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The Fifth Labour of Heracles: Cleaning the Linnean stable of names for grass snakes (*Natrix astreptophora*, *N. helvetica*, *N. natrix* sensu stricto)

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Abstract

We scrutinize scientific names erected for or referred to Natrix astreptophora (Seoane, 1884), Natrix helvetica (Lacepède, 1789), and Natrix natrix (Linnaeus, 1758). As far as possible, we provide synonymies for the individual subspecies of each species, identify each name with one of the mtDNA lineages or nuclear genomic clusters within these taxa, and clarify the whereabouts of type material. In addition, we feature homonyms and names erroneously identified with grass snakes. For Natrix astreptophora (Seoane, 1884), we recognize a second subspecies from North Africa under the name Natrix astreptophora algerica (Hecht, 1930). The nominotypical subspecies occurs in the European part of the distribution range (Iberian Peninsula, adjacent France). Within Natrix helvetica (Lacepède, 1789), we recognize four subspecies. The nominotypical subspecies occurs in the northern distribution range, Natrix helvetica sicula (Cuvier, 1829) in Sicily, mainland Italy and adjacent regions, Natrix helvetica cetti Gené, 1839 on Sardinia, and Natrix helvetica corsa (Hecht, 1930) on Corsica. However, the validity of the latter subspecies is questionable. For Natrix Cetti Gené, 1839, we designate a lectotype from Sardinia to stabilize current usage of this name. Furthermore, we give Coluber siculus Cuvier, 1829 and Tropidonotus natrix var. astreptophorus Seoane, 1884 precedence over four previously overlooked senior synonyms that we qualify as nomina oblita according to the requirements of the International Code of Zoological Nomenclature. Coluber bipedalis Bechstein, 1802 and Vipera vissena Rafinesque, 1814 are nomina oblita for Coluber siculus Cuvier, 1829. Coluber distinctus Gravenhorst, 1807 and Tropidonotus sparsus Schreiber, 1875 are nomina oblita for Tropidonotus natrix var. astreptophorus Seoane, 1884. For Natrix natrix (Linnaeus, 1758) we recognize tentatively five subspecies, some of which hybridize broadly. The nominotypical subspecies matches the 'yellow mtDNA lineage' and the 'yellow microsatellite cluster' and lives in Scandinavia and Central Europe. For Natrix vulgaris Laurenti, 1768, we designate a neotype and resurrect this name for the previously characterized 'red mtDNA lineage' of Natrix natrix that also corresponds to a distinct nuclear genomic cluster (Natrix natrix vulgaris Laurenti, 1768). Pure populations of this subspecies are restricted to southern and southeastern Central Europe. The 'green mtDNA lineage' of Natrix natrix, also distinct with respect to nuclear genomic markers, corresponds to Natrix natrix scutata (Pallas, 1771). This subspecies occurs in most of the eastern distribution range. Natrix natrix persa (Pallas, 1814) is characterized by another mtDNA lineage endemic to the Transcaucasus und northern Iran. We restrict this subspecies to populations in these regions, while the taxonomic status of grass snakes from the Balkans and Asia Minor, previously also assigned to Natrix natrix persa, demands further research. Finally, we tentatively recognize Natrix natrix syriaca (Hecht, 1930) as valid. This subspecies is characterized by yet another mtDNA lineage endemic to southeastern Turkey. Based on genetic evidence, the following subspecies should not be recognized: Natrix natrix fusca Cattaneo, 1990, Natrix natrix gotlandica Nilson & Andrén, 1981, and Natrix natrix schweizeri Müller, 1932. Some other names can be unambiguously identified with distinct mtDNA lineages and could represent distinct taxa. However, without additional nuclear genomic evidence, we refrain from potentially premature taxonomic decisions.

Key words

Nomenclature, Natricidae, Serpentes, Squamata, subspecies, taxonomy.



Introduction

Among the 110 snake species known to Linnaeus (1758) was the grass snake, which he described under the name Coluber Natrix. Later it was generally thought that this species, now Natrix natrix (Linnaeus, 1758), is distributed across much of the Palearctic Region. Within its vast range, from the Iberian Peninsula and the Maghreb region to Lake Baikal, a variable number of morphologically distinct subspecies was recognized since the 20th century (MERTENS & MÜLLER, 1928, 1940; HECHT, 1930; MERTENS, 1947; MERTENS & WERMUTH, 1960; THORPE, 1979; Kabisch, 1999), ranging from 4 (Thorpe, 1979) to 20 (HECHT, 1930). Two additional species of grass snake, Natrix megalocephala and Natrix cetti proposed by Орлов & Туниев [Orlov & Tuniyev] (1987) and Vanni & Cim-MARUTA (2011), were subsequently synonymized with Natrix natrix (Fritz et al., 2012; Kindler et al., 2013).

However, based on genetic evidence, Pokrant et al. (2016) and Kindler et al. (2017) split recently grass snakes into three species. According to their results, Natrix astreptophora (Seoane, 1884) is widely distributed on the Iberian Peninsula and in adjacent southern France. In addition, it has a disjunct distribution range with several isolated occurrence patches in the Maghreb region. Natrix helvetica (Lacepède, 1789) lives in Western Europe north of the Pyrenees to the Rhine region, in Britain, on Corsica, Sardinia, Sicily, and in mainland Italy. Recently, GLAW et al. (2019) showed that the distribution of Natrix helvetica extends northward across the Alps to southernmost Bavaria. Natrix natrix (Linnaeus, 1758) sensu stricto ranges from the Rhine region through much of Europe eastward to Lake Baikal in Central Asia. Its distribution range also includes Fennoscandia, the Balkan Peninsula, and parts of the Middle East including Asia Minor and Transcaucasia.

Several recent studies (FRITZ et al., 2012; KINDLER et al., 2013, 2017, 2018a, b; KINDLER & FRITZ, 2018; SCHULTZE et al., 2020) found many conflicts between morphologically defined subspecies and genetic lineages of grass snakes. Kindler et al. (2013, 2018a) and SCHULTZE et al. (2020) identified three distinct mtDNA lineages within Natrix astreptophora, seven within Natrix helvetica, and eight within Natrix natrix, and most of these lineages conflict with morphologically defined subspecies. Most prominently, the traditional subspecies Natrix natrix persa (WERNER, 1938; MERTENS, 1947; MERTENS & WERMUTH, 1960; KABISCH, 1999) corresponds to seven of the eight mtDNA lineages of N. natrix, and certain of these mtDNA lineages occur in morphologically very different populations (KINDLER et al., 2013). Some mtDNA lineages match nuclear genomic clusters as identified by analyses of microsatellite loci, others do not (Kindler et al., 2017, 2018a; Schultze et al., 2020). The most pronounced conflict between mitochondrial and nuclear genomic differentiation was revealed for mainland Italy and Sicily, where one nuclear genomic cluster corresponds to no fewer than five, in part deeply divergent, mtDNA lineages (SCHULTZE *et al.*, 2020). Yet, for many mtDNA lineages it is still unknown how they match nuclear genomic differentiation, even though preliminary data (KINDLER *et al.*, 2017, 2018a) suggest that no additional species are involved.

The present study aims at clarifying the genetic identity of the many synonyms of the three grass snake species to lay the foundation for the proper naming of subspecies. One may argue that it is not worth spending much time on the clarification of the subspecific taxonomy because the usage of subspecies should be simply abandoned. This disregards in general the fact that many taxa originally identified as subspecies were later recognized as full species. Their nomenclature can only rest on solid ground when the identity of the subspecies names is clarified. Moreover, evolution also acts below the species level, resulting in biologically meaningful population clusters that ultimately may evolve to distinct species. Such clusters, infraspecific taxa, need to be named because only named taxa are visible within and beyond science.

Only when biologically meaningful, conspecific entities bear names, they can be comprehended as distinct—in science, by the public, in politics, and conservation. This is of particular relevance when conspecific taxa are endangered. Recognizing them nomenclaturally allows their protection.

Subspecies are the only accepted Linnean category below the species level (ICZN, 1999). As with species, a problem is the lacking consensus what criteria should be used to delineate subspecies (ZACHOS, 2016). This leads sometimes to grotesque situations, as described by GIP-POLITI (2020), when recognized subspecies have nothing to do with meaningful biological entities. Recently, KINDLER & FRITZ (2018) suggested identifying subspecies with Evolutionarily Significant Units (as defined by Moritz, 1994) that are capable of complete genetic amalgamation in secondary contact zones. Within that framework, subspecies represent distinct nuclear genomic clusters and are characterized by distinct mtDNA lineages (except for cases of mitochondrial capture), i.e., they need to be confirmed by two independent lines of genetic evidence. Morphology, traditionally used for subspecies delineation (e.g., MAYR, 1969), is not a criterion and not an obligatory prerequisite. This acknowledges that morphology is influenced by a multitude of environmental factors, so that morphology can, but does not necessarily, reflect genetic and evolutionary divergence. Important is that massive gene flow in both directions is expected in geographic contact zones of subspecies, causing widereaching and ever expanding introgression. When coming into secondary contact, subspecies typically establish a wide unimodal hybrid zone where only hybrid genotypes¹, but no pure parental genotypes, are present. This

We use the term 'genotype' for the nuclear genomic makeup of an organism, i.e., we apply this term to its diploid genetic information encoded in the chromosomes, in contrast to the haplotypic genetic information of mitochondrial DNA (mtDNA).

subspecies definition closely resembles that of AVISE & BALL (1990).

If the Kindler & Fritz (2018) definition for subspecies is applied, most traditionally and currently recognized subspecies of grass snakes (Mertens & Wermuth, 1960; Kabisch, 1999; Kreiner, 2007; Geniez, 2015) need to be critically reassessed and taxonomically revised. Only for Natrix helvetica has this task already been undertaken (Schultze et al., 2020), and the nomenclatural situation has been subsequently largely resolved (FRITZ et al., 2020). For Natrix astreptophora and Natrix natrix it still remains unclear how traditionally recognized subspecies and genetic clusters match, which subspecies are valid, and how these redefined subspecies should be named. The present study cannot disentangle this situation completely, but it can lay the nomenclatural foundations for future revisions because the geographic distribution of the 18 distinct mtDNA lineages of Natrix astreptophora, Natrix helvetica and Natrix natrix sensu stricto is well known (KINDLER et al., 2013, 2014, 2017, 2018a, b; Pokrant et al., 2016; Schultze et al., 2019, 2020; Asztalos et al., 2020) and can serve as a basis for the taxonomic identification of scientific names.

To this end, we scrutinize type localities and availability of all currently known scientific names for the three grass snake species according to the requirements of the International Code of Zoological Nomenclature (henceforth 'the Code;' ICZN, 1999). In addition, we match whenever possible mtDNA lineages, microsatellite clusters, and scientific names to facilitate naming individual subspecies. It needs to be kept in mind that it is the nature of subspecies that they are able to secondarily amalgamate completely. In a unimodal hybrid zone of subspecies only hybrid genotypes occur but no pure parental genotypes. Our understanding is that Article 23.8 of the Code precludes the usage of any name founded on such subspecies hybrids for either of its parental taxa, "even if [the respective name] is older than all other available names." However, such names can be unambiguously referred to the species to which the hybridizing subspecies belong.

We used as a starting point for the present study the checklist of Mertens & Wermuth (1960) and re-examined each scientific name listed there. Names that were erected too late to be included in this sixty-year-old work were added, as well as names that were overlooked by MERTENS & WERMUTH (1960), as far as we were aware of them. In addition, the names listed as synonyms of *Tropi*donotus natrix and Natrix natrix in Boulenger (1893) and WALLACH et al. (2014), respectively, were compared to those of Mertens & Wermuth (1960). Where necessary, we commented on unjustified conclusions by MERTENS & WERMUTH (1960) or other authors. In the following, we discuss all names and provide information on namebearing types, type localities, and genetic and taxonomic identity. The sequence of names is chronologically by the year of publication and, when more than one name was introduced per year, alphabetically.

We use throughout the paper the original spelling of any species group name, except when we apply the respective name for a recognized species or subspecies. Then, the used name may differ from the original spelling as required by the current Code (ICZN, 1999: Articles 27, 28, 32). However, in one case, the original spelling represents an obvious inadvertent error. Here, the corrected name is used (Coluber bipedalis Bechstein, 1802) and the misspelling is explained. If in the original description the term 'var.' = 'varietas' (Latin for variety) was used as a prefix of a new species group name, this abbreviation is also shown in the original spelling. This prefix is of feminine gender. Therefore, epithets for varieties formed by Latin adjectives appeared often, but not always, as inflected feminine forms, even when the genus has another gender (e.g., Tropidonotus natrix var. picturata Jan, 1864). If such names would be used as valid, their gender would have to be adapted to that of the respective generic name (ICZN, 1999: Article 32.2). Names that were erroneously identified in the literature as synonyms of grass snakes are shown in quotation marks in the respective subheadings. We also use quotation marks when we refer to subsequent usages of names that differ from the original spellings.

We frequently refer below to the numbers or letters and colour codes for mtDNA lineages from Kindler et al. (2013, 2014, 2017, 2018a, b), POKRANT et al. (2016), and Schultze et al. (2019, 2020) to characterize grass snakes genetically. This letter and colour system was originally introduced to avoid the premature identification of an mtDNA lineage with a particular taxon. It has to be highlighted that one publication (KINDLER & FRITZ, 2014) was an exception with respect to the colour code used. This article reported the results of Kindler et al. (2013) in German language for local field herpetologists and citizen scientists. For copyright reasons, the figures from KIN-DLER et al. (2013) were redrawn and shown in Kindler & Fritz (2014) with other symbols and other colours. In the present study we use the general colour code of the other mentioned studies and not that from Kindler & Fritz (2014).

At the end of this article, we provide, whenever possible, full synonymies for the individual subspecies and indicate their genetic identity. Furthermore, we identify names that pertain to distinct mtDNA lineages and that may refer to additional subspecies, pending further study. Finally, we summarize *nomina dubia* and *nomina nuda* that have been erroneously identified with grass snakes.

Coluber Natrix Linnaeus, 1758

Norén & Åhlander (2020) recently discussed the complicated history and identity of *Coluber Natrix* Linnaeus, 1758. They clarified the situation by designating a neotype (Swedish Museum of Natural History in Stockholm, NRM 8260, collected by M. Norén on 14 May 2018 at the Fada mill pond, approximately two kilometres southeast of the Berga-Tuna Estate, Nyköping, Sweden). Its collection site represents the type locality of *Coluber Natrix* (ICZN, 1999: Article 76.3).

The type locality lies within the distribution range of the 'yellow mtDNA lineage' ('lineage 3;' Kindler *et al.*,

2013) of Natrix natrix. The nuclear genomic identity of Swedish grass snake populations matches their mtDNA lineage in that they represent a pure cluster (the 'yellow cluster') in analyses using microsatellite loci (KINDLER et al., 2017). Consequently, the nominotypical subspecies of *Natrix natrix* (Linnaeus, 1758) is to be identified with the 'yellow mtDNA lineage' (lineage 3) and the 'yellow cluster' of Kindler et al. (2013, 2017), which occurs in Scandinavia and Central Europe. Towards the south and southeast, Natrix natrix natrix hybridizes extensively with adjacent subspecies and in two narrow hybrid zones in the Rhine region and northeastern Italy, with Natrix helvetica (see Kindler et al., 2017; Schultze et al., 2019, 2020). A further hybrid zone with Natrix helvetica is expected in southernmost Bavaria and adjacent Austria (GLAW et al., 2019).

Natrix Gronoviana Laurenti, 1768

This species was described in the dissertation of Josephus Nicolaus Laurenti (1735–1805). This work was issued in two versions in the same year (LAURENTI, 1768a, b). One version is the dissertation itself (LAURENTI, 1768a), printed obviously only in a few copies, and the other version was issued as a book (LAURENTI, 1768b). Both versions differ mainly by 11 additional pages in LAURENTI (1768a) that contain no nomenclaturally relevant information (OHLER *et al.*, 2018).

The description of Natrix Gronoviana was based on figure 1 of plate XXXIII in SEBA (1735). This figure shows definitely not a grass snake but a specimen that we identify either as Spalerosophis diadema (Schlegel, 1837) or Coronella austriaca Laurenti, 1768 (see reproduction of plate XXXIII in our Fig. 1). Müsch et al. (2001: p. 558) suggested instead that Seba's figure could represent a whip snake ("Coluber sp.," we assume that Hierophis was meant). Figure 2 of the same plate in Seba (1735) shows a snake resembling Natrix astreptophora (Seoane, 1884) and figure 3, another one that could be a Natrix helvetica (Lacepède, 1789). However, Laurenti (1768a, b. p. 75) explicitly referred to figure 1. LAURENTI's description does not match Seba's figure 1 completely; in particular, the greyish-blue general coloration mentioned in the original description conflicts with the brownish colour of the snake depicted in Seba (1735). The latter author (p. 33) characterized this snake correctly as "Serpens, Arabica, fusca, maculis, nigricantibus, flammatis, notata." According to Seba, the grass snakes in figures 2 and 3 also originated from Arabia, which is obviously incorrect. Conversely, Spalerosophis diadema occurs across the whole Arabian Peninsula and beyond (GENIEZ, 2015). It cannot be ruled out that Laurenti (1768a, b) erroneously referred to figure 1 instead of figure 3; the grass snake shown in figure 3 has an unnaturally bluish-green coloration, perhaps from the preservative (see our Fig. 1).

In any case, *Natrix Gronoviana* cannot be unambiguously identified with a grass snake and should be regarded as a *nomen dubium*. Discussing other aspects, Müller & Mertens (1932a) arrived at the same conclu-

sion. This was and is of some relevance because Hecht (1929, 1930) identified *Natrix Gronoviana* with what is now *Natrix helvetica* (Lacepède, 1789).

Later, Mertens & Wermuth (1960) listed "Natrix gronoviana Laurenti" as a synonym of Natrix natrix (Linnaeus, 1758) and restricted, without justification and validity, the type locality to "Wien" (Vienna, Austria). "Natrix gronoviana" also appears in the synonymy of Tropidonotus natrix and Natrix natrix of Boulenger (1893: p. 219) and Wallach et al. (2014: p. 477), respectively.

Natrix vulgaris Laurenti, 1768

This name was listed by Mertens & Wermuth (1960: p. 187) as a junior synonym of *Natrix natrix natrix* (Linnaeus, 1758). However, the identity of *Natrix vulgaris* Laurenti, 1768 is far from straightforward.

This species was also described in the dissertation of Laurenti (1768a, b: p. 75). He introduced *Natrix vulgaris* in his "Tabula Reptilium," the first chapter of his dissertation, and mentioned plates IV (figures 1–3) and X (figures 1–3; our Fig. 2) in Seba (1735) as illustrating his new species. In addition, Laurenti characterized two varieties of *Natrix vulgaris* "in Museo Illustrissimi Comitis Turriani" [in the museum of the illustrious Count Turrianus], the private collection of Count Franz Anton Hannibal von Thurn und Valsassina (1699–1768) (Ohler *et al.*, 2018), without naming them. The whereabouts of the Turrianus collection are unknown (Böhme & Klaver, 1997: p. 56; Ohler *et al.*, 2018). Both the specimens figured in Seba (1735) and the specimens in the Turrianus collection represent syntypes of *Natrix vulgaris* Laurenti, 1768.

In the second chapter "Historia Reptilium Austriacorum," Laurenti detailed his description of Natrix vulgaris, gave some information on habitats and behaviour, and presented two experiments relating to the venomousness of this snake species (pp. 180-184). This, together with Laurenti's complaint (Præloquium, p. 15) that he would have liked to include animals from remote parts of the world but had to use reptiles from Lower Austria, strongly suggests that his description was also based on grass snakes from Lower Austria, which have to be regarded as syntypes as well. That LAURENTI chose the species epithet 'vulgaris' supports that he knew well the local and common grass snake (cf. also Ohler et al., 2018). Elsewhere, Laurenti did not mention explicitly the geographic provenance of any 'grass snakes' except for his remark on page 75 that the snakes in Seba's plate X are not from Egypt.

However, Seba (1735: p. 6), who lived in Amsterdam, specified in the Latin and French text for plate IV that the snakes shown there are native. This implies Seba knew grass snakes from the province of Holland; however, he specifically mentioned West Frisia, Germany, and Italy. Seba's figures in plate IV are not of good quality, a fact already criticized by Wagler in Michahelles (1833: columns 904–905). Seba's figure 1 cannot be identified with any species. The snakes in figures 2 and 3 show a

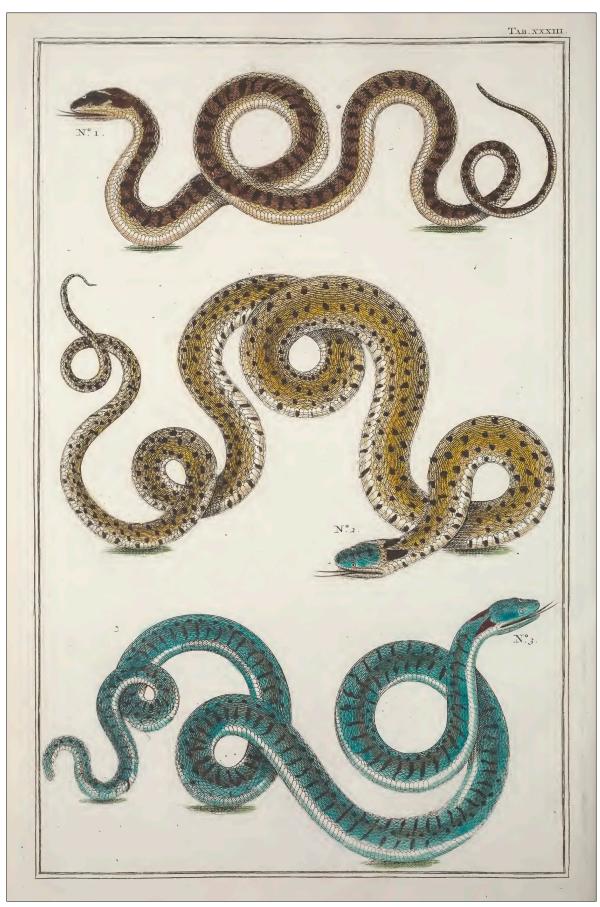


Fig. 1. Reproduction of plate XXXIII of Seba (1735), showing (1) a snake of unclear identity on which the descriptions of *Natrix Gronoviana* Laurenti, 1768 and *Coluber arabicus* Gmelin, 1789 were based, and two snakes resembling (2) *Natrix astreptophora* (Seoane, 1884) and (3) *Natrix helvetica* (Lacepède, 1789).

spotted dorsal pattern and a closed collar, resembling juvenile *Natrix astreptophora* (Seoane, 1884).

In Seba's plate X (our Fig. 2), of better quality than plate IV, are also three snakes shown that, for the same reasons, match *Natrix astreptophora*. According to Seba (1735: p. 11), the snake in figure 1 came from Egypt, where it lives along the Nile; for the snakes in figures 2 and 3, he gave America as origin.

MERTENS & WERMUTH (1960: p. 187) designated "Wien" (Vienna, Austria) as type locality of *Natrix vulgaris* Laurenti, 1768, reflecting that Laurenti worked for his dissertation at the local university. This type locality gained wide acceptance in herpetology (e.g., Kabisch, 1999; SCHMIDTLER, 2019). However, the Code (ICZN, 1999) requires the designation of a lectotype or neotype for the restriction of type locality, rendering the type locality designation in Mertens & Wermuth (1960) invalid. Consequently, and in agreement with Article 73.2.3 of the Code, the type locality of Natrix vulgaris Laurenti, 1768 encompasses all places of origin of its syntypes (by indication the figured and described grass snakes in Seba, 1735), except for those with evidently erroneous provenance (Egypt, America), plus the Lower Austrian specimens. The material in the Turrianus collection of unknown provenance is here irrelevant. Thus, the type locality of Natrix vulgaris includes parts of the Netherlands (Holland, West Frisia), Germany, Italy, and Lower Austria. Moreover, the Iberian Peninsula and adjacent southern France (Occitany) have to be added because Natrix astreptophora, figured by SEBA (1735: plates IV, figs 2, 3 and X, figs 1-3; our Fig. 2), occurs there (it seems unlikely that the depicted snakes originated from the Maghreb, where Natrix astreptophora occurs as well, because the species is extremely rare there; KINDLER et al., 2018a).

This composite type locality makes clear that *Natrix vulgaris* was based on three distinct *Natrix* species. In the Netherlands, western Germany, and most of Italy *Natrix helvetica* (Lacepède, 1789) occurs in two currently recognized subspecies, the nominotypical subspecies in the Netherlands and western Germany and *Natrix helvetica sicula* (Cuvier, 1829) in mainland Italy and Sicily. In northeastern Italy, central and eastern Germany and Lower Austria *Natrix natrix* (Linnaeus, 1758) is distributed. In addition, the snakes figured by Seba (1735) represent *Natrix astreptophora* (Seoane, 1884).

SEBA's second collection, to which the figured material belonged, was sold after his death and some specimens still survive in European natural history museums (MÜSCH *et al.*, 2001; see also BAUER & GÜNTHER, 2013). However, there is no evidence that the physical syntypes for the plates cited by LAURENTI (1768a, b) are still extant.

Based on the invalid type locality designation by Mertens & Wermuth (1960), Schmidtler (2019) recently considered the use of the name *Natrix vulgaris* Laurenti, 1768 for grass snakes of mtDNA lineage 4 (the so-called 'red lineage') of Kindler *et al.* (2013, 2017). To validate this usage and to clarify the taxonomic identity and type locality of *Natrix vulgaris* Laurenti, 1768 according to

Article 75.3.1 (ICZN, 1999), we designate here a neotype for this nominal species. This also precludes that this name poses a threat to the well-established names *Natrix astreptophora* (Seoane, 1884) and *Natrix helvetica* (Lacepède, 1789). To this end, we select a specimen from the collection of the Natural History Museum Vienna (Naturhistorisches Museum Wien) that has been genetically studied and that unambiguously represents the 'red lineage,' also with respect to its nuclear genomic identity (KINDLER *et al.*, 2017):

Neotype: Naturhistorisches Museum Wien, NMW 36405: 2, Oberedlitz, Gemeinde Thaya, Niederösterreich (Lower Austria), Austria, collected April 2001. Genotyped at 13 microsatellite loci and mtDNA sequenced by Kindler *et al.* (2017).

Description of the neotype: Ethanol-preserved large female grass snake (2.8 cm head length, 65.8 cm snoutvent length, 10.2 cm tail length). Tail ventrally slightly damaged. Head with 1/1 (left/right) preocular scales, no suboculars, 2/2 postoculars, 1-3/1-3 temporals, 7/7 supralabials (each third and fourth supralabial contacting eye), 1/1 loreals. Keeled dorsal body scales, counts at a head length behind the head, at midbody, and at a head length before the vent: 19/19/17, with 177 ventrals, 37 countable subcaudals; anal scale divided. Head and body dorsally overall greenish brown, with a few small black body spots. Pronounced light occipital crescents with black posterior rim of approximately the same width. Head cream-coloured ventrally; body ventrally with decreasing cream-coloured and increasing blackish areas; ventral scales in the last third of the body completely blackish; subcaudals blackish (Figs 3 and 4).

With the present neotype designation, the name Natrix vulgaris Laurenti, 1768 can be used in the combination Natrix natrix vulgaris Laurenti, 1768 for the Central European subspecies corresponding, with respect to their mitochondrial and nuclear genomic identity, to the 'red lineage' and 'red cluster' of Kindler et al. (2013, 2017). Natrix natrix vulgaris broadly hybridizes with geographically adjacent subspecies. Genotypically pure populations seem to be restricted to southern and southeastern Central Europe, in some regions with cytonuclear discordance (Kindler et al., 2017; Schultze et al., 2020; see the maps in these studies). Further research is needed to find out whether Natrix natrix vulgaris can be told apart morphologically from the nominotypical subspecies. It is unclear whether the striped morphotypes mainly known from the southern part of the distribution range of the 'red lineage' (KINDLER et al., 2013, 2017) result from hybridization of Natrix natrix vulgaris with genetic lineages from the southern Balkans.

Coluber scutatus Pallas, 1771

Pallas (1771: p. 459) described this species and mentioned that it is "in Iaico aquaticus, in terram tamen exiens," i.e., that the species is in the Iaico River aquatic but leaves the water [to go] onto the land. On page 429, Pallaves the water [to go] onto the land.

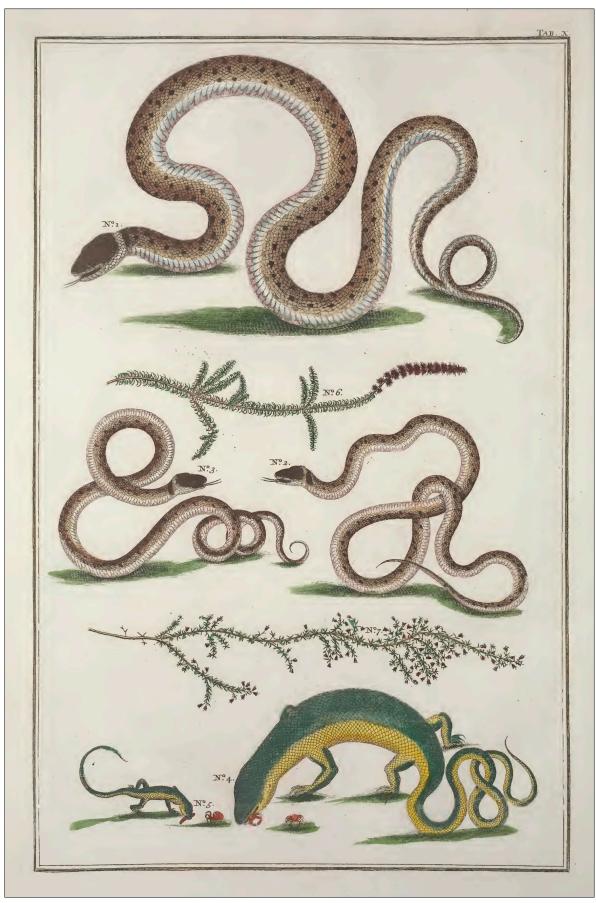


Fig. 2. Reproduction of plate X of Seba (1735), showing three specimens of *Natrix astreptophora* (Seoane, 1884). Specimen (2) is the only known syntype of *Coluber distinctus* Gravenhorst, 1807. These snakes were originally also syntypes of *Coluber Natrix* Linnaeus, 1758 (see Norén & ÅHLANDER, 2020) and *Natrix vulgaris* Laurenti, 1768.

LAS mentioned *Coluber scutatus* in German besides for the "Iaik" also for the environs of "Gurjef," now named Atyrau, a settlement at the lower Iaico. The Iaico or Iaik is now known as the Ural River. Thus, the type locality of *Coluber scutatus* is the lower Ural River near Atyrau. There are no type specimens.

MERTENS & WERMUTH (1960) and MERTENS (1966) used PALLAS' name for the easternmost subspecies of Natrix natrix (Linnaeus, 1758) that occurs, according to these authors, on the Crimea and east of the Dniepr River. MERTENS (1966) believed that the easternmost records for grass snakes from the Transbaikal Region also belong to this subspecies (see below under Natrix vibakari continentalis Nikolsky, 1925). Much of this distribution range matches that of mtDNA lineage 8, the 'green lineage' of Kindler *et al.* (2013, 2014, 2017). However, this lineage also occurs beyond the putative range of Natrix natrix scutata (Pallas, 1771) in Anatolia, western Transcaucasia and Finland, with the westernmost records in Finland, Gotland, the Kaliningrad Oblast (Russia), and along the eastern Polish border (KINDLER et al., 2013, 2014, 2017). According to the results of Kindler et al. (2017) using microsatellite data, this 'green mtDNA lineage' also constitutes another nuclear genomic cluster compared to the more western 'red' and 'yellow lineages,' i.e., to Natrix natrix natrix (Linnaeus, 1758) and Natrix natrix vulgaris Laurenti, 1768. Therefore, we identify the 'green lineage' with Natrix natrix scutata. The genetically verified easternmost records of this subspecies are known from the Emba (Zhem) River and Edylsor Lake, Kazakhstan (KINDLER et al., 2013, 2017). This is more than 3,700 km from the easternmost records of Natrix natrix scutata in the Transbaikal Region (see below under *Natrix vibakari* continentalis Nikolsky, 1925).

Currently, morphological variation in *Natrix natrix scutata* is not well understood. Mertens (1966) suggested that in this subspecies the light lunar spots fuse to form a closed collar, like in juvenile *Natrix astreptophora* (Seoane, 1884). However, other authors identified *Natrix natrix scutata* with grass snakes with well-separated lunar spots that can be orange or even red (e.g., Орлов & Туниев [Orlov & Tuniyev], 1987; Kabisch, 1999; Kreiner, 2007; Geniez, 2015).

Coluber arabicus Gmelin, 1789

This nominal species is not listed by Mertens & Wermuth (1960) as a synonym of *Natrix natrix* (Linnaeus, 1758), but Schreiber (1875: p. 237) identified it with his "var. a" of *Tropidonotus natrix*. Also, Boulenger (1893: p. 219) and Wallach *et al.* (2014: p. 478) included it in their synonymies of *Tropidonotus natrix* and *Natrix natrix*, respectively.

GMELIN (1789: p. 1102) based his *Coluber arabicus* on figure 1 of plate XXXIII (see our Fig. 1), the accompanying description in SEBA (1735: p. 33, erroneously given as 32 in GMELIN, 1789) and some other works (GRONOVIUS, 1756: p. 61, no. 22 and 1781: p. 22, no. 108; BODDAERT, 1783: p. 24, no. 28). The identity of the de-

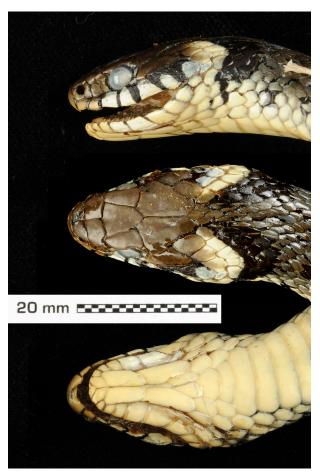


Fig. 3. Lateral, dorsal and ventral aspects of the head of the neotype of *Natrix vulgaris* Laurenti, 1768 (Naturhistorisches Museum Wien, NMW 36405:2, female, Oberedlitz, Gemeinde Thaya, Niederösterreich, Austria). Photos: Alice Schumacher (Naturhistorisches Museum Wien).

picted snake is unclear (see above under *Natrix Gronoviana* Laurenti, 1768). All additional sources (Gronovius, 1756, 1781; Boddaert, 1783) cited by Gmelin (1789) were based on the same figure in Seba (1735) and contain no new information, so that they do not clarify the matter. Thus, *Coluber arabicus* Gmelin, 1789 is a *nomen dubium*.

However, why did Schreiber (1875) and Boulenger (1893) identify *Coluber arabicus* with a grass snake? Gmelin (1789: p. 1101) mentioned Seba's (1735) figure 1 of plate XXXIII not only in his description of *Coluber arabicus* but also under *Coluber Gronovianus*. Both Schreiber (1875: p. 237) and Boulenger (1893: p. 219) treated "*Coluber gronovianus* Laur." as a synonym of *Tropidonotus natrix*, and since Gmelin characterized the two species with the same figure, Schreiber and Boulenger concluded that they represent the same species.

Coluber bipes Gmelin, 1789

This name has been discussed in FRITZ et al. (2020). It is a nomen oblitum (type locality: Dolomiti di Fiemme/



Fig. 4. Dorsal and ventral aspects of the neotype of *Natrix vulgaris* Laurenti, 1768 (Naturhistorisches Museum Wien, NMW 36405:2, female, Oberedlitz, Gemeinde Thaya, Niederösterreich, Austria). Photos: Alice Schumacher (Naturhistorisches Museum Wien).

Fleimser Alpen, Italy) to be identified with *Natrix hel-vetica sicula* (Cuvier, 1829). Grass snakes in this region harbour mtDNA lineage C (SCHULTZE *et al.*, 2020). See also below under *Coluber scopolianus* Daudin, 1803.

Coluber Capite-triangulatus Lacepède, 1789² (unavailable name)

This name was listed by Wallach *et al.* (2014: p. 478) as a "nomen rejiciendum" among the synonyms of Natrix natrix (Linnaeus, 1758). We agree that this name is unavailable according to Opinion 1463 (ICZN, 1987). Moreover, Coluber Capite-triangulatus Lacepède, 1789 was founded on material labelled as "Vipère de'l Isle Saint-Eustache" in the Cabinet du Roi (Lacepède, 1789: p. 132), today the Muséum national d'Histoire naturelle, Paris. This island is nowadays known as Sint Eustatius, Lesser Antilles, making the identification with a grass snake highly unlikely. Neither Mertens & Wermuth (1960) nor Boulenger (1893) identified Coluber Capite-triangulatus with a grass snake.

Coluber Helveticus Lacepède, 1789

This is the currently used name for the barred grass snake and its northern subspecies, as discussed in Fritz *et al.* (2020). *Coluber Helveticus* Lacepède, 1789 has been conserved as an available name by the International Commission on Zoological Nomenclature (ICZN, 1992: Opinion 1686), despite having been published in a rejected work.

LACEPÈDE (1789: Table méthodique, p. 100 and p. 326) introduced *Coluber Helveticus* as a *nomen novum* for *Coluber vulgaris* Razoumowsky, 1789 with type locality of Jorat, Switzerland (see also below under *Coluber vulgaris* Razoumowsky, 1789).

The type locality Jorat, a hill range north of Lake Geneva, was erroneously identified with "Mont Jura" by MERTENS & MÜLLER (1940: p. 53) and MERTENS & WERMUTH (1960: p. 188).

The first author who used *Coluber Helveticus* for a western subspecies of *Natrix natrix* was Mertens (1934: p. 15); its taxonomic distinctness has been first claimed under the name *Tropidonotus natrix gronovianus* (Laurenti, 1768) by Hecht (1929: p. 559) and, more importantly, in Hecht's (1930) much-criticized (Müller & Mertens, 1931, 1932a, b; Mertens, 1947) revision of grass snakes.

The type locality of *Coluber Helveticus* Lacepède, 1789 lies within the distribution range of mtDNA lineage E of Kindler *et al.* (2013, 2017) that matches a distinct nuclear genomic cluster (Kindler *et al.*, 2017), qualifying it as the distinct subspecies *Natrix helvetica helvetica* (Lacepède, 1789) (Kindler *et al.*, 2017; Kindler & Fritz, 2018; Schultze *et al.*, 2019, 2020). Adult individuals of this subspecies are often lacking lunar spots and have a silvery grey overall coloration with dark lateral bars, eponymous for its vernacular name 'barred grass snake' (e.g., Kabisch, 1999). Some representatives of the southern subspecies *Natrix helvetica sicula* (Cuvier, 1829) are morphologically difficult to tell apart from *Natrix helvetica helvetica*, even though the southern subspecies is frequently more colourful and more contrastingly patterned.

Coluber Semimonile Lacepède, 1789

(unavailable name)

This unavailable name (ICZN, 1987: Opinion 1463) was listed by Wallach *et al.* (2014: p. 478) as a "nomen rejiciendum" under the synonyms of Natrix natrix (Linnaeus, 1758). Lacepède (1789: p. 173) based this species on a snake from Japan in the Cabinet du Roi. Together with the figure of this individual in his plate VIII, this prevents the identification with any grass snake. Neither Mertens & Wermuth (1960) nor Boulenger (1893) identified Coluber Semimonile with a grass snake.

Coluber Torquatus Lacepède, 1789

(unavailable name)

This name, identified by MERTENS & WERMUTH (1960: p. 186) with *Natrix natrix* (Linnaeus, 1758) but not with a particular subspecies, is unavailable (ICZN, 1987: Opinion 1463). For a long time, especially until the 19th century, the species epithet *torquatus* or *torquata* was frequently used for grass snakes, a tradition dating back to pre-Linnean times (e.g., GESNERUS, 1587: paragraph 63; ALDROVANDI, 1640: p. 287; RAIUS, 1693: p. 334).

According to the sources on which Lacepède (1789: p. 147) based his description, *Coluber Torquatus* is composed of *Natrix natrix*, *Natrix helvetica* and black *Hierophis viridiflavus*. The latter is evident from Lacepède's remark that this snake is called "en Sardaigne Colubro nero" and further supported by some other names (Serpe nero, Carbon, Carbonazzo) listed by Lacepède for this species. Until today, *Hierophis viridiflavus* is known in some regions of Italy under the name 'carbonazzo' or similar dialectal forms. Thus, in addition of being unavailable, *Coluber Torquatus* Lacepède, 1789 is also a *nomen dubium*.

Coluber tyrolensis Gmelin, 1789

This name refers to a southern subspecies of the barred grass snake, *Natrix helvetica sicula* (Cuvier, 1829), and was discussed in Schmidtler (2019) and Fritz *et al.* (2020). The latter authors fixed, according to Article 23.9

The spelling of the author name 'Lacepède' has been repeatedly debated and several variants occur even in publications by the author himself or by other authors (see Dubois, 2008; Bour, 2010; David et al., 2011). The name is given as "De la Cépède" on the title page of the second volume of the 'Histoire naturelle des quadrupèdes ovipares et des serpens,' in which many new snake names appeared. To the best of our knowledge, this variant, with or without the nobiliary particle, has not been used in recent years in herpetology. We use instead Lacepède, as the author himself in later years (Bour, 2010). If we cite different spellings by other authors, these are shown in quotation marks.

of the Code (ICZN, 1999), *Coluber tyrolensis* Gmelin, 1789 as a *nomen oblitum* in relation to the *nomen protectum Coluber siculus* Cuvier, 1829.

Coluber tyrolensis Gmelin, 1789 and Coluber bipes Gmelin, 1789 (see above) were published in the same work (GMELIN, 1789: p. 1102 and p. 1099, respectively) and founded on the same source (SCOPOLI, 1769). Both names have the same type locality (Dolomiti di Fiemme/ Fleimser Alpen, Italy). In this region occur barred grass snakes of mtDNA lineage C (SCHMIDTLER, 2019; SCHULTZE et al., 2020). If snakes with mtDNA lineage C should be regarded as a distinct subspecies in future, we give Coluber tyrolensis Gmelin, 1789 precedence over the name Coluber bipes Gmelin, 1789 according to the First Reviser Principle (ICZN, 1999: Article 24.2). Consequently, the name combination to be used then would be Natrix helvetica tyrolensis (Gmelin, 1789).

Coluber vulgaris Razoumowsky, 1789

This name was frequently overlooked (e.g., Boulenger, 1893; Mertens & Wermuth, 1960; Wallach *et al.*, 2014). It is the oldest name for the northern subspecies of *Natrix helvetica* (Lacepède, 1789).

RAZOUMOWSKY (1789: p. 121) described Coluber vulgaris from Jorat, Switzerland (Canton of Vaud). However, Coluber vulgaris Razoumowsky, 1789 becomes a junior secondary homonym of Natrix vulgaris Laurenti, 1768 when transferred to the genus Natrix and becomes, therefore, invalid (ICZN, 1999: Article 57.3.1). Consequently, the younger replacement name Coluber Helveticus Lacepède, 1789 has to be used instead of Coluber vulgaris Razoumowsky, 1789 (Fritz et al., 2020). In addition, Coluber vulgaris Razoumowsky, 1789 is also a senior primary homonym of *Coluber vulgaris* Bonnaterre, 1790 (a subjective junior synonym of Coluber viridiflavus Lacepède, 1789 = Hierophis viridiflavus; MERTENS & WERMUTH, 1960: p. 174), making Coluber vulgaris Bonnaterre, 1790 permanently invalid (ICZN, 1999: Article 57.2).

"Coluber azureus Donndorff, 1798"

(see Wallach et al., 2014: p. 478)

In contrast to Mertens & Wermuth (1960) and Boulenger (1893), Wallach et al. (2014: p. 478) listed "Coluber azureus Donndorff, 1798" among the synonyms of Natrix natrix (Linnaeus, 1758). Wallach et al. (2014: p. 556) mentioned Coluber azureus also as a synonym of Coluber irregularis Leach in Bowdich, 1819 (now Philothamnus irregularis) and, attributed to Merrem (1820) as describer, as a nomen dubium (p. 819).

However, Donndorff (1798: p. 204) only mentioned, but did not describe, "Coluber Azureus," which was described by Bonnaterre (1790: p. 13). Both Bonnaterre (1790: p. 13) and Donndorff (1798: p. 204) identified this species with "L'Azurée" (Coluber Caeruleus) of Lacepède (1789: p. 276 and p. 100 of the Table méthodique) from "Cap Vert," or in Latin the "promontorium

viride," i.e., the Cape Verde Peninsula in the region of the city of Dakar, Senegal. This makes the identity of *Coluber azureus* with any grass snake impossible.

Coluber Helvetus Donndorff, 1798

MERTENS & WERMUTH (1960: p. 188) treated *Coluber Helvetus* Donndorff, 1798 as a replacement name for "*Coluber helveticus* Lacépède, 1789." However, the Code (ICZN, 1999: Article 72.7, Glossary) requires that a replacement name is expressly proposed as such, which is not the case with *Coluber Helvetus*.

We regard *Coluber Helvetus* Donndorff, 1798 as a taxonomically irrelevant incorrect spelling of '*Coluber Helveticus*' and identify it with the nominotypical subspecies of *Natrix helvetica* (Lacepède, 1789).

"Coluber aesculapii Sturm, 1799"

(see Wallach et al., 2014: p. 478)

Wallach et al. (2014: p. 478) listed "Coluber aesculapii Sturm, 1799" erroneously under the synonyms of *Natrix* natrix (Linnaeus, 1758). STURM (1799) neither intended to describe a new species nor did he use this name for a grass snake, a species well known to him. In his unpaginated work, STURM (1799) treated and figured under the name "Coluber Aesculapii" the Aesculapian snake Zamenis longissimus (Laurenti, 1768), as did many contemporary authors. However, Coluber Aesculapii Linnaeus, 1758 refers to another species, now known as Erythrolamprus aesculapii (Linnaeus, 1758). It is beyond the scope of the present article to evaluate the confusing history of these names. In any case, "Coluber aesculapii Sturm, 1799" does not refer to any grass snake species. To indicate the misunderstanding by WALLACH et al. (2014), we cite "Coluber aesculapii Sturm, 1799" in quotation marks.

Coluber Gronovius Bechstein, 1802

This name is an incorrect spelling for "Coluber Gronovianus." Bechstein (1802: p. 175) referred "Coluber Gronovius" explicitly to Laurenti (1768a, b), the describer of Natrix Gronoviana, and did not expressly propose Coluber Gronovius as a replacement name, as required by the Code (ICZN, 1999: Article 72.7, Glossary). Therefore, the treatment of "Coluber gronovius Bechstein, 1802" by Mertens & Wermuth (1960: p. 187) as a replacement name for Natrix Gronoviana Laurenti, 1768 is erroneous.

Coluber bipedalis Bechstein, 1802 Original spelling: Coluber pipedalis

Coluber bipedalis was inadvertently misspelled in the original description (Bechstein, 1802: p. 174) and corrected by Schreiber (1875: p. 237) and later authors according to Article 32.5.1 of the Code (ICZN, 1999). This name was overlooked in Fritz *et al.* (2020).

Bechstein (1802: p. 174) based his description entirely on Scopoli's (1769) observation of a two-foot-long snake in South Tyrol. Coluber bipes Gmelin, 1789 and Coluber tyrolensis Gmelin, 1789 were founded on the same source as well (see above). The type localities of all three nominal species are the Dolomiti di Fiemme/Fleimser Alpen, Italy (see Fritz et al., 2020), within the distribution range of mtDNA lineage C of Natrix helvetica sicula (Cuvier, 1829). Thus, Coluber bipedalis Bechstein, 1802 threatens the usage of *Coluber siculus* Cuvier, 1829 for the southern mainland subspecies of *Natrix helvetica*. To maintain current usage, we qualify in accordance with Article 23.9.2 of the Code *Coluber siculus* Cuvier, 1829 as a nomen protectum that has precedence over the nomen oblitum Coluber bipedalis Bechstein, 1802 (see also below under the paragraph on Coluber siculus Cuvier, 1829).

Coluber scopolianus Daudin, 1803

This name was recently discussed in Fritz *et al.* (2020). It is a *nomen oblitum* with respect to *Coluber siculus* Cuvier, 1829. Daudin (1803: p. 328) introduced *Coluber scopolianus* explicitly as a replacement name for *Coluber bipes* Gmelin, 1789.

GMELIN'S (1789: p. 1099) description of *Coluber bipes* was entirely based on observations by Scopoli (1769: p. 39), who used in his Latin text the adjective "bipedalis" to characterize the observed snake. As DAUDIN (1803: p. 329) explained, the choice of GMELIN'S species epithet is a misinterpretation, either of the paired copulatory organs of a male snake or referring to the size, meaning 'two feet long.' As a replacement name, *Coluber scopolianus* has the same type locality as *Coluber bipes* Gmelin, 1789 (Dolomiti di Fiemme/Fleimser Alpen, Italy; ICZN, 1999: Article 72.7). Both names refer to lineage C of *Natrix helvetica sicula* that occurs in this region (FRITZ *et al.*, 2020; SCHULTZE *et al.*, 2020).

Coluber decorus Gravenhorst, 1807

This name was listed among the synonyms of *Natrix natrix* (Linnaeus, 1758) by Wallach *et al.* (2014: p. 478). The detailed description in Gravenhorst (1807: p. 410) makes clear that this nominal species cannot be a grass snake. We speculate that Wallach *et al.* (2014) were misled by Gravenhorst's closing sentence "Größe einer mittelmäßigen Ringelnatter" [size of an average grass snake].

As indicated by the addition "(n. sp.)" after the species name, Gravenhorst (1807) indeed intended to describe a new species and did not just use the already existing name *Coluber decorus* for another species, as suggested by Schlegel (1837: p. 231), who identified Gravenhorst's species with *Xenodon rhabdocephalus* (Wied-Neuwied, 1824). Thus, *Coluber decorus* Gravenhorst, 1807 is a junior primary homonym of *Coluber decorus* Shaw, 1802 = *Dendrelaphis pictus* (Gmelin, 1789) (see Wallach *et al.*, 2014: p. 219) and cannot be used

as a valid name (Principle of Homonymy, ICZN, 1999: Article 52).

Coluber distinctus Gravenhorst, 1807

This generally overlooked name is listed by WALLACH et al. (2014: p. 478) among the synonyms of Natrix natrix (Linnaeus, 1758), too. Gravenhorst (1807: pp. 404, 405) specified that his new species Coluber distinctus is identical to the snake in figure 2 of plate X in Seba (1735) showing a Natrix astreptophora (Seoane, 1884) (see our Fig. 2). Additional type material was putatively in Gravenhorst's collection in Breslau (now Wrocław, Poland). It has to be considered lost (Borczyk & Skawiński, 2019). Since the only available type material is the snake figured in Seba (1735), Coluber distinctus Gravenhorst, 1807 has to be identified with Tropidonotus natrix var. astreptophorus Seoane, 1884. According to our knowledge, Coluber distinctus Gravenhorst, 1807 has not been used as a valid name after 1899. To maintain the current usage of Natrix astreptophora (Seoane, 1884), we qualify Tropidonotus natrix var. astreptophorus Seoane, 1884 as a nomen protectum with respect to the nomen oblitum Coluber distinctus Gravenhorst, 1807 (cf. ICZN, 1999: Article 23.9), see the account on *Tropidonotus natrix* var. astreptophorus Seoane, 1884 below.

Coluber irroratus Gravenhorst, 1807

This is another overlooked name treated by WALLACH et al. (2014: p. 478) as a junior synonym of Natrix natrix (Linnaeus, 1758). There seems to be no surviving type material (Borczyk & Skawiński, 2019), and Gravenhorst's (1807: p. 407) description does not allow an unambiguous identification with any snake species. Moreover, the description does not mention any trait characteristic for a grass snake. We hypothesize that WALLACH et al. (2014) were misled by the last sentence of Gravenhorst's description, mentioning "C. natrix." However, this sentence "Größe eines mittelmäßigen C. natrix" [size of an average C. natrix] specifies, as in Coluber decorus Gravenhorst, 1807, only the size of the snake in question relative to the size of a grass snake. We conclude that Coluber irroratus Gravenhorst, 1807 cannot be identified with any snake species and has to be regarded as a nomen dubium.

Coluber minutus Pallas, 1814

PETER SIMON PALLAS' work 'Zoographia Rosso-Asiatica' appeared in three volumes. Coluber minutus and Coluber persa (see below) were described in volume 3. Its publication date has been controversial (see for instance Zhao & Adler, 1993: p. 392). According to Opinion 212 (ICZN, 1954), the year 1814 has to be accepted for this volume, even though its title page shows the date 1831

Pallas' (1814: p. 41) description of *Coluber minutus* was based on a single juvenile grass snake from "Persia."

Grass snakes from Iran represent mtDNA lineage 1 of Kindler *et al.* (2013).

Coluber minutus bears, like Pallas' Coluber persa (see below), two longitudinal back stripes. Eichwald (1841: p. 133) gave the name Coluber persa Pallas, 1814 precedence over the simultaneously published Coluber minutus (ICZN, 1999: Article 24.2, First Reviser Principle). Since then, Coluber minutus has been generally regarded as a synonym of Coluber persa. The whereabouts of the holotype of Coluber minutus are unknown. It is not present in the collection of the Zoological Institute of the Russian Academy of Sciences, St. Petersburg (К. Д. Мильто [К. D. Milto], pers. comm., 22 June 2020).

Coluber persa Pallas, 1814

Since Werner (1938) and Mertens (1947), the name Natrix natrix persa (Pallas, 1814) has been generally applied to grass snakes with two longitudinal back stripes from the Balkans and the Middle East inclusive of Asia Minor and Transcaucasia (e.g., Mertens & Wermuth, 1960; Gruber, 1989; Kabisch, 1999; Arnold & Oven-DEN, 2002; GENIEZ, 2015), even though MERTENS (1947: p. 21) already acknowledged a certain degree of morphological variability in that not all snakes in these populations are striped. Later, Kindler et al. (2013) showed that populations identified with *Natrix natrix persa* correspond to seven out of the eight mtDNA lineages of Natrix natrix. Some of these seven mtDNA lineages occur completely within the range of the putative subspecies Natrix natrix persa. Others are also distributed beyond the range, and grass snakes lack there the back stripes, even though mtDNA and STRUCTURE analyses (PRITCHARD et al., 2000) using microsatellite loci showed no genetic differentiation compared to populations with striped snakes (Kindler et al., 2017).

Pallas (1814: p. 41) erected his Coluber persa based on one specimen with two back stripes, collected by Samuel Gottlieb Gmelin (1744-1774) during his expedition to Persia. It is unknown whether the holotype still exists; it could be not located in the collection of the Zoological Institute of the Russian Academy of Sciences, St. Petersburg (К. Д. Мильто [К. D. Milto], pers. comm., 22 June 2020). GMELIN's (1774) detailed itinerary allows reconstructing that his way led from Derbent (Dagestan) through what is now the independent state of Azerbaijan to Gilan and Mazandaran in Iran. GMELIN (1774: pp. 482, 483, 503) explicitly mentioned "Schlangen" [snakes] for Mazandaran and Gilan. In these two Iranian provinces live, as in Azerbaijan, grass snakes with mtDNA lineage 1 of Kindler et al. (2013), which has to be identified with Coluber persa Pallas, 1814.

Without additional nuclear genomic evidence, the delineation of the subspecies *Natrix natrix persa* remains speculative. Yet, the available data (Kindler *et al.*, 2013, 2017) strongly suggest that this subspecies does not occur on the Balkan Peninsula, where four distinct mtDNA lineages are found (lineages 3, 4, 5, and 7 of Kindler *et al.*, 2013). Lineage 1 does not occur there, and the

geographically closest records are in Transcaucasia, approximately 2,000 km away from the Balkans (KINDLER et al., 2013). Thus, we tentatively identify grass snakes of mtDNA lineage 1 from Azerbaijan and Iran with Natrix natrix persa (Pallas, 1814), while the identity of grass snakes from the Balkan remains undetermined (see also below under Coluber bilineatus Bibron & Bory de Saint-Vincent, 1833).

It remains unclear why Pallas (1814) used the species epithet 'persa' obviously in female gender, even though Coluber is masculine and treated as such by Pallas in other cases (p. 40: Coluber quadrilineatus, p. 41: Coluber minutus, p. 45 [page number transposed to 54]: Coluber pictus, Coluber cupreus, p. 46: Coluber caucasius). However, Coluber maeota Pallas, 1814 (p. 47), a questionable synonym of Elaphe dione (Pallas, 1773) (Mertens & Wermuth, 1960: p. 178; Wallach et al., 2014: p. 262), seems to be in feminine gender as well. We treat 'persa' (and 'maeota') as nouns in the nominative singular standing in apposition to the genus name (ICZN, 1999: Article 11.9.1.2), even though this is irrelevant for the currently used combination Natrix natrix persa because Natrix is of feminine gender.

Coluber viperinus Rafinesque, 1814

Wallach et al. (2014: p. 478) listed Coluber viperinus Rafinesque, 1814 as a junior synonym of Natrix natrix (Linnaeus, 1758). Otherwise, this name is rarely mentioned, perhaps because it is confused with its senior homonym Coluber viperinus Latreille in Sonnini & Latreille, 1801. However, RAFINESQUE (1814a: p. 104) described Coluber viperinus in his 'Prodromo di Erpetologia Siciliana' explicitly as a new species ("Raf. N. Sp."), gave some scale counts and mentioned that it is totally black, with a tawny tinge. This leaves no doubt that Coluber viperinus Rafinesque, 1814 represents a distinct nominal species. According to its type locality Sicily, it refers to mtDNA lineage A of Natrix helvetica sicula (Cuvier, 1829), distributed in Sicily and Calabria (Kindler et al., 2013; Kindler & Fritz, 2018; Schultze et al., 2020).

RAFINESQUE (1814a) explained that Coluber viperinus is called in Sicilian "Vissena niura" (black vissena). The words 'vis(s)ena,' 'guisina' or variants thereof are still widely used for grass snakes in Sicily (La Mantia & Vaccaro, 2008: p. 452). However, especially melanistic grass snakes are often confused with the local black whipsnake, Hierophis viridiflavus carbonarius (Bonaparte, 1833), so that 'vissena niura' could refer to either species (F. Marrone, pers. comm., 8 June 2020), although La Mantia & Vaccaro (2008: p. 452) believed that the 'vissena niura' is a black grass snake. Regardless of its identity, Coluber viperinus Rafinesque, 1814 cannot be used as a valid name because it is a junior primary homonym of Coluber viperinus Latreille in Sonnini & Latreille, 1801. The latter name is a junior synonym of Coluber maurus Linnaeus, 1758 = Natrix maura (see MERTENS & WERMUTH, 1960: p. 185).

Vipera vissena Rafinesque, 1814

This name was listed by Mertens & Wermuth (1960: p. 185) as a synonym of *Natrix maura* (Linnaeus, 1758). However, *Natrix maura* does not occur on Sicily (Schätti, 1999), from where *Vipera vissena* Rafinesque, 1814 has been described. Perhaps Mertens & Wermuth (1960) were misled because Rafinesque (1814b: p. 15) mentioned an overall yellowish brown coloration with black spots, which also matches *Natrix maura*. In the face of its origin, Wallach *et al.* (2014: p. 478) referred *Vipera vissena* correctly to *Natrix natrix* (Linnaeus, 1758) sensu lato.

RAFINESQUE (1814b: p. 15) detailed that Vipera vissena is observed in Sicily, where the "nom vulgaire Vissena" is used for it. Until today, grass snakes are known under 'vis(s)ena' or 'guisina' in Sicily (La Mantia & Vaccaro, 2008; F. Marrone, pers. comm., 8 June 2020). Thus, there is no doubt that Vipera vissena Rafinesque, 1814 refers to grass snakes. On Sicily, mtDNA lineage A of Natrix helvetica sicula (Cuvier, 1829) occurs (see above under Coluber viperinus Rafinesque, 1814), and this island is also the type locality of Coluber siculus Cuvier, 1829. Consequently, Vipera vissena Rafinesque, 1814 is a senior synonym of Coluber siculus Cuvier, 1829, which is currently used in the combination Natrix helvetica sicula. Since Vipera vissena Rafinesque, 1814 has never been regarded as the valid name of any species after RAFINESQUE (1814a, b), it is a nomen oblitum with respect to Coluber siculus Cuvier, 1829. To maintain current usage, we qualify the latter name in the respective paragraph below as a nomen protectum.

Natrix hybridus Merrem, 1820

MERREM (1820: p. 125) described this species from Switzerland, and MERTENS & WERMUTH (1960: p. 188) treated it as a junior synonym of "Coluber helveticus Lacépède, 1789." WALLACH et al. (2014: p. 478) listed it under the synonyms of "Coluber natrix Linnaeus, 1758." There is no type material.

Merrem (1820) chose the species epithet not to indicate a hybrid origin, rather to express his doubts on the distinctness of his species. This is supported by his comment that *Natrix hybridus* is perhaps a variety of the "geringelte Natter *Natrix torquatus*" (Merrem, 1820: pp. 124, 125) and by his German name for *Natrix hybridus*, "unächte Natter."

Across northeastern Switzerland runs a narrow hybrid zone of *Natrix helvetica* and *Natrix natrix* (Thorpe, 1979; Kindler *et al.*, 2017), so that Merrem's name after two centuries gains an inadvertent connotation because it could refer to *Natrix helvetica*, *Natrix natrix* or to their hybrids. Moreover, the name also refers to the smooth snake, *Coronella austriaca* Laurenti, 1768, since Merrem (1820: p. 125) identified *Natrix hybridus* with *Coluber versicolor* Razoumowsky, 1789. The latter name is a junior synonym of *Coronella Austriaca* Laurenti, 1768 (see Mertens & Wermuth, 1960: p. 175; Wallach *et al.*, 2014: p. 185). Therefore, *Natrix hybridus* Merrem, 1820 has to be regarded as a *nomen dubium*.

"Coluber scopolii Risso, 1826"

(see Wallach et al., 2014: p. 478)

This name is erroneously listed as a junior synonym of *Natrix natrix* (Linnaeus, 1758) in WALLACH *et al.* (2014: p. 478).

Risso (1826: p. vii) specified in the introduction of his book that six out of the 15 'ophidian species' he treated are new; Risso's ophidians are lizards (slow worms, Anguis), for which he described two new species, and true snakes, for which he described four new species. Risso (1826) always indicated new species by an "(N.)" [Nobis = ours] after the species name. Coluber Scopolii (p. 90) is neither marked by an "(N.)" nor does it belong to the four new snake species (Coluber guttatus, Coluber palustris, Coluber rupestris, Coluber strigatus). Coluber Scopolii was actually already described by MERREM (1820: p. 104). It is a junior synonym of Zamenis longissimus (Laurenti, 1768) (Mertens & Wermuth, 1960: p. 179). This identification is also evident from the references for Coluber Scopolii cited in Risso (1826). "Coluber scopolii Risso, 1826" is consequently not a new name.

Tropidonotus Oppelii Boie, 1827

Boie (1827: column 534) diagnosed this species from southern Europe ("im südlichen Europa zu Hause") by the presence of two whitish back stripes. Boie (1827: column 534) gave Duméril as authority for this name, perhaps referring to an unpublished manuscript by André-Marie-Constant Duméril (1774–1860). Therefore, Wallach *et al.* (2014: p. 476) cited this name as "*Tropidonotus oppelii* Duméril in F. Boie, 1827."

Tropidonotus Oppelii is a nomen dubium. If it refers to a grass snake, the type locality would imply that it was based on specimens from the Balkan Peninsula because this is the only part of southern Europe where striped grass snakes occur. Then, Tropidonotus Oppelii cannot be referred to a particular mtDNA lineage (see above under Coluber persa Pallas, 1814). This conclusion is similar to that of Mertens & Wermuth (1960: p. 186), who listed Tropidonotus Oppelii Boie, 1827 as a synonym of Natrix natrix (Linnaeus, 1758) but did not identify it with any subspecies. An alternative view is found in Wallach et al. (2014: p. 476). These authors assigned "Tropidonotus oppelii" to the synonymy of Natrix maura (Linnaeus, 1758), also a species with striped morphotypes.

Coluber siculus Cuvier, 1829

This name, with type locality of Sicily (CUVIER, 1829: p. 84), has been used for a long time for a southern subspecies either of *Natrix natrix* (Linnaeus, 1758) or *Natrix helvetica* (Lacepède, 1789). The usage of *Coluber siculus* Cuvier, 1829 for this subspecies is or was threatened by several older names. Fritz et al. (2020) qualified *Coluber siculus* as a nomen protectum with respect to the nomina oblita Coluber bipes Gmelin, 1789, Coluber tyrolensis Gmelin, 1789, and Coluber scopolianus Dau-

din, 1803, all with the same type locality (Dolomiti di Fiemme/Fleimser Alpen, Italy), and referred these names to mtDNA lineage C of *Natrix helvetica sicula*. In the present study, we further qualify *Coluber siculus* Cuvier, 1829 as a *nomen protectum* having precedence over the *nomina oblita Coluber bipedalis* Bechstein, 1802 and *Vipera vissena* Rafinesque, 1814 that were overlooked in FRITZ *et al.* (2020).

To this end, we cite in fulfilment of Article 23.9.1.2 of the Code (ICZN, 1999) the following 25 articles from the preceding 50 years with more than 10 different authors that used *Coluber siculus* as the valid name of a subspecies of *Natrix natrix* or *Natrix helvetica*: Lanza (1973, 1983), Mezzena & Dolce (1977), Stefani (1983), Gruber (1989), Shine (1994), Turrisi & Vaccaro (1998), Mazzotti *et al.* (1999), Lo Valvo & Longo (2001), Arnold & Ovenden (2002), Di Cerbo & Manenti (2004), Luiselli *et al.* (2005), Kreiner (2007), Di Cerbo & D'Amico (2008), Kwet (2010), Göcmen *et al.* (2011), Kindler *et al.* (2013, 2017), Geniez (2015), Speybroeck *et al.* (2016), Bruni (2017), Kindler & Fritz (2018), Di Nicola (2019), Fritz *et al.* (2020), and Schultze *et al.* (2020).

In the herpetological collection of the Muséum national d'Histoire naturelle, Paris, the specimen MNHN-RA-0.3317 (Fig. 5) is identified as the holotype of *Coluber siculus* Cuvier, 1829. However, MNHN-RA-0.3317 has to be regarded as a syntype because it is not clear from the original description that Cuvier based his new species only on a single specimen. In addition, BIBRON & BORY DE SAINT-VINCENT (1833: p. 73) mention that *Coluber siculus* was "établie par Cuvier d'après des individus trouvés par l'un de nous (M. Bibron) en Sicile," indicating that Cuvier had more than one specimen at his disposal.

Tropidonotus ater Eichwald, 1831

Based on melanistic grass snakes, Eichwald (1831: p. 173) described this species from islands in the Volga River near Astrakhan. The type locality lies within the distribution range of mtDNA lineage 8, the 'green lineage' of Kindler et al. (2013, 2014, 2017). Thus, Tropidonotus ater Eichwald, 1831 represents a junior synonym of Coluber scutatus Pallas, 1771 and not of Coluber persa Pallas, 1814 as suggested by Mertens & Wermuth (1960: p. 188). It is possible that type material of Tropidonotus ater Eichwald, 1831 is in the collection of the Zoological Institute of the Russian Academy of Sciences, St. Petersburg (К. Д. Мильто [К. D. Milto], pers. comm., 22 June 2020).

"Tropidonotus persicus Eichwald, 1831"

(see Mertens & Wermuth, 1960: p. 188)

MERTENS & WERMUTH (1960: p. 188) identified this name, like the preceding, with *Coluber persa* Pallas, 1814 and treated *Tropidonotus persicus* Eichwald, 1831 as a replacement name for Pallas' name. According to Eich-

WALD (1831: p. 173), *Tropidonotus persicus* occurs in Mazandaran and has two white back stripes. Therefore, this name clearly refers to the same taxon and the same mtDNA lineage as *Coluber persa* Pallas, 1814.

EICHWALD (1831) credited *Tropidonotus persicus* to PALLAS but did not expressly state that he intended to replace PALLAS' original name, as required by Article 72.7 and the Glossary of the Code (ICZN, 1999) for *nomina nova*. Therefore, it is clear that *Tropidonotus persicus* is merely an incorrect subsequent spelling (ICZN, 1999: Article 33.3) and not a distinct new name. Interestingly, EICHWALD (1841: p. 132) referred later to the same species under the name "*Tropidonotus persa*," using the original species name obviously in apposition and turning back to PALLAS' original spelling.

Coluber niger Dvigubsky, 1832

Двигубский [Dvigubsky, also transliterated as Dwigubskij, Dwigubski or Dwigubsky] (1832: p. 26) described this species in his treatise on the natural history of the Russian Empire in a superficial way and without mentioning a locality. There is no type material. Никольскій [Nikolsky, also transliterated as Nikolskij] (1916: p. 43) listed Coluber niger as a synonym of "Coluber natrix Linné." Mertens & Wermuth (1960: p. 189) inferred that the type locality of Coluber niger is southeastern Transcaucasia and relegated it into the synonymy of Coluber scutatus Pallas, 1771.

Двигубский (1832) characterized the coloration of Coluber niger as dorsally black with small light brown spots and ventrally white. Most importantly, he described the head as laterally and ventrally reddish, which is not expected in a grass snake. Moreover, a light neck collar or lunar spots were not mentioned. This questions the identification as a grass snake. Another snake species, widely distributed in the southwest of the former Russian Empire, matches Двигубский's description better. Dolichophis caspius (Gmelin, 1789) can show both a reddish head coloration and a speckled body pattern (GRUBER, 1989; Ščerbak & Böhme, 1993). However, keeled scales, mentioned by Двигубский (1832) for Coluber niger, do not occur in Dolichophis caspius (see Gruber, 1989). Consequently, Coluber niger Dvigubsky, 1832 cannot be unambiguously identified with any species. It represents a nomen dubium and should be removed from the synonymy of Coluber Natrix Linnaeus, 1758.

"Coluber ponticus Ménétries, 1832"

(see Nikolsky, 1916: p. 43 and Wallach *et al.*, 2014: p. 478)

Никольскій (1916: р. 43) and Wallach *et al.* (2014: р. 478) listed *Coluber ponticus* Ménétries, 1832 among the synonyms of *Natrix natrix* (Linnaeus, 1758). However, Ménétries (1832: р. 69) did not describe a new species with that name but only cited *Coluber ponticus* Pallas, 1814, a junior synonym of the dice snake *Natrix tessellata* (Laurenti, 1768) (Mertens & Wermuth, 1960:



Fig. 5. Dorsal and ventral aspects of a syntype of *Coluber siculus* Cuvier, 1829 (Muséum National d'Histoire naturelle, Paris, MNHN-RA-0.3317, Sicily, Italy). Photos: Antoine Fraysse (Muséum national d'Histoire naturelle, Paris, RECOLNAT project 2018, ANR-11-IN-BS-0004).

p. 190). Consequently, *Coluber ponticus* as mentioned by Ménétries (1832) is not a new name and does not refer to the synonymy of any grass snake species.

Tropidonotus Natrix var. minax Fitzinger, 1832

This and the following name (Tropidonotus Natrix var. murorum Fitzinger, 1832) have a complicated and convoluted history. Boulenger (1893: p. 219), Mertens & WERMUTH (1960: p. 188), and WALLACH et al. (2014: p. 478) credited both names to Bonaparte (1834 in Bo-NAPARTE, 1832–1841), who used them in the combinations "Natrix Torquata var. Minax" and "Natrix Torquata var. Murorum" in his unpaginated 'Iconografia della fauna italica' and gave brief morphological descriptions. Accordingly, Mertens & Wermuth (1960) treated the two names as junior synonyms of "Natrix natrix helvetica (Lacépède, 1789)" with type locality of Italy. However, FITZINGER (1832: p. 326) already characterized both varieties in his 'Ausarbeitung einer Fauna des Erzherzogthumes Oesterreich,' referring to grass snakes from the Archduchy of Austria.

We take the stance that the diagnostic characters mentioned by Fitzinger ("schwarz" [black] for minax; "gelbstreifig" [striped yellow] and "zweistreifig" [bearing two stripes for *murorum*) suffice to make the names available for the purposes of the Code (ICZN, 1999). This view is supported by the fact that these traits do not translate into the scientific names in Latin, as expected for nomina nuda, even though Fitzinger combined the traits as adjectives with the respective German vernacular names. Furthermore, the Latin adjective "Mihi" [= mine] after "Tropidonotus Natrix, var. minax" and "Tropidonotus Natrix, var. murorum" indicates that Fitzinger (1832) intended to describe these two varieties as new to science, in contrast to Bonaparte (1834 in Bonaparte, 1832–1841), who merely used the names of these varieties for snakes matching Fitzinger's (1832) brief descriptions.

Tropidonotus Natrix var. minax was characterized by FITZINGER (1832: p. 326) as "Schwarze Wasser= Ringel= Kron= oder Haus=Natter" that differs therefore by its black coloration from the regular "Tropidonotus Natrix." FITZINGER mentioned "Schreibers" (see below) as an earlier authority for this variety and specified that the variety minax had the same distribution as "Tropidonotus Natrix." However, he mentioned that the variety was very rare and more typical for the southern regions. Thus, Tropidonotus Natrix var. minax was based on black grass snakes from the Archduchy of Austria, corresponding more or less to the current Austrian states of Oberösterreich (Upper Austria) and Niederösterreich (Lower Austria).

In Upper Austria both the 'yellow' and the 'red mtDNA lineage' (lineages 3 and 4 of Kindler et al., 2013) occur, in Lower Austria only the 'red lineage' (Kindler et al., 2013, 2017). However, many grass snakes in the two states are genotypically admixed according to microsatellite analyses, even though pure representatives of the 'red cluster' also occur (Kindler et al., 2017). In the face

of this complex situation, *Tropidonotus Natrix* var. *minax* cannot be unambiguously referred to a particular subspecies or genetic lineage of *Natrix natrix* (Linnaeus, 1758).

In an earlier work, Fitzinger (1826: p. 58) had already mentioned the two varieties as *nomina nuda*, using the combinations "*Coluber Natrix minax*" and "*Coluber Natrix murorum*." For the former name he cited "Schreibers" again as earlier authority. "Schreibers" is to be identified with Karl Franz Anton Ritter von Schreibers (1775–1852), former director of the Vereinigte k. k. Naturalien-Kabinette in Wien, later known as Naturhistorisches Museum Wien. Fitzinger (1826, 1832) referred with some certainty to one of von Schreibers' unpublished manuscripts that was destroyed by a fire during the 1848 revolution in Vienna (Scholler, 1953).

Type material of both *Tropidonotus Natrix* var. *minax* and *Tropidonotus Natrix* var. *murorum* Fitzinger, 1832 is or was most likely in the collection of the Naturhistorisches Museum Wien. Gemel *et al.* (2019) did not list any types for these taxa, implying either that the specimens are unidentified or were lost in the same fire as von Schreibers' manuscripts.

Tropidonotus Natrix var. murorum Fitzinger, 1832

The history of this name resembles that of *Tropidonotus Natrix* var. *minax* Fitzinger, 1832 (see above). Important differences are that Fitzinger (1832: p. 326) characterized this variety by the presence of two yellow stripes, a description repeated by Bonaparte (1834 in Bonaparte, 1832–1841). According to Fitzinger, the distribution of *Tropidonotus Natrix* var. *murorum* is identical with that of *Tropidonotus Natrix* var. *murorum* can only be assigned to *Natrix natrix* (Linnaeus, 1758) but not to a particular subspecies or genetic lineage.

FITZINGER (1826: p. 58) had already used the epithet *murorum* as a *nomen nudum* in the combination "*Coluber Natrix murorum*." In both works, FITZINGER (1826, 1832) indicated "Vest" as previous authority for this name ("*Coluber murorum* Vest" *nomen nudum*). This may refer to a conversation with or an unpublished manuscript by the Austrian physician and botanist Lorenz Chrysanth von Vest (1776–1840) of Klagenfurt and Graz, who studied in Vienna.

Coluber bilineatus Bibron & Bory de Saint-Vincent, 1833

This species was described based on material collected and observed on the Peloponnesus during the French Morea expedition (1828–1833). As implied by the species epithet, BIBRON & BORY DE SAINT-VINCENT (1833: p. 73) diagnosed their new species *Coluber bilineatus* by the presence of two yellow back stripes. A syntype was figured on their plate XIV (figures 2 and 2a, b) of the Atlas volume, published in 1835 (see our Fig. 6). The speci-

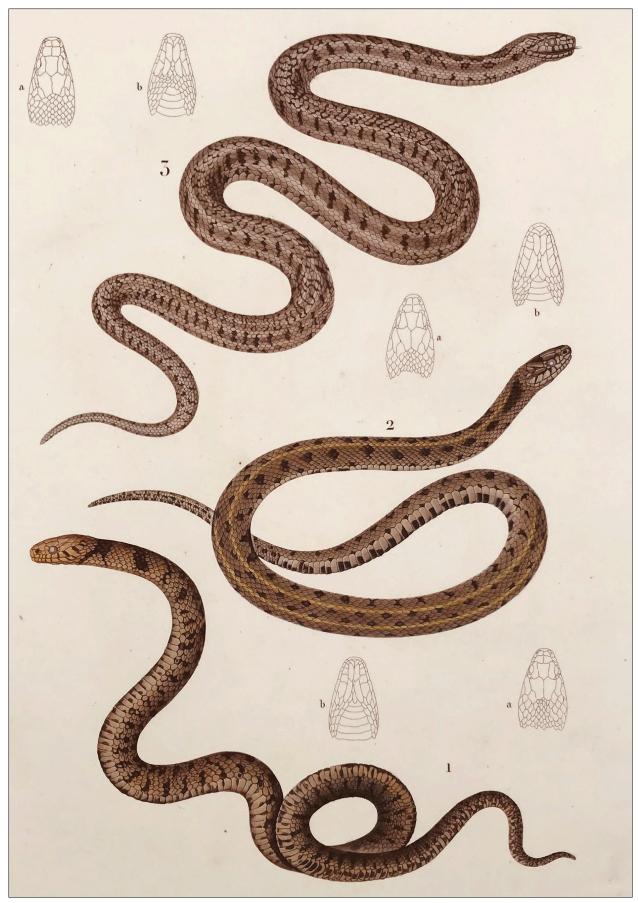


Fig. 6. Reproduction of plate XIV of BIBRON & BORY DE SAINT-VINCENT (1835). The original caption reads: (1) Couleuvre à Collier noir, Coluber Siculus Cuv.; (2) Couleuvre à deux raies, Coluber Bilineatus Bib. et Bory; (3) Couleuvre Léopardine, Coluber Leopardinus C. Bonap. [= Zamenis situla (Linnaeus, 1758)].



Fig. 7. Dorsal and ventral aspects of a syntype of *Coluber bilineatus* Bibron & Bory de Saint-Vincent, 1833 (Muséum National d'Histoire naturelle, Paris, MNHN-RA-0.3468, Peloponnesus, Greece). Same specimen as in Figure 6 (2). Photos: Antoine Fraysse (Muséum national d'Histoire naturelle, Paris, RECOLNAT project 2018, ANR-11-INBS-0004).

men is still present in the herpetological collection of the Muséum national d'Histoire naturelle, Paris (MNHN-RA-0.3468; Fig. 7).

BIBRON & BORY DE SAINT-VINCENT (1833: p. 73) believed that *Coluber bilineatus* occurs along with another, more common, grass snake species on the Peloponnesus, which they identified as *Coluber siculus* Cuvier, 1829 (Fig. 6). Both were diagnosed from "*Coluber natrix*, Linn." by the presence of a black collar and the absence of light lunar spots. According to BIBRON & BORY DE SAINT-VINCENT, *Coluber bilineatus* differs from *Coluber siculus* only by the presence of the two yellow stripes.

Acknowledging the presence of back stripes, MERTENS & WERMUTH (1960: p. 188) treated Coluber bilineatus Bibron & Bory de Saint-Vincent, 1833 as a junior synonym of Coluber persa Pallas, 1814, a conclusion that is not supported by preliminary genetic data (see also above under the account for Coluber persa Pallas, 1814, which we identify with the Transcaucasian mtDNA lineage 1 of Kindler et al., 2013). Grass snakes from the Peloponnesus belong to mtDNA lineage 5 of Kindler et al. (2013). However, further research is needed to resolve their nuclear genomic identity. According to analyses using microsatellite loci (KINDLER et al., 2017), Peloponnesian grass snakes belong to a distinct nuclear genomic cluster that corresponds to up to four mtDNA lineages (lineages 3, 4, 5, and 7 of Kindler et al., 2013), like most Balkan populations. This situation could parallel that in mainland Italy and Sicily, where several mtDNA lineages together represent one nuclear genomic continuum and a single subspecies (Schultze et al., 2020). Alternatively, additional fine-scale analyses, preferably using additional nuclear genomic markers, could resolve this Balkan cluster into several units. Until this is clarified, the possibility remains that the nuclear genomic cluster from the Balkans corresponds to four distinct mtDNA lineages, perhaps even to additional ones occurring further east.

With respect to nomenclature, *Coluber bilineatus* Bibron & Bory de Saint-Vincent, 1833 is a younger primary homonym of *Coluber bilineatus* Latreille in Sonnini & Latreille, 1801, and thus permanently invalid (ICZN, 1999: Article 57.2).

Coluber bilineatus Latreille in Sonnini & Latreille, 1801 is rarely mentioned. It seems that Latreille (in Sonnini & Latreille, 1801: pp. 110, 111) copied his description largely from Lacepède (1789: Table méthodique, p. 88 and p. 220) without citing him. Lacepède (1788) used the same name for a specimen of unknown provenance from the "collection de Sa Majesté." Lacepède's name was ruled to be unavailable (ICZN, 1987: Opinion 1463). Wallach et al. (2014: p. 34) identify Coluber bilineatus Lacepède, 1789 with Amphiesma stolatum (Linnaeus, 1758).

Coluber bilineatus Bibron & Bory de Saint-Vincent, 1833 is also a primary homonym of Coluber bilineatus Schinz, 1833, described in the same year (Schinz, 1833: p. 148). Coluber bilineatus Schinz, 1833 is a junior synonym of Coluber scalaris Schinz, 1822 = Zamenis scalaris (see Mertens & Wermuth, 1960: p. 182; Wallach et al., 2014: p. 809).

In addition to these primary homonyms, there are two further names that were temporarily senior secondary homonyms of *Coluber bilineatus* Bibron & Bory de Saint-Vincent, 1833 (SHERBORN, 1922–1932). However, these names are irrelevant because they are now placed as junior synonyms into other genera: *Hurria bilineata* Daudin, 1803 is now a junior synonym of *Cerberus rynchops* (Schneider, 1799), and *Elaps bilineatus* Schneider, 1801 is now another junior synonym of *Amphiesma stolatum* (Linnaeus, 1758) (WALLACH *et al.*, 2014: p. 155 and p. 34, respectively). It is beyond the scope of the present study to clarify the history of these two names in more detail.

Coluber natrix var. dalmatina Schinz, 1833

Schinz (1833: p. 144) described this variety based on grass snakes from Dalmatia with two white back stripes. Figure 1 of Schinz' plate 58 illustrates this well. No surviving type material is known. Mertens & Wermuth (1960: p. 188) listed *Coluber natrix* var. *dalmatina* Schinz, 1833 as a synonym of *Coluber persa* Pallas, 1814.

MtDNA lineages 4 and 5 of *Natrix natrix* occur in Dalmatia (KINDLER *et al.*, 2013), and the nuclear genomic identity of Balkan grass snakes is still unclear (see above under *Coluber bilineatus* Bibron & Bory de Saint-Vincent, 1833). Thus, *Coluber natrix* var. *dalmatina* Schinz, 1833 cannot be identified with a particular mtDNA lineage or subspecies and can only be referred to *Natrix natrix* (Linnaeus, 1758).

Natrix Cetti Gené, 1839

GENÉ (1839: p. 272) described *Natrix Cetti* from Sardinia and Corsica and mentioned three specimens, two adults from Sardinia and a juvenile from southern Corsica. Although not stated explicitly, it may be inferred that these specimens were in the collection of the Royal Zoological Museum Turin, now Museo Regionale di Scienze Naturali, Torino, because Carlo Giuseppe [Josephus] Gené (1800–1847) worked there as a professor and co-director of the museum.

The Sardinian syntypes were a male from the Monte di San Giovanni d'Iglesias (southern Sardinia) and a gravid female from Fonni (Nuoro province, central Sardinia). Gené (1839) illustrated the female and the juvenile syntypes on his plate IV (see our Fig. 8). The male syntype, with everted hemipenes, was later figured in JAN & SORDELLI (1868: plate I, fig. 2).

According to Gené (1839), a further putatively Sardinian specimen was in the collection of the "Museum Karalitanum," i.e., the museum of Cagliari, Sardinia. This specimen has to be regarded as another syntype. It was obviously lost by the late 19th century because Camerano (1891: p. 21) mentioned only two specimens from the Cagliari museum, but these were not collected early enough (1861, 1884) to qualify as Gené's syntype. Camerano provided measurements of one of the

Cagliari specimens and the three syntypes from Torino (p. 18). Tortonese (1942: p. 221) tentatively identified a badly preserved juvenile from Sardinia from the Torino museum as one of GENÉ's syntypes and stated that he could not find the syntype from Corsica. Later, ELTER (1981: p. 102) mentioned three Sardinian grass snakes (R211 = 505, 1 specimen; R1734 = 504, 2 specimens) in the Torino museum. Today, only one lot of Natrix helvetica cetti is present; two other lots with the old numbers 503 and 505 are lost (F. Andreone, pers. comm., 25 June 2020, MZUT R1734). The jar numbered MZUT R1734 (old number 504) contains an adult female, a juvenile, and an egg. The two snakes match the syntypes figured on Gené's (1839) plate IV, i.e., the female from Fonni, Sardinia, and the juvenile from southern Corsica (Figs 8 and 9). Despite the long period of preservation, the female can be bend easily into the same twisted position as shown in Gené's plate (see our Fig. 8), so that there is no doubt that these two specimens are syntypes.

Mertens & Müller (1928: p. 49) restricted the type locality of *Natrix Cetti* to one of the sites mentioned in Gené (1839), the Monte di San Giovanni d'Iglesias, Sardinia. Following this step, *Natrix Cetti* Gené, 1839 has generally been identified with grass snakes from Sardinia (e.g., Hecht, 1930; Mertens & Wermuth, 1960; Thorpe, 1979; Kabisch, 1999; Vanni & Cimmaruta, 2011; Genez, 2015). However, as Mertens & Müller (1928) did not designate a lectotype, their restriction of the type locality is invalid.

Since Gené (1839) described his grass snake species based on material from Sardinia and southern Corsica, all localities together (i.e., both islands) constitute the type locality (ICZN, 1999: Article 73.2.3). This automatically renders *Tropidonotus natrix corsus* Hecht, 1930, a name later widely used for the subspecies from Corsica, a junior subjective synonym of *Natrix Cetti* Gené, 1839. To resolve this intricate situation and maintain the current usage of subspecies names, we here designate the female syntype from Fonni, Sardinia, as lectotype of *Natrix Cetti* Gené, 1839.

Genetically, Natrix Cetti Gené, 1839 corresponds to the deeply divergent mtDNA lineage B of Natrix helvetica. Barred grass snakes from Corsica also belong to the same lineage (Kindler et al., 2013; Kindler & Fritz, 2018; Schultze et al., 2020). In microsatellite analyses (SCHULTZE et al., 2020), Sardinian and Corsican grass snakes were not differentiated, even though grass snakes from both islands together represent a distinct cluster compared to Natrix helvetica from the mainland and Sicily. The lack of genetic differentiation between Sardinian and Corsican grass snakes suggests that they are synonymous. However, the results of Schultze et al. (2020) should be regarded as preliminary because they could study only a few samples from Corsica and Sardinia. Since Sardinian grass snakes are seriously threatened and listed in the IUCN category 'Critically Endangered' (EUROPEAN REPTILE AND AMPHIBIAN SPECIALIST GROUP, 1996), a premature synonymization of their name with that of the Corsican subspecies could have negative implications for the conservation of Sardinian grass snakes. Therefore, Schultze *et al.* (2020) refrained from taxonomic conclusions and recommended further research. In the face of this situation, we stress the need for additional investigations but tentatively accept both subspecies as valid.

Tropidonotus Natrix var. colchica Nordmann in Démidoff, 1842

MERTENS & WERMUTH (1960: p. 188) treated this name as a synonym of Coluber persa Pallas, 1814 and gave 1840 as year of publication. Démidoff's report about his 1837 expedition, for which Alexander von Nordmann (Александр фон Нордман, 1803 – 1866) supervised and at least partially wrote the 'Observations sur la faune pontique' (Damkaer, 2002: p. 266; Adler, 2012: pp. 109, 110), appeared in several volumes. The volume containing the 'Observations' indeed appeared in 1840 (Nord-MANN in Démidoff, 1840). However, under the description of Tropidonotus natrix (p. 350) neither the name "Tropidonotus Natrix var. colchica" nor "Tropidonotus Natrix var. nigra" is mentioned, even though the two varieties were described morphologically and the plates in the Atlas volume of 1842 were cited. Only in the legends of two plates, plate 12 and 11, respectively, do the two names appear (Nordmann in Démidoff, 1842), so that their publication date is 1842. "Tropidonotus Natrix var. colchica," which differs in coloration from typical grass snakes (Nordmann in Démidoff, 1840: p. 350), is shown in figure 1 of plate 12 (Nordmann in Démidoff, 1842).

On page 350 of the 1840 volume, Nordmann mentioned that grass snakes were collected in "Abasie" and on the Crimea. The whereabouts of this material is unclear. Since no further information is given, "Abasie" and the Crimean Peninsula have to be regarded as the compound type locality of *Tropidonotus Natrix* var. *colchica* Nordmann in Démidoff, 1842. According to a map in the Atlas volume (Démidoff, 1842), "Abasie" corresponds to a large part of the northern Transcaucasian Black Sea coast, from Anapa (Russia) to Anaklia (Georgia). Mertens & Wermuth (1960: p. 188) misidentified this region with the Russian Kuban Region north of the Greater Caucasus.

In the western Transcaucasus and on the Crimea mtDNA lineage 8 occurs, i.e., the 'green lineage' (KINDLER et al., 2013, 2017), to which we assign the name Natrix natrix scutata (Pallas, 1771); see above under Coluber scutatus Pallas, 1771. Thus, Tropidonotus Natrix var. colchica Nordmann in Démidoff, 1842 is a junior synonym of Coluber scutatus Pallas, 1771.

Tropidonotus Natrix var. *nigra* Nordmann in Démidoff, 1842

This is the second variety described and named by Nord-Mann in Démidoff (1840: p. 350; 1842: plate 11, figure 1)—a melanistic grass snake. Nordmann in Démidoff (1840) mentioned explicitly that this variety is from



Fig. 8. Reproduction of plate IV of Gené (1839), showing the adult syntype from Fonni, Sardinia, and the juvenile syntype from southern Corsica. This hand-coloured plate displays the original coloration and pattern of the depicted specimens that faded over time. Copies of Gené (1839) with hand-coloured plates are rare; mostly copies with plain plates were distributed.

"Abasie," so that this region, but not the Crimea, represents the type locality. As the preceding variety, *Tropidonotus Natrix* var. *nigra* Nordmann in Démidoff, 1842 is to be identified with *Natrix natrix scutata* (Pallas, 1771).

Tropidonotus Natrix var. nigra Nordmann in Démidoff, 1842 is a primary homonym of several other names. Most important is Tropidonotus niger Holbrook, 1842, which in turn is a junior synonym of Nerodia sipedon (Linnaeus, 1758) (Wallach et al., 2014: p. 485). With-

out having investigated the exact publication dates of Démidoff (1842) and Holbrook (1842), we cannot establish which of the two homonyms is the senior one. According to Article 24.1 of the Code (ICZN, 1999), the name proposed at higher rank, *Tropidonotus niger* Holbrook, 1842, would take precedence, if published simultaneously.

Younger homonyms are *Tropidonotus tessellatus* var. nigra de Betta, 1857 = Natrix tessellata (Laurenti, 1768) (see below under Natrix torquata var. nigrescens de Bet-

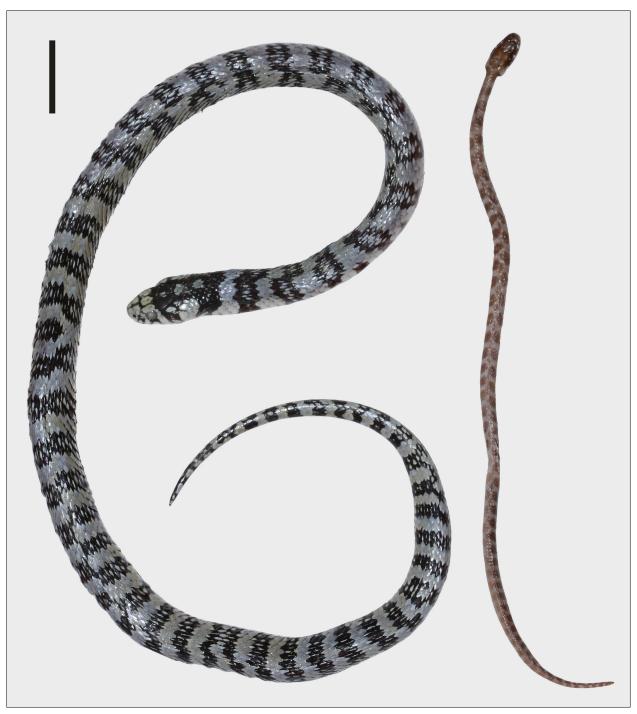


Fig. 9. Lectotype (left, female, Fonni, Nuoro province, Sardinia) and paralectotype (right, juvenile, southern Corsica) of *Natrix Cetti* Gené, 1839 (Museo Regionale di Scienze Naturali, Torino, MZUT R1734). Same specimens as in Figure 8. Scale bar = 2 cm. Photos: Franco Andreone.

ta, 1853), Tropidonotus natrix var. nigra Jan, 1864 (see below under Tropidonotus natrix var. nigra Jan, 1864), and Tropidonotus [Natrix] viperinus aberratio nigra Mosauer & Wallis, 1927 = Natrix maura (Linnaeus, 1758) (see Mosauer & Wallis, 1927; Mertens & Wermuth, 1960: p. 186; Wallach et al., 2014: p. 477). However, according to Article 45.6.2 of the Code, we deem Tropidonotus [Natrix] viperinus aberratio nigra Mosauer & Wallis, 1927 to be an infrasubspecific name and, thus, it is not available (ICZN, 1999: Article 45.5).

Coluber Jenisonii Gistel, 1848

GISTEL (1848: p. 100) based *Coluber Jenisonii* on black snakes caught in 1833 in the Gümmlingermoos near Bern, Switzerland. The whereabouts of the type specimens is unknown. The description was later repeated verbatim in GISTEL & BROMME (1850: p. 328), with "Gistl" [sic] indicated as describer. Accordingly, MERTENS & WERMUTH (1960: p. 188) and WALLACH *et al.* (2014: p. 478) credited the name to GISTEL in GISTEL & BROMME (1850).

MERTENS & WERMUTH (1960: p. 188) listed *Coluber Jenisonii* with a question mark as a junior synonym of "*Coluber helveticus* Lacépède, 1789." We share the view that the identification with a melanistic grass snake is most likely. It is mtDNA lineage E of *Natrix helvetica* that occurs in the vicinity of Bern, which corresponds to a distinct nuclear genomic cluster and the nominotypical subspecies of that taxon (KINDLER *et al.*, 2013, 2017; SCHULTZE *et al.*, 2019, 2020). Consequently, we regard *Coluber Jenisonii* Gistel, 1848 as a subjective junior synonym of *Coluber Helveticus* Lacepède, 1789.

Natrix torquata var. nigrescens de Betta, 1853

This variety was described by DE BETTA (1853: p. 22) based on a single melanistic snake, collected in June 1853 in the "Provincia Vicetina" (Vicenza province, Italy) and housed in the Museo di Storia Naturale, Verona. However, DE BETTA (1857: p. 222) explained later that he originally misidentified this snake, with the exact locality Sette Comuni, and that this specimen actually represents a dice snake (*Natrix tessellata*). Based on the same museum specimen, DE BETTA (1857) proposed another name, *Tropidonotus tessellatus* var. *nigra*, to correct his previous mistake. Consequently, both *Natrix torquata* var. *nigrescens* de Betta, 1853 and *Tropidonotus tessellatus* var. *nigra* de Betta, 1857 are synonyms of *Natrix tessellata* (Laurenti, 1768) and not of any grass snake species.

Boulenger (1893) mentioned neither of these names coined by DE BETTA (1853, 1857). MERTENS & WERMUTH (1960) overlooked only the publication by DE BETTA (1857) and listed *Natrix torquata* var. *nigrescens* de Betta, 1853 as a junior synonym of "Coluber helveticus Lacépède, 1789" (p. 188). WALLACH et al. (2014: p. 478) mentioned both "Tropidonotus torquata nigrescens Betta, 1853" and "Tropidonotus tessellatus nigrescens Betta, 1857" [sic] among the synonyms of Natrix natrix (Linnaeus, 1758).

Natrix torquata var. Senescens Minà Palumbo, 1863

This is a generally overlooked name. We are only aware of WALLACH et al. (2014: p. 478), who listed it as a synonym of Natrix natrix (Linnaeus, 1758). Minà Palumbo (1863: p. 406) used this name for aged grass snakes from Sicily without a neck collar. MINA PALUMBO stated that this name originates with Bonaparte ("1840" = 1834 in Bonaparte, 1832–1841). Indeed, Bonaparte used the abbreviation "Senesc." in his unpaginated text and on the first of the two plates that illustrate "Natrix Torquata" but not in the sense of a variety. Bonaparte simply explained the difference between an aged ("Senesc.") and a juvenile ("Juv.") grass snake. Thus, "Natrix torquata var. Senescens" has been introduced by MINA PALUMBO (1863) and not by Bonaparte (1834 in Bonaparte, 1832–1841). Natrix torquata var. Senescens Miná Palumbo, 1863 is a junior synonym of Natrix helvetica sicula (Cuvier, 1829) and refers to mtDNA lineage A, which is widely distributed in Sicily (KINDLER et al., 2013; SCHULTZE et al., 2020).

Tropidonotus natrix var. bilineata Jan, 1864

The publication date of Jan's 'Enumerazione sistematica degli Ofidi appartenenti al gruppo Potamophilidae' is a matter of debate. Savage & McDiarmid (2017: p. 15) concluded that the second fascicle of volume III of the 'Archivio per la Zoologia, l'Anatomia e la Fisiologia,' in which Jan's work appeared, was published only in 1865. However, a nomenclaturally relevant preprint was already issued in 1864. This preprint differs merely in the pagination from the later version, and we refer to the page numbers of the 1864 version.

JAN (1864: p. 4) used the name *Tropidonotus natrix* var. bilineata for a variety from Dalmatia and regarded it as identical with the "var. murorum Fitz." = Tropidonotus Natrix var. murorum Fitzinger, 1832. WALLACH et al. (2014: p. 478) listed "Tropidonotus natrix bilineata Jan, 1863" (meaning the 1864 publication) as a nomen nudum in the synonymy of *Natrix natrix* (Linnaeus, 1758). However, Jan (1864) gave a brief morphological diagnosis on page 8, explaining that this variety is characterized by two whitish lines on the body. Moreover, he mentioned there that this variety, Tropidonotus natrix var. nigra Jan, 1864, and Tropidonotus natrix var. subbilineata Jan, 1864 (see below) also occur in other southern [European] countries. This renders the identification of these varieties with a certain mtDNA lineage impossible, even though Tropidonotus natrix var. bilineata Jan, 1864 can be referred to the species *Natrix natrix* (Linnaeus, 1758) because striped morphotypes are unknown in Natrix astreptophora (Seoane, 1884) and Natrix helvetica (Lacepède, 1789). Yet, within *Natrix natrix*, the identification with an mtDNA lineage or subspecies is impossible

The epithet 'bilineatus' or 'bilineata' for grass snakes and related Natrix species has a convoluted nomenclatural history (see above under Coluber bilineatus Bibron & Bory de Saint-Vincent, 1833). The synonymy of Natrix natrix persa (Pallas, 1814) in Mertens & Wermuth (1960: p. 189) suggests that Tropidonotus natrix var. bilineata Jan, 1864 is a junior secondary or primary homonym of three other names. This is true for Coluber bilineatus Bibron & Bory de Saint-Vincent, 1833 and Tropidonotus viperinus var. bilineata Jan, 1863, respectively. The latter name, a junior synonym of Coluber maurus Linnaeus, 1758 = Natrix maura (see Mertens & Wer-MUTH, 1960: p. 186), was only mentioned in JAN (1863: p. 71) but was made available by reference to the description of the "Tropidonote chersoïde" in Duméril et al. (1854: p. 562). Consequently, Tropidonotus viperinus var. bilineata Jan, 1863 invalidates its junior primary homonym Tropidonotus natrix var. bilineata Jan, 1864 (ICZN, 1999: Article 57.2). However, the third name listed by Mertens & Wermuth (1960), "Natrix viperina var. bilineata Bonaparte, 1839" [sic], is a nomen nudum because Bonaparte (1840: p. 437) failed to provide any

reference to a description or a description beyond mentioning the name.

The type material of *Tropidonotus natrix* var. *bilineata* Jan, 1864 and of the following varieties described by Jan (1864) was originally in the Museo Civico di Storia Naturale di Milano (Jan, 1864: p. 4) but lost during the Allied bombing of Milan in World War II (SCALI, 1996).

Tropidonotus natrix var. nigra Jan, 1864

This is a nomen dubium introduced by JAN (1864: p. 4) for melanistic grass snakes, with the diagnostic character given on page 8 ("sono affato ... neri"). As the preceding name Tropidonotus natrix var. bilineata Jan, 1864, it has a type locality including Dalmatia and "altri paesi più meridionali," making the identification with a particular mtDNA lineage or subspecies impossible. Tropidonotus natrix var. nigra Jan, 1864 cannot even be referred to a particular species because melanistic individuals also occur in *Natrix helvetica* (Lacepède, 1758). Fortunately, Tropidonotus natrix var. nigra Jan, 1864 is a junior primary homonym of *Tropidonotus niger* Holbrook, 1842 and Tropidonotus Natrix var. nigra Nordmann in Démidoff, 1842 and thus permanently invalid (ICZN, 1999: Article 57.2). For further homonyms, see under Tropidonotus Natrix var. nigra Nordmann in Démidoff, 1842.

Tropidonotus natrix var. picturata Jan, 1864

This variety was named by Jan (1864: p. 4) based on one specimen from "Elisabethpol, Crimea" in the Museo Civico di Storia Naturale di Milano (figured in Jan & Sordelli, 1868: plate I, fig. 1) and further material without locality data in the museum of Geneva, Switzerland. Elisabethpol, now Ganja, Azerbaijan, was erroneously assumed to be located within the Crimea by Jan (see below). The type material in Milan is lost (Scali, 1996). On page 9, Jan (1864) mentioned another specimen of this variety from Trabzon, Anatolia, which was most likely in the Natural History Museum of Genoa, and which has to be regarded as another syntype.

JAN (1864: p. 9) diagnosed his variety 'picturata' by its peculiar dorsal black coloration with many white spots. This coloration type is known to occur in many parts of the distribution range of what is now *Natrix helvetica* (Lacepède, 1789) and *Natrix natrix* (Linnaeus, 1758) (MÜLLER & MERTENS, 1932b).

Müller & Mertens (1932b: p. 24) highlighted that Jan (1864) erroneously located Elisabethpol within the Crimea, but surprisingly Mertens & Wermuth (1960: p. 190) later listed both Elisabethpol and the Crimea as type locality. Mertens & Wermuth (1960) identified *Tropidonotus natrix* var. *picturata* Jan, 1864 as a junior synonym of *Natrix natrix scutata* (Pallas, 1771). This matches the occurrence of mtDNA lineage 8 along the Turkish Black Sea coast (Kindler *et al.*, 2013), where Trabzon is situated (see above under *Coluber scutatus* Pallas, 1771). According to the results of Kindler *et al.* (2013), another mtDNA lineage of *Natrix natrix* (line-

age 2), however, is expected to occur in the region of Ganja, Azerbaijan. Moreover, the identity of the Geneva material mentioned by Jan (1864) remains unclear; it may represent *Natrix helvetica* (Lacepède, 1768), which occurs in this region of Switzerland. Pending further evidence, we treat *Tropidonotus natrix* var. *picturata* Jan, 1864 as a *nomen dubium*.

Tropidonotus natrix var. subbilineata Jan, 1864

This is another name of questionable identity that can, however, be unambiguously referred to *Natrix natrix* (Linnaeus, 1758) but not to a particular genetic lineage or subspecies.

Jan (1864: p. 4) based his description of *Tropidonotus natrix* var. *subbilineata* on grass snakes from Dalmatia and other southern [European] countries, see above under *Tropidonotus natrix* var. *bilineata* Jan, 1864. According to Jan (1864: p. 8), *Tropidonotus natrix* var. *subbilineata* is darker than *Tropidonotus natrix* var. *bilineata* and with paler stripes.

Tropidonotus fallax Fatio, 1872

MERTENS & WERMUTH (1960: p. 188) listed this species as a junior synonym of "Coluber helveticus Lacépède, 1789." FATIO (1872: pp. 153–156) based his description of Tropidonotus fallax on a publication by STUDER (1870), who described a putatively new snake species without naming it. STUDER described one specimen from the collection of the Naturhistorisches Museum Bern that matches a melanistic grass snake. According to the label, the specimen was collected in Switzerland ("Schweiz").

In Switzerland both *Natrix helvetica* (Lacepède, 1789) and *Natrix natrix* (Linnaeus, 1758) occur, which hybridize in a narrow belt in the northeast of the country (KINDLER *et al.*, 2017). Since the collection site of the holotype is unknown, *Tropidonotus fallax* Fatio, 1872 has to be regarded as a *nomen dubium* because it cannot be unambiguously identified with either species or a hybrid.

Tropidonotus sparsus Schreiber, 1875

MERTENS & WERMUTH (1960: p. 186) listed *Tropidonotus sparsus* Schreiber, 1875 in the synonymy of *Natrix natrix* (Linnaeus, 1758) but did not assign Schreiber's name to any subspecies.

Schreiber (1875: p. 243) diagnosed this nominal species by its speckled dorsal pattern and specified that he found such grass snakes "im südlichen Illyrien" [in the southern Illyria] and in the Austrian Crown Land of Salzburg. Within the former Austro-Hungarian Empire, Illyria is to be identified with what is now more or less southwestern Slovenia, Istria, and the adjacent regions of Italy. In addition, Schreiber had seen an unspecified number of specimens of *Tropidonotus sparsus* from Spain in the "kaiserliches Cabinet" (now Naturhistorisches Museum Wien).

Grass snakes in Slovenia, Istria, and northeastern Italy represent mtDNA lineage 4 of Natrix natrix (Linnaeus, 1758) (KINDLER et al., 2013, 2017; SCHULTZE et al., 2020). However, with respect to their nuclear genomic identity, the grass snakes of this region are admixed (KINDLER et al., 2017), preventing the identification with any subspecies of N. natrix. The species in Spain is Natrix astreptophora (Seoane, 1884) (Pokrant et al., 2016). Thus, it is obvious that *Tropidonotus sparsus* Schreiber, 1875 was based on two distinct species and potentially threatens the usage of the well-established name for Iberian grass snakes. However, after its description, Tropidonotus sparsus has not been used by any other author as a valid species name and we, therefore, declare it as another nomen oblitum with respect to Tropidonotus natrix var. astreptophorus Seoane, 1884, the nomen protectum according to Article 23.9 of the Code (ICZN, 1999); see the account on Tropidonotus natrix var. astreptophorus Seoane, 1884 below.

Four *Natrix astreptophora* in the herpetological collection of the Naturhistorisches Museum Wien match the description of *Tropidonotus sparsus* and were early enough present to have been seen by Schreiber (1875). These specimens should be regarded as syntypes of *Tropidonotus sparsus* Schreiber, 1875: NMW 20515:1 and 2, La Sanabria and Terrol, Spain; NMW 21960:1, Bilbao, Spain; NMW 21978:1, La Sanabria, Spain (S. Schweiger, pers. comm., 15 October 2020).

Tropidonotus natrix var. concolor Ninni, 1880

MERTENS & WERMUTH (1960: p. 188) listed this name in the synonymy of "Coluber helveticus Lacépède, 1789." However, Ninni (1880: p. 72) mentioned that he collected specimens of this coloration variety in the "R. [Regio] Bosco Montello (Provincia di Treviso)," Venetia, and deposited these in the Museo Civico di Venezia (now Museo di Storia Naturale di Venezia). It is unclear whether the specimens are still present (N. Novarini, pers. comm., 15 June 2020). Their collection site and, thus, type locality, lies in the hybrid zone of Natrix natrix (mtDNA lineage 4) and Natrix helvetica sicula (mtDNA lineage C; Schultze et al., 2020), so that Tropidonotus natrix var. concolor Ninni, 1880 cannot be unambiguously identified with any of these taxa and could potentially also refer to interspecific hybrids. Thus, the name represents currently a nomen dubium, pending a future taxonomic assessment of the type material, if still in existence.

However, *Tropidonotus natrix* var. *concolor* Ninni, 1880 is a junior primary homonym of *Tropidonotus tessellatus* var. *concolor* Jan, 1864 = *Natrix tessellata* (Laurenti, 1768) and therefore permanently invalid (ICZN, 1999: Article 57.2). Therefore, the taxonomic identity of *Tropidonotus natrix* var. *concolor* Ninni, 1880 is irrelevant.

Boulenger (1893: p. 220) credited the name *Tropidonotus natrix* var. *concolor* to Müller (1885: p. 681), who used it in his supplement of the holdings of the Naturhistorisches Museum Basel for a grass snake from

Wylerrain near Basel, Switzerland. Even though MÜLLER (1885) did not indicate NINNI (1880) as authority for this name, we hypothesize that MÜLLER was aware of NINNI's name and did not intend to describe a new variety, because he did not add 'nov. var.' to "*Tropidonotus natrix* Kuhl var. *concolor*," which he did for all the other cases for which he intended to describe new taxa (e.g., p. 700: "*Amphisbaena leonina* nov. sp.").

Tropidonotus natrix var. lineata Ninni, 1880

This is another name listed by MERTENS & WERMUTH (1960: p. 188) in the synonymy of "Coluber helveticus Lacépède, 1789." NINNI (1880: p. 74) introduced the variety lineata for Italian grass snakes with two back stripes and identified it with previously described varieties for striped grass snakes ("murorum. Vest," "Tr. natrix var. bilineata, Jan," "subbilineata, Jan"). Unlabelled type material of Tropidonotus natrix var. lineata Ninni, 1880 may exist in the collection of the Museo di Storia Naturale di Venezia (N. Novarini, pers. comm., 15 June 2020).

It seems likely that Ninni referred to striped grass snakes from Venetia (Veneto) because Ninni worked in Venice and striped grass snakes occur only in the northeast of Italy (Lapini *et al.*, 1999). Accordingly, *Tropidonotus natrix* var. *lineata* Ninni, 1880 can be assigned to mtDNA lineage 4 of *Natrix natrix* (Linnaeus, 1758) but not to a particular subspecies because grass snakes in this region have an admixed nuclear genomic identity (for more information, see above under *Tropidonotus sparsus* Schreiber, 1875).

"Tropidonotus natrix var. *nigrescens* Ninni, 1880"

(see Mertens & Wermuth, 1960: p. 188)

This is another name treated by MERTENS & WERMUTH (1960: p. 188) as a junior synonym of "Coluber helveticus Lacépède, 1789." However, NINNI (1880: p. 73) did not establish a new name "Tropidonotus natrix var. nigrescens," he merely used this name which was already introduced by DE BETTA (1853) in the combination Natrix torquata var. nigrescens.

Tropidonotus natrix var. nigri-torquata Ninni, 1880

This name was interpreted by Mertens & Wermuth (1960: p. 190, misspelled as "nigro-torquatus") as a replacement name for Coluber siculus Cuvier, 1829. However, Ninni (1880: p. 74) did not establish the name for his variety expressly as a nomen novum, as required by the Code (ICZN, 1999: Article 72.7, Glossary) but cited the Sicilian Coluber siculus as an older synonym. Thus, Tropidonotus natrix var. nigri-torquata Ninni, 1880 is a regular new name and a junior synonym of Coluber siculus Cuvier, 1829. Type material of Tropidonotus natrix var. nigri-torquata Ninni, 1880 could be in the Museo di Storia Naturale di Venezia.

Tropidonotus natrix var. bulsanensis Gredler, 1882

This name for a variety from South Tyrol was overlooked by Mertens & Wermuth (1960). Wallach *et al.* (2014: p. 478) synonymized it with "*Coluber natrix* Linnaeus, 1758."

Gredler (1882: pp. 24, 25) described this coloration variety, characterized by many irregular snow-white speckles, from the environs of Bozen (Bolzano, South Tyrol), Italy, based on a killed snake found by "Hr. Mulser." This specimen, at the time of description in Mulser's private collection, is the holotype of *Tropidonotus natrix* var. *bulsanensis*. The specimen is today in the Gredler collection of the Naturhistorisches Kabinett of the Franziskanergymnasium in Bozen and registered under number 1094. It is well preserved, and the label specifies that it was collected near Terlan (Terlano), a village approximately 7 km northwest of Bozen (D. Lorenz, pers. comm., 2 October 2020).

The type locality lies within the distribution range of mtDNA lineage C of *Natrix helvetica sicula* (Cuvier, 1829) (KINDLER *et al.*, 2013; SCHULTZE *et al.*, 2020). Consequently, *Tropidonotus natrix* var. *bulsanensis* Gredler, 1882 is a junior synonym of *Coluber siculus* Cuvier, 1829.

Tropidonotus natrix var. moreoticus Bedriaga, 1882

MERTENS & WERMUTH (1960: p. 189) listed *Tropidonotus natrix* var. *moreoticus* as a synonym of *Coluber persa* Pallas, 1814 and dated the publication of this name to 1881. This matches the release date of the first two issues of volume 56 of the 'Bulletin de la Société Impériale de Moscou.' However, Bedriaga's article 'Die Amphibien und Reptilien Griechenlands' appeared in several parts. The description of *Tropidonotus natrix* var. *moreoticus* was published in issue 4 that appeared only in 1882, as evident from the date on the cover page of the "Seconde Partie" (= issues 3 and 4) of volume 56.

Bedriaga (1882: p. 289) described this variety based on material in the "Athener Museum," i.e., the Natural History Museum of Athens University, Greece. According to information provided by "Prof. v. Heidreich" [the director of the museum, Theodor von Heidreich, 1822–1902], the material was collected on the northern Peloponnesus (Bedriaga, 1882). Tropidonotus natrix var. moreoticus was characterized by Bedriaga as a black variety with two narrow yellow back stripes. From the Peloponnesus, only mtDNA lineage 5 is known (KIN-DLER et al., 2013, 2017). Since the older name Coluber bilineatus Bibron & Bory de Saint-Vincent, 1833, also described from the Peloponnesus, is a junior primary homonym of Coluber bilineatus Latreille in Sonnini & Latreille, 1801 and permanently invalid (ICZN, 1999: Article 57.2, see above), Tropidonotus natrix var. moreoticus Bedriaga, 1882 would have to be used as the valid subspecies name if and when grass snakes of lineage 5 were deemed taxonomically distinct.

Tropidonotus natrix var. astreptophorus Seoane, 1884

Since Mertens & Müller (1928), this name has been generally used for a subspecies of *Natrix natrix* (Linnaeus, 1758) or, since Pokrant *et al.* (2016), for a distinct species of grass snake, which is distributed across the Iberian Peninsula, southwestern France (Occitany), and in the northern Maghreb.

SEOANE (1884: p. 15) described *Tropidonotus natrix* var. *astreptophorus*³ based on material from Galicia, stressing the complete absence of the neck collar—as reflected in the Latin epithet '*astreptophorus*.' This trait, however, develops only with age, and juvenile snakes possess a pronounced, typically closed, collar (MERTENS, 1966; POKRANT *et al.*, 2016).

SEOANE (1884: pp. 17, 18) stated that he sent fresh material from coastal Galicia to several museums (Madrid, St. Petersburg, Berlin, London, Vienna "y otros muchos"); a shed skin was in the "Instituto de Pontevedra" (p. 16). It is likely that additional specimens were in Seoane's private collection. All of these specimens have to be regarded as syntypes of *Tropidonotus natrix* var. astreptophorus.

However, the recently published type catalogue for amphibians and reptiles in the collection of the Museo Nacional de Ciencias Naturales, Madrid, mentions no type material for Tropidonotus natrix var. astreptophorus Seoane, 1884 (González-Fernández et al., 2017), and in this museum are neither specimens of Natrix astreptophora collected by Seoane nor any from his former private collection (M. Calvo Revuelta, pers. comm., 28 October 2020). Also, Никольскій [Nikolsky] (1916) did not list any specimens from Seoane among the grass snake material of the St. Petersburg museum, and no syntypes can be located in the Museum für Naturkunde Berlin as well (F. Tillack, pers. comm., 8 July 2020). In contrast, Boulenger (1893: p. 220) mentioned for the British Museum of Natural History (now Natural History Museum, London) one female from "Corunna," received from Seoane. This specimen bears the catalogue number NHMUK 1884.11.20.99 (P. Campbell, pers. comm., 22 October 2020). Another syntype from La Coruña, Spain, is in the Naturhistorisches Museum Wien (NMW 22174:1; S. Schweiger, pers. comm., 8 July 2020; not mentioned in GEMEL et al., 2019). Five additional syntypes are in the Muséum national d'Histoire naturelle, Paris (MNHN-RA-1889.580, MNHN-RA-1889.582, MNHN-RA-1889.583, MNHN-RA-2012.459, Galicia, Spain; MNHN-RA-1889.581, Cuntis, Pontevedra, Spain; see our Figs 10 and 11 for two of these syntypes).

The usage of *Tropidonotus natrix* var. *astreptophorus* Seoane, 1884 is threatened by two older names, *Coluber distinctus* Gravenhorst, 1807 and *Tropidonotus sparsus*

³ Parenthetically it should be noted that Seoane (1884: p. 16) inadvertently used in the original description the combination *Tropidonotus* astreptophorus as well.



Fig. 10. Dorsal and ventral aspects of a juvenile syntype of *Tropidonotus natrix* var. *astreptophorus* Seoane, 1884 (Muséum National d'Histoire naturelle, Paris, MNHN-RA-1889.581, Cuntis, Pontevedra, Spain). Photos: Antoine Fraysse (Muséum national d'Histoire naturelle, Paris, RECOLNAT project 2018, ANR-11-INBS-0004). Compare this specimen to the snakes depicted by Seba (1735), see our Figures 1 and 2.

Schreiber, 1875 (see also above under the respective accounts). Yet, to the best of our knowledge, neither name has ever been used as valid for any snake species after the original descriptions. Therefore, we declare both Coluber distinctus Gravenhorst, 1807 and Tropidonotus sparsus Schreiber, 1875 nomina oblita with respect to Tropidonotus natrix var. astreptophorus Seoane, 1884. To qualify the latter name as nomen protectum according to Article 23.9 (ICZN, 1999), we list here 25 works, published by at least 10 authors in the immediately preceding 50 years and encompassing a span of not less than 10 years. These publications used Tropidonotus natrix var. astreptophorus Seoane, 1884 as the valid name for a subspecies of *Natrix* natrix (Linnaeus, 1758) or for the distinct species Natrix astreptophora (Seoane, 1884): THORPE (1979); MALK-MUS (1982, 1997, 2003); ENGELMANN et al. (1986); CRESPO & Oliveira (1989); Gruber (1989); Braña (1998); Ka-BISCH (1999); ARNOLD & OVENDEN (2002); KREINER (2007); Guicking et al. (2008); Kindler et al. (2013, 2018a); GENIEZ (2015); POKRANT et al. (2016, 2018); SPEYBROECK et al. (2016, 2020); ESCORIZA & BEN HASSINE (2017); Escoriza (2018); Kalboussi & Achour (2018); Blain et al. (2019); Massary et al. (2019); Fernández-Ortín et al. (2019).

As confirmed by genetic research (Pokrant et al., 2016; Kindler et al., 2018a; Asztalos et al., 2020), Na-

trix astreptophora occurs both in southwestern Europe (Iberian Peninsula, adjacent France) and in the Maghreb. However, the European populations are distinct from the Maghrebian ones in mtDNA and nuclear genomic markers (microsatellites), allowing their classification as distinct subspecies. According to the type locality Galicia, European populations represent the nominotypical subspecies *Natrix astreptophora astreptophora* (Seoane, 1884). These populations correspond to mtDNA lineage Eu of Kindler et al. (2013).

Tropidonotus natrix var. albo-torquata Camerano, 1891

This name was overlooked by Mertens & Wermuth (1960). Camerano (1891: p. 21) introduced this variety for grass snakes with a more or less pronounced yellowish-white collar and stated that this coloration type of medium-sized adults is more frequent in the Padan Plain and peninsular Italy than in Sicily. This implies that the type locality of *Tropidonotus natrix* var. *albo-torquata* is mainland Italy and Sicily. There is no type material known. In mainland Italy and Sicily two distinct species of grass snake occur, *Natrix helvetica* (with the subspecies *sicula*) and *Natrix natrix*. Since *Tropidonotus natrix* var. *albo-torquata* cannot be unambiguously identified



Fig. 11. Dorsal and ventral aspects of an adult syntype of *Tropidonotus natrix* var. *astreptophorus* Seoane, 1884 (Muséum National d'Histoire naturelle, Paris, MNHN-RA-1889.582, Galicia, Spain). Photos: Antoine Fraysse (Muséum national d'Histoire naturelle, Paris, RECOLNAT project 2018, ANR-11-INBS-0004).

with one of these taxa, it has to be regarded as a *nomen dubium*.

Tropidonotus natrix var. albiventris Dürigen, 1897

There is no type material for this variety. DÜRIGEN (1897: p. 278) described in his book 'Deutschlands Amphibien

und Reptilien' Tropidonotus natrix var. albiventris for grass snakes with white belly. Therefore, MERTENS & WERMUTH (1960: p. 186) inferred "Deutschland" as its type locality. However, DÜRIGEN never restricted his descriptions and enumerations of varieties to Germany. Since he did not specify the geographic origin for Tropidonotus natrix var. albiventris, it could refer to any region and any species of grass snake and therefore represents a nomen dubium.

Tropidonotus natrix var. fasciatus Dürigen, 1897

No type material exists for this variety either. DÜRIGEN (1897: p. 278, 279) specified that it has no continuous distribution but is virtually lacking in Central and Northern Europe and not rare in southern and southeastern regions. This conflicts with his morphological description, which resembles *Natrix helvetica*, a species that does not occur in the southeast of Europe. Consequently, also *Tropidonotus natrix* var. *fasciatus* Dürigen, 1897 should be regarded as a *nomen dubium*.

Tropidonotus natrix var. subfasciatus Boulenger, 1913

This is a generally overlooked name (but see Hecht, 1930: p. 254, who included it in his enumeration of scientific names for grass snakes and related species). Boulenger (1913: pp. 154, 155) mentioned this variety from Austria and Corfu. It is characterized by a white belly with black bars occupying the free edges of each ventral shield. Boulenger credits the name of this variety to the Viennese zoologist Franz Werner (1867–1939), with whom he was obviously in direct contact (Boulenger, 1913: p. 225). We are not aware of any publication by Werner that uses this name.

Tropidonotus natrix var. subfasciatus Boulenger, 1913 is a nomen dubium without known type material. This name cannot be identified with a particular genetic lineage or taxon. Pre-World War I Austria comprised a fair part of eastern Central Europe, spanning from what is now Austria across the current Czech Republic to southeastern Poland and western Ukraine and southward to the Adriatic Sea and northeastern Italy. In this area, and in Corfu (Kerkyra, Greece), three distinct mtDNA lineages of Natrix natrix occur (lineages 3, 4, and 5; KINDLER et al., 2013, 2017); in Vorarlberg (Austria) lineage E of Natrix helvetica occurs (ZANGL et al., 2020), and in South Tyrol (Italy), lineage C of Natrix helvetica is present (SCHULTZE et al., 2020). Lineage C is also expected in Tyrol (Austria).

Natrix vibakari continentalis Nikolsky, 1925

This nominal taxon was overlooked by Mertens & Wermuth (1960). Никольский [Nikolsky] (1925: p. 124) described this taxon as a subspecies of the East Asian keelback *Natrix vibakari* (Boie, 1826), now *Hebius vibakari*, based on two specimens from Забайкалье [Transbaikal] that he received from П. С. Михно (Р. S. Mikhno, 1867—1938, one of the founders of the local museum in Кяхта, Бурятия = Kyakhta, Buryatia). Терентьев & Чернов [Телент'еv & Chernov] (1949: p. 233) placed *Natrix vibakari continentalis* into the synonymy of *Natrix natrix*, and Mertens (1966) identified it with the subspecies *Natrix natrix scutata* (Pallas, 1771).

Only one of the two syntypes could be located in the collection of the Зоологический институт РАН, Санкт-Петербург [Zoological Institute of the Russian Academy

of Sciences, St. Petersburg]. This specimen (Fig. 12) bears the catalogue number ЗИСП [ZISP] 16073 and was collected by П. С. Михно in the vicinity of Троицкосавск (Troitskosavsk), Kyakhta, Republic of Buryatia, Russia (К. Д. Мильто [К. D. Milto], pers. comm., 10 June 2020). This snake from the Russian-Mongolian border south of Lake Baikal morphologically matches *Natrix natrix scutata* (Pallas, 1771) as defined by Mertens (1966). The light lunar spots on the neck form a closed collar, a character that occurs only in this subspecies and in juveniles of *Natrix astreptophora* (Seoane, 1884). This supports the view that *Natrix vibakari continentalis* Nikolsky, 1925 is a junior synonym of *Coluber scutatus* Pallas, 1771. However, this tentative conclusion should be corroborated genetically.

One of the four specimens mentioned by MERTENS (1966) as on loan to him from the Leningrad museum is the second lost syntype. This specimen (ZIL 14236) was also collected by Михно in 1907 ("Troitzkosawskij Rayon, Tschernoe Ozero;" MERTENS, 1966). The head of this specimen is shown in MERTENS' figure 1 and closely resembles that of the extant syntype. None of the syntypes are mentioned in Никольский (1916), neither under *Natrix vibakari* nor *Natrix natrix*.

Tropidonotus natrix algericus Hecht, 1930

This subspecies is frequently synonymized with *Tropidonotus natrix* var. *astreptophorus* Seoane, 1884 following Mertens & Wermuth (1960: p. 187). *Tropidonotus natrix algericus* Hecht, 1930 is one of the 10 subspecies erected by Hecht (1930), each based on only one or a few individuals and disregarding individual variation. This shortcoming was soon criticized severely (Müller & Mertens, 1931, 1932a, b; see also Mertens, 1947). Consequently, the majority of Hecht's subspecies were not regarded as valid (Mertens, 1947; Mertens & Wermuth, 1960), even though some of them were revalidated later (see below).

HECHT (1930: p. 306) based his Tropidonotus natrix algericus only on the holotype, a specimen (ZMB 19636) from "Südalgier" in the Zoologisches Museum Berlin, now Museum für Naturkunde, collected by "Schaposchnikoff." Mertens & Wermuth (1960: p. 187) identified the type locality with southern Algeria ("Süd-Algerien"), a region far beyond the distribution range of Natrix astreptophora (cf. the map in Kindler et al., 2018a). According to the acquisition catalogue of the herpetological collection of the Berlin museum, the batch of 31 specimens from Schaposchnikoff that contained ZMB 19636 was registered on 7 May 1905 with locality "Touggourt," a town south of Chott Melghir (F. Tillack, pers. comm., 11 July 2017). This is in northern, not in southern, Algeria but still approximately 300 km south of the known distribution range of Natrix astreptophora. Some letters exchanged between Ch. Schaposchnikoff, a Russian from Tbilisi then collecting in Algeria and Tunisia, and the museum are still present, and correspondence from May 1905 clarifies that the 31 specimens were



Fig. 12. Dorsal and ventral aspects of a syntype of *Natrix vibakari continentalis* Nikolsky, 1925 (Зоологический институт РАН, Санкт-Петербург, ЗИСП 16073, Троицкосавск, Кяхта, Бурятия = Troitskosavsk, Kyakhta, Buryatia, Russia). Photos: К. Д. Мильто.

only dispatched from Touggourt. Thus, the type locality of *Tropidonotus natrix algericus* Hecht, 1930 has to be corrected because it seems likely that the holotype originated within the known range of *Natrix astreptophora* in northern Algeria.

In Algeria and Tunisia occurs a distinct mtDNA lineage of *Natrix astreptophora* (lineage Tu of Kindler *et al.*, 2013) that also represents a distinct nuclear genomic cluster in analyses using microsatellite loci (Kindler *et al.*, 2018a). This situation qualifies Algerian and Tunisian populations as a distinct subspecies according to the criteria of Kindler & Fritz (2018), and we propose to use the new combination *Natrix astreptophora algerica* (Hecht, 1930) for these grass snakes.

Tropidonotus natrix bithynius Hecht, 1930

This is another subspecies name based on a single specimen (Hecht, 1930: pp. 268, 269), placed by Mertens (1947: p. 23) and Mertens & Wermuth (1960: p. 189) into the synonymy of *Natrix natrix persa* (Pallas, 1814). The holotype of *Tropidonotus natrix bithynius* Hecht, 1930 is in the Museum für Naturkunde Berlin (ZMB 31425). Its collection site ("Alem Dagh bei Skutari," a hill approx. 30 km from Shkodër, Albania) lies within the distribution range of mtDNA lineage 5 of *Natrix natrix* (KINDLER *et al.*, 2013, 2017). Until the nuclear genomic identity of Balkan grass snakes is clarified, *Tropidonotus natrix bithynius* Hecht, 1930 cannot be identified with a

particular subspecies (see above under the account for *Coluber bilineatus* Bibron & Bory de Saint-Vincent, 1833).

Tropidonotus natrix britannicus Hecht, 1930

HECHT (1930: pp. 303–305) described this subspecies based on two specimens each from the museums in Berlin and Copenhagen and three specimens from Norfolk in an unspecified private collection ("Privatbesitz," HECHT, 1930: p. 305). The holotype is in the Museum für Naturkunde Berlin (ZMB 33060, England). MERTENS (1947: p. 29) and MERTENS & WERMUTH (1960: p. 188) treated *Tropidonotus natrix britannicus* Hecht, 1930 correctly as a junior synonym of "*Coluber helveticus* Lacépède, 1789."

British grass snakes represent the nominotypical subspecies of the barred grass snake, *Natrix helvetica helvetica* (Lacepède, 1789), which is genotypically distinct and characterized by mtDNA lineage E (KINDLER *et al.*, 2013, 2017; SCHULTZE *et al.*, 2020).

Tropidonotus natrix bucharensis Hecht, 1930

This is another subspecies name based on a single specimen (HECHT, 1930: pp. 285, 286). The holotype originates from Eduard Friedrich Eversmann's (1794-1860) expedition to Central Asia (1820) and is in the collection of the Museum of Naturkunde Berlin (ZMB 1943). HECHT (1930: p 286) indicated "Bucharei" (i.e., the region around Bukhara, Uzbekistan) as geographic origin. However, grass snakes are unknown from Uzbekistan (Банников [Ванников] *et al.*, 1977). Неснт (1930) specified "Fundort rekonstr.: Niederungen östlich von den Mugosarskischen Bergen" [reconstructed collection site: lowlands east of the mountains of Mugosarsk]. This statement seems to have originated with LICHTEN-STEIN in EVERSMANN (1823: p. 145), who described the morphology of the same specimen under the name "Coluber natrix Lin.," providing exactly the same collection site, without mentioning Bukhara. According to Evers-MANN (1823) the 'mountains of Mugosarsk' are not in the region of Bukhara. Rather, they were described as the foothills of the Ural Mountains that terminate at the Aral Sea (EVERSMANN, 1823: p. 67). This reveals that ZMB 1943 was not collected in Uzbekistan but further north, somewhere in the Kazakh steppe east of the Aral Sea.

Mertens (1947: p. 26) speculated that *Tropidonotus* natrix bucharensis Hecht, 1930 could be either a synonym of Natrix natrix persa (Pallas, 1814) or Natrix natrix scutata (Pallas, 1771). Mertens & Wermuth (1960: p. 190) accepted "Buchara" (not "Bucharei") as type locality and placed it into the synonymy of Natrix natrix scutata. In face of the type locality referring to a site further north, in Kazakhstan east of the Aral Sea, this taxonomic allocation seems justified.

Tropidonotus natrix cephallonicus Hecht, 1930

Another subspecies described by HECHT (1930: pp. 270, 271) based on a single specimen. The holotype, with two faint back stripes, is in the Museum für Naturkunde Berlin (ZMB 18422, "Insel Kephallonia, Argostoli"). MERTENS (1947: p. 23) and MERTENS & WERMUTH (1960: p. 189) placed this subspecies into the synonymy of *Natrix natrix persa* (Pallas, 1814).

Even though no grass snakes from Kefalonia have been studied genetically, this island lies directly off the coastal region of western Greece where only mtDNA lineage 5 of *Natrix natrix* is distributed (KINDLER *et al.*, 2013, 2017). Since the nuclear genomic identity of Balkan grass snakes is unclear, *Tropidonotus natrix cephallonicus* Hecht, 1930 cannot be identified with a particular subspecies (see above under the account for *Coluber bilineatus* Bibron & Bory de Saint-Vincent, 1833).

Tropidonotus natrix corsus Hecht, 1930

This is another subspecies described by HECHT (1930: pp. 308, 309) using only one specimen. HECHT (1930: p. 309) stated that the holotype from "Korsika" is in the collection of the Zoologisches Museum Berlin (now Museum für Naturkunde Berlin), but a catalogue number was not provided. This specimen cannot be located currently (F. Tillack, pers. comm., 18 July 2020).

While Mertens (1947: p. 31) treated Tropidonotus natrix corsus Hecht, 1930 as a synonym of Natrix Cetti Gené, 1839, he later supported the validity of the Corsican subspecies (Mertens, 1957: pp. 188–190; Mertens & WERMUTH, 1960: p. 187). However, further research is needed to clarify this situation. Today, both taxa are accepted as subspecies of Natrix helvetica (see Kindler et al., 2017; Kindler & Fritz, 2018; Schultze et al., 2020). Natrix helvetica corsa shares with Natrix helvetica cetti the same distinct mtDNA lineage (lineage B of KINDLER et al., 2013), and the two taxa together constitute a nuclear genomic cluster distinct from barred grass snakes from Sicily and the mainland (Natrix helvetica helvetica, N. h. sicula). However, Corsican and Sardinian grass snakes seem not to be differentiated genetically from one another (SCHULTZE et al., 2020). This suggests that Tropidonotus natrix corsus Hecht, 1930 may be indeed a synonym of *Natrix Cetti* Gené, 1839 (see above under the account for the latter taxon).

Tropidonotus natrix cypriacus Hecht, 1930

This subspecies was also based on a single specimen (Museum für Naturkunde Berlin, ZMB 16122, "Cypern;" Hecht, 1930: pp. 267, 268), and the name was treated for a long time as a junior synonym of *Natrix natrix persa* (Pallas, 1814) (Mertens, 1947: p. 23; Mertens & Wermuth, 1960: p. 189). The subspecies *Natrix natrix cypriaca* (Hecht, 1930) was later resurrected for the endangered Cypriot grass snakes as a consequence

of the unpublished doctoral thesis of BLOSAT (1998) and recognized by Baier et al. (2009) and Baier & Wiedl (2010) as a valid subspecies. However, preliminary genetic data using mtDNA do not support the distinction of an endemic Cypriot subspecies. Grass snakes from the southeastern Balkans, western Turkey, and Cyprus share the same mtDNA lineage (lineage 7 of KINDLER et al., 2013), but their nuclear genomic identity has not been examined yet (KINDLER et al., 2013, 2017). However, if grass snakes with mtDNA lineage 7 from those regions should represent a distinct subspecies, it would have to be named Natrix natrix cypriaca (Hecht, 1930). Further investigations are needed here, not least because Böhme & Wiedl (1994: p. 31) concluded that Cypriot grass snakes are "certainly not identical with populations on the opposite Turkish coast." Yet, Cypriot grass snakes are morphologically highly variable, as later described and figured by Baier et al. (2009).

Tropidonotus natrix dystiensis Hecht, 1930

HECHT (1930: pp. 269, 270) described this striped subspecies on the basis of one specimen in the Zoologisches Museum Berlin (now Museum für Naturkunde Berlin), two specimens in the Muséum national d'Histoire naturelle, Paris, and another one in the Senckenberg Museum Frankfurt, all from the island of Euboea (Εύβοια), Greece. The holotype is in the Berlin museum (ZMB 13594, "Dystos auf Euböa"). The name of this subspecies was declared a junior synonym of *Natrix natrix persa* (Pallas, 1814) soon after its description (MERTENS, 1947: p. 23; MERTENS & WERMUTH, 1960: p. 189).

Until now, no grass snakes from Euboea have been studied genetically (KINDLER *et al.*, 2013, 2017). Yet, in microsatellite analyses, all studied grass snakes from the southern Balkans represent a distinct cluster that corresponds to four mtDNA lineages of *Natrix natrix* (Linnaeus, 1758) (KINDLER *et al.*, 2017). Therefore, grass snakes from Euboea most likely belong to the same microsatellite cluster. Until the taxonomic identity of grass snakes from the southern Balkans is clarified, *Tropidonotus natrix dystiensis* Hecht, 1930 can only be identified with *Natrix natrix* but not with a particular subspecies (see also above under *Coluber persa* Pallas, 1814 and *Coluber bilineatus* Bibron & Bory de Saint-Vincent, 1833).

Tropidonotus natrix schirvânae Hecht, 1930

This subspecies was described on the basis of three specimens in the Museum für Naturkunde Berlin from the same locality ("Schirvân" = Şirvan, Azerbaijan), another specimen from the same museum from "Pjatigorsk" (= Пятигорск, Ставропольский край, Russia), and a fifth paratype from Tbilisi, Georgia, in the Muséum national d'Histoire naturelle, Paris. The holotype is from Şirvan and bears the catalogue number ZMB 1938. Mertens (1947: p. 26) treated *Tropidonotus natrix schirvânae* Hecht, 1930 in the account of *Natrix natrix scutata* (Pallas, 1771) and stressed that the original description

contains no useful diagnostic characters. Mertens & Wermuth (1960: p. 190) listed Hecht's name accordingly as a synonym under the latter subspecies. However, the type locality of *Tropidonotus natrix schirvânae* lies within the distribution range of mtDNA lineage 1 (Kindler *et al.*, 2013) and the name is, therefore, most probably synonymous with *Coluber persa* Pallas, 1814.

Tropidonotus natrix syrae Hecht, 1930

HECHT (1930: p. 269) based this subspecies on a single specimen in the collection of the Museum für Naturkunde Berlin (ZMB 13533, "Insel Syra" = island of Siros or Syros [Σύρος], Cyclades, Greece). Mertens (1947: p. 23) and Mertens & Wermuth (1960: p. 189) identified this subspecies with *Natrix natrix persa* (Pallas, 1814). No grass snakes from Siros have been studied genetically (Kindler *et al.*, 2013, 2017). Thus, the identity of *Tropidonotus natrix syrae* Hecht, 1930 remains unclear and parallels the situation in *Tropidonotus natrix dystiensis* Hecht, 1930. In both cases, the presence of an endemic subspecies that fulfils the criteria outlined in Kindler & Fritz (2018) seems unlikely (see also below under the account for *Natrix natrix schweizeri* Müller, 1932).

Tropidonotus natrix syriacus Hecht, 1930

HECHT (1930: pp. 266, 267) described this subspecies based on a type series of 11 specimens in the collection of the Museum für Naturkunde Berlin and identified ZMB 13768 as holotype. All specimens originated from "Sendschirli" [Zincirli, İslahiye/Gaziantep, Turkey].

Despite severe criticism of Hecht's work, Mertens (1947: pp. 24, 25) recognized *Natrix natrix syriaca* (Hecht, 1930) as a valid subspecies based on one non-type specimen in the Senckenberg Museum Frankfurt (SMF 17261, "Jafa, Palästina"). This snake represents a misidentified *Natrix tessellata* (see Grillitsch & Werner, 2009). In the checklist of Mertens & Wermuth (1960) the name *Tropidonotus natrix syriacus* was omitted.

KINDLER et al. (2013) assigned two genetically distinct samples from the Gulf of İskenderun to Natrix natrix syriaca (mtDNA lineage 6). Yet, these samples were collected west of the Amanus Mountains (Nur Dağları), while the type locality of Tropidonotus natrix syriacus lies east of this mountain chain. Further studies are needed to clarify to which lineage the grass snakes from the type locality belong. For the time being, we tentatively follow Kindler et al. (2013) and recognize Natrix natrix syriaca as a distinct subspecies characterized by mtDNA lineage 6. However, we underline that further research is needed to clarify the taxonomic identity of grass snakes from southeastern Turkey.

Natrix natrix schweizeri Müller, 1932

This subspecies was based on an unspecified number of syntypes collected by Hans Schweizer on Milos (M $\eta\lambda$ o ς), Cyclades, Greece (MULLER, 1932). Three syntypes in the

Zoologische Staatssammlung München have been lost during the Second World War (Franzen & Glaw, 2007: p. 256). It remains unclear whether some of the 10 specimens from Milos mentioned by Mertens (1947: p. 25) represent additional syntypes or not. SMF 32478–32482 and SMF 40083 were collected in 1924 and 1932, respectively, i.e., early enough to be part of the type material mentioned by Müller (1932). These specimens, and further grass snakes collected by Hans Schweizer on Milos, are still present in the Senckenberg Museum Frankfurt (L. Mogk, pers. comm., 27 May 2020).

KINDLER et al. (2013, 2017) studied two grass snake samples from Milos. Both bore mitochondrial haplotypes of the 'yellow lineage' (lineage 3) corresponding to Natrix natrix natrix, whereas another grass snake from the island of Paros (Πάρος), approximately 60 km northeast of Milos, yielded a haplotype of the "red lineage" (lineage 4) corresponding to Natrix natrix vulgaris. With respect to microsatellite data, the two snakes from Milos were admixed. No microsatellite data could be generated for the grass snake from Paros. Yet, the genetic identity of the Milos samples and the different haplotype of the Paros sample indicate that these populations are admixed, as grass snakes from the southern Balkans in general (KIN-DLER et al., 2017). Thus, Natrix natrix schweizeri should not be treated as a distinct subspecies. This conclusion refers to the taxa described from other Cycladic islands (Natrix natrix syrae Hecht, 1930 from Siros; Natrix natrix fusca Cattaneo, 1990 from Kea) and Euboea (Natrix natrix dystiensis Hecht, 1930) as well.

Natrix natrix lanzai Kramer, 1970

Kramer (1970: p. 671) described this subspecies based on 49 specimens from northern and central mainland Italy. The holotype of *Natrix natrix lanzai* Kramer, 1970 is an adult male collected by Benedetto Lanza on the 11 July 1970 near the 'Croci di Calenzàno,' Calenzàno, province of Firenze (Florence), at the Ritortolo creek, a right confluent of the Sieve River, 290 m a.s.l. (Kramer, 1970: p. 671). Originally the holotype was in the private collection of Eugen Kramer (1921–2004), catalogued with the number 12422. Together with 44 of the 48 additional specimens mentioned in the original description, the holotype is now in the herpetological collection of the Muséum d'Histoire naturelle Genève, Switzerland, and has the catalogue number MHNG 1324.094 (A. Schmitz, pers. comm., 12 June 2020).

Barred grass snakes from Tuscany, where the type locality lies, represent mtDNA lineage F of *Natrix helvetica sicula* (see Kindler *et al.*, 2013; Schultze *et al.*, 2020). This lineage corresponds, together with four other Italian lineages (A, C, D, G) to one and the same nuclear genomic cluster and the same subspecies (Schultze *et al.*, 2020).

Natrix natrix gotlandica Nilson & Andrén, 1981

NILSON & Andrén (1981) diagnosed this subspecies from Gotland, Sweden, using scalation and coloration charac-

ters. The holotype and 11 paratypes from Gotland are in the Göteborg Natural History Museum, Sweden. The holotype (GNM-Ba.Re.Su 1031) was collected by G. Nilson and C. Andrén on 6 June 1976 at Muske mire on southern Gotland, 1.5 km east-northeast of Sundre church.

KINDLER *et al.* (2014, 2017) examined three grass snakes from Gotland genetically. Each corresponded to a different mtDNA lineage (lineages 3, 4, and 8 = the 'yellow,' 'red,' and 'green lineages' of KINDLER *et al.*, 2013). All three mtDNA lineages occur in countries abutting the Baltic Sea. Only one sample (lineage 8) could be genotyped using microsatellite loci (KINDLER *et al.*, 2017); its nuclear genomic identity matched in the hierarchical STRUCTURE analyses the 'red and yellow cluster' (to be identified with *Natrix natrix vulgaris* and *Natrix natrix natrix*) but not *Natrix natrix scutata*, the subspecies characterized by mtDNA lineage 8 (see above).

The island of Gotland was never connected to the Scandinavian Peninsula or the southern Baltic coast. It started to emerge out of the Baltic Ice Lake 10,300 years ago (BJÖRCK, 1995). Therefore, KINDLER *et al.* (2014, 2017) concluded that the grass snakes on Gotland must result from natural or human-mediated overseas dispersal. This, together with the diverse genetic identity of the Gotland snakes and the young age of the island, precludes the recognition of *Natrix natrix gotlandica* Nilson & Andrén, 1981 as a distinct subspecies.

Natrix natrix calabra Vanni & Lanza in Lanza, 1983

Using 40 male and 46 female grass snakes from Calabria, Italy, Vanni & Lanza (in Lanza, 1983: p. 179) described this subspecies, based on coloration differences and a high number of subcaudal scales in males. The holotype is in the Museo di Storia Naturale dell'Università di Firenze, Sezione di Zoologia 'La Specola' (MZUF 23405). It was collected by B. Lanza and N. Nisticò on 29 April 1978 at Novalba di Cardinale, 560 m a.s.l. (10 km NNE of Serra San Bruno, Catanzaro province), Italy.

KINDLER et al. (2013) published mtDNA sequences of a grass snake from the Serra San Bruno. According to their results, mtDNA lineage A occurs near the type locality, which matches the nuclear genomic cluster of *Natrix helvetica sicula* (Cuvier, 1829) (KINDLER & FRITZ, 2018; SCHULTZE et al., 2020). Hence, *Natrix natrix calabra* Vanni & Lanza in Lanza, 1983 is a junior synonym of *Coluber siculus* Cuvier, 1829.

Natrix megalocephala Orlov & Tuniyev, 1987

Based on 19 specimens, OPJOB & TYHHEB (ORLOV & TUNIYEV, also transliterated as ORLOW & TUNIJEW, 1987) described this species from the Colchis Region in the Caucasus, with a range extending eastward to central Azerbaijan. In 1992, an expanded English translation of the description was published that "combines material previously published in Russian by Orlov and Tuniyev

(1986a) [sic] with additional information" (ORLOV & TUNIYEV, 1992: p. 42). The content of the two publications differs in several places considerably, without highlighting the modifications.

The publication date of the original description requires clarification. The title page of volume 158 of the Труды Зоологического Института АН СССР (Proceedings of the Zoological Institute, USSR Academy of Sciences) has the date "1986" imprinted. However, the description of *Natrix megalocephala*, starting on page 116, shows "1987," and 1987 has later also been used by the authors as publication date of the description (Orlow & Tunijew, 1999). This date has to be accepted in accordance with Article 21 of the Code (ICZN, 1999).

The holotype of *Natrix megalocephala* is in the Zoological Institute of the Russian Academy of Sciences, St. Petersburg (then Leningrad, 3ИН [ZIN], now 3ИСП [ZISP] 11846) and was collected by К. Сатунин (К. Satunin) 1909 at Пицунда, Абхазия (Pitsunda, Abkhazia). *Natrix megalocephala* was diagnosed by its massive, wide head with enlarged frontal and temporal scales and its thick body (Орлов & Туниев, 1987: p. 117; ORLOV & TUNIYEV, 1992: p. 44).

According to this distribution range, Natrix megalocephala should be occurring in broad sympatry with Natrix natrix (Linnaeus, 1758). However, the validity of *Natrix megalocephala* was soon challenged (HILLE, 1997; Вöhme, 1999; Jandzík, 2005; Frotzler et al., 2011; GÖÇMEN et al., 2011). It was highlighted that the two species are morphologically difficult to tell apart (Jandzík, 2005). Moreover, big-headed grass snakes were also reported from several parts of the distribution range of *Natrix natrix* sensu lato (Gredler, 1882; GÖÇMEN et al., 2011), suggestive of age-dependent variation, with big-headed snakes representing simply old individuals. Using mtDNA sequences, Kindler et al. (2013) examined three 'Natrix megalocephala.' They found no differences compared to mtDNA lineage 8 of Natrix natrix and synonymized the two taxa. Since we identify in the present study mtDNA lineage 8 with Natrix natrix scutata, Natrix megalocephala Orlov & Tuniyev, 1987 becomes a junior synonym of *Coluber* scutatus Pallas, 1771.

Natrix natrix fusca Cattaneo, 1990

Based on three preserved specimens in his private collection, an additional roadkill (not preserved), and observations of at least two further grass snakes, Cattaneo (1990: pp. 214–218) described this subspecies from the island of Kea (Kéa), western Cyclades, Greece, based on coloration and scalation differences. The holotype (male, field number NN/KEA 10[2]) was collected by A. Cattaneo on the 20 May 1988 on Kea near Otzias ($O\tau\zeta\iota\dot{\alpha}\varsigma$). The specimen is still in his private collection (A. Cattaneo, pers. comm., 2 June 2020).

There are no genetic data available for grass snakes from Kea (KINDLER *et al.*, 2013, 2017). Nevertheless, the validity of this subspecies seems questionable; see above

under the account for *Natrix natrix schweizeri* Müller, 1932.

"Coluber bicephalus Hufeland & Osann, 1825" (see Wallach et al., 2014)

Wallach et al. (2014: p. 478) listed "Coluber bicephalus Hufeland & Osann, 1825" as a synonym of Natrix natrix (Linnaeus, 1758), without providing a source under their references. The name Coluber bicephalus was published in volume 4 of the 'Journal der practischen Heilkunde,' which was only edited by Christoph Wilhelm Hufeland (1762–1836) and Emil Osann (1787–1842). However, the name appeared in an article by a "Geheimer Hofrat [privy court counsellor] Sachse." Coluber bicephalus Sachse, 1825 is a nomen nudum (Sachse, 1825: p. 5), and it is impossible to identify this name with any species.

"Coluber bipedalis Scopoli, 1788"

(see Wallach *et al.*, 2014)

This is another name listed by Wallach *et al.* (2014: p. 478) as a synonym of *Natrix natrix* (Linnaeus, 1758). However, *Coluber bipedalis* is not mentioned in Scopoli (1788), even though some other *Coluber* species are treated on pages 38–41 and figured on plates XIX and XX. It seems likely that the mentioning of the name *Coluber bipedalis* Scopoli, 1788 in Wallach *et al.* (2014) is a *lapsus calami* for *Coluber bipedalis* Bechstein, 1802, which these authors omitted.

"Natrix rubetaria Bonaparte, 1840"

(see Wallach et al., 2014)

This is another name and authorship combination in the synonymy of *Natrix natrix* (Linnaeus, 1758) in Wallach *et al.* (2014: p. 478). Bonaparte (1840) did not describe a new species with the name *rubetaria*. Rather, he cited "*Natrix rubetaria* Aldrov." among the synonyms of *Natrix torquata* on page 438, referring to a pre-Linnean work (Aldrovandi, 1640).

Summary and Conclusions

The results of our present study are summarized below, as far as possible, as classical synonymies. Names that can be only referred to one of the three grass snake species, but not to a particular subspecies, are listed only for the respective species. All names that refer unambiguously to a certain subspecies, also the nominotypical subspecies, appear only under that subspecies.

We indicate for each name its genetic identity, whenever possible also for those names that currently cannot be unambiguously referred to a certain taxon (Balkan and Middle Eastern mtDNA lineages, see above under

the accounts of *Coluber persa* Pallas, 1814 and *Coluber bilineatus* Bibron & Bory de Saint-Vincent, 1833). In particular the taxonomic identity of mtDNA lineage 2, recorded from central northern and northeastern Transcaucasia (eastern Georgia and Dagestan, Russia; KINDLER *et al.*, 2013), remains unclear. In Transcaucasia three distinct mtDNA lineages meet (lineages 1, 2, and 8; KINDLER *et al.*, 2013), but currently nothing is known about the nuclear genomic differentiation in this region.

Finally, both *nomina dubia* (names that cannot be identified with a certain grass snake species or that do not refer to a grass snake species at all) and *nomina nuda* are summarized in two lists.

Synonymies

Natrix astreptophora (Seoane, 1884)

Natrix astreptophora astreptophora (Seoane, 1884)

- 1807 Coluber distinctus Gravenhorst (nomen oblitum, this study). Syntype: specimen in figure 2 of plate X in Seba (1735). Inferred type locality: Iberian Peninsula and Occitany (Occitanie), France.
- 1875 Coluber sparsus Schreiber (partim, nomen oblitum, this study). Syntypes: material from Spain in the Naturhistorisches Museum Wien (NMW 20515:1, 2; NMW 21960: 1; NMW 21978:1). Type locality: southern Illyria, Salzburg, Spain.
- 1884 Tropidonotus natrix var. astreptophorus Seoane (nomen protectum; this study). Syntypes: according to Seoane (1884: pp. 17, 18) deposited in the natural history museums of Berlin, London, Madrid, St. Petersburg, Vienna, and the "Instituto de Pontevedra." Confirmed syntypes are in London (NHMUK 1884.11.20.99), Paris (MNHN-RA-1889.580–1889.583, MNHN-RA-2012.459), and Vienna (NMW 22174:1). Type locality: Galicia, Spain.

Remarks: The Iberian and southern French populations of Natrix astreptophora correspond to mtDNA lineage Eu of Kindler et al. (2013) and constitute a distinct microsatellite cluster (Kindler et al., 2018a). These populations represent the nominotypical subspecies.

Distribution: Iberian Peninsula and Occitany (Occitanie), France.

Natrix astreptophora algerica (Hecht, 1930)

1930 Tropidonotus natrix algericus Hecht. Holotype: Museum für Naturkunde Berlin, ZMB 19636. Type locality: northern Algeria.

Remarks: The Algerian and Tunisian populations of Natrix astreptophora correspond to mtDNA lineage Tu of Kindler et al. (2013) and represent a distinct microsatellite cluster (Kindler et al., 2018a) and the distinct subspecies Natrix astreptophora algerica.

Distribution: Mediterranean region of central and eastern Algeria, Tunisia.

Natrix helvetica (Lacepède, 1789)

Natrix helvetica helvetica (Lacepède, 1789)

- 1789 Coluber vulgaris Razoumowsky (invalid name; junior secondary homonym of Natrix vulgaris Laurenti, 1768 = Natrix natrix vulgaris when transferred to the genus Natrix).
 No type specimens designated in original description. Type locality: Jorat, Switzerland.
- 1789 Coluber Helveticus Lacepède (nomen novum for Coluber vulgaris Razoumowsky, 1789). Type locality: Jorat, Switzerland.
- 1798 Coluber Helvetus Donndorff (incorrect subsequent spelling).
- 1848 *Coluber Jenisonii* Gistel. Type material: unknown. Type locality: Gümmlingermoos near Bern, Switzerland.
- 1930 Tropidonotus natrix britannicus Hecht. Holotype: Museum für Naturkunde Berlin, ZMB 33060. Type locality: England.

Remarks: Despite having been published in a rejected work, Coluber Helveticus Lacepède, 1789 has been conserved as an available name (ICZN, 1992: Opinion 1686). The nominotypical subspecies of Natrix helvetica corresponds to mtDNA lineage E of Kindler et al. (2013) and a distinct microsatellite cluster (Kindler et al., 2017; Schultze et al., 2020).

Distribution: Western Europe, from the Pyrenees to the Rhine region, Great Britain.

Natrix helvetica cetti Gené, 1839

1839 Natrix Cetti Gené. Lectotype (designated in the present study): Museo Regionale di Scienze Naturali, Torino, MZUT R1734, adult female, Fonni, Nuoro province, Sardinia, Italy.

Remarks: This endangered subspecies shares with the more abundant Natrix helvetica corsa (Hecht, 1930) the same mtDNA lineage (lineage B of Kindler et al., 2013), and the two taxa constitute together only one microsatellite cluster (Schultze et al., 2020). Therefore, the Sardinian and Corsican subspecies could be synonymous.

Distribution: Sardinia (Italy).

Natrix helvetica corsa (Hecht, 1930)

1930 Tropidonotus natrix corsus Hecht. Holotype: Museum für Naturkunde Berlin, lost. Type locality: Corsica.

Distribution: Corsica (France).

Natrix helvetica sicula (Cuvier, 1829)

- 1789 Coluber bipes Gmelin (nomen oblitum; Fritz et al., 2020). No type specimens designated in original description. Type locality: Dolomiti di Fiemme/Fleimser Alpen, Italy.
- 1789 Coluber tyrolensis Gmelin (nomen oblitum; FRITZ et al., 2020). No type specimens designated in original description. Type locality: Dolomiti di Fiemme/Fleimser Alpen, Italy.
- 1802 Coluber pipedalis (typographical error) = Coluber bipedalis
 Bechstein (nomen oblitum; this study). No type specimens

- designated in original description. Type locality: Dolomiti di Fiemme/Fleimser Alpen, Italy.
- 1803 Coluber scopolianus Daudin (nomen novum for Coluber bipes Gmelin, 1789 and nomen oblitum; Fritz et al., 2020).
 Type locality: Dolomiti di Fiemme/Fleimser Alpen, Italy.
- 1814 Coluber viperinus Rafinesque (permanently invalid name; junior primary homonym of Coluber viperinus Latreille in Sonnini & Latreille, 1801 = Natrix maura [Linnaeus, 1758]). No type specimens designated in original description. Type locality: Sicily.
- 1814 Vipera vissena Rafinesque (nomen oblitum; this study). No type specimens designated in original description. Type locality: Sicily.
- 1829 Coluber siculus Cuvier (nomen protectum; FRITZ et al., 2020; this study). Syntype: Muséum national d'Histoire naturelle, Paris, MNHN-RA-0.3317. Type locality: Sicily.
- 1863 Natrix torquata var. Senescens Minà Palumbo. Type material: unknown. Type locality: Sicily.
- 1880 Tropidonotus natrix var. nigri-torquata Ninni. Type material: perhaps in the Museo di Storia Naturale di Venezia. Type locality: Sicily.
- 1882 *Tropidonotus natrix* var. *bulsanensis* Gredler. Holotype: Naturhistorisches Kabinett am Franziskanergymnasium Bozen, Gredler collection 1094. Type locality: Terlan (Terlano) northwest of Bozen (Bolzano), South Tyrol, Italy.
- 1970 Natrix natrix lanzai Kramer. Holotype: Muséum d'Histoire naturelle Genève, MHNG 1324.094. Type locality: 'Croci di Calenzàno,' Calenzàno, province of Firenze (Florence), Italy, at the Ritortolo creek, a right confluent of the Sieve River, 290 m a.s.l.
- 1983 Natrix natrix calabra Vanni & Lanza in Lanza. Holotype: Museo di Storia Naturale dell'Università di Firenze, Sezione di Zoologia 'La Specola,' MZUF 23405. Type locality: Novalba di Cardinale, 560 m a.s.l. (10 km NNE of Serra San Bruno, Catanzaro province, Calabria), Italy.

Remarks: Coluber bipes Gmelin, 1789, Coluber tyrolensis Gmelin, 1789, Coluber bipedalis Bechstein, 1802, Coluber scopolianus Daudin, 1803, and Tropidonotus natrix var. bulsanensis Gredler, 1882 correspond to mtDNA lineage C of Kindler et al. (2013). If grass snakes with this mtDNA lineage should be regarded as a distinct subspecies in future, the name to be used is Natrix helvetica tyrolensis (Gmelin, 1789) because we here give precedence to Coluber tyrolensis Gmelin, 1789 over the simultaneously published name Coluber bipes Gmelin, 1789 (First Reviser Principle; ICZN, 1999: Article 24.2). This precedence was already implied in FRITZ et al. (2020).

Coluber siculus Cuvier, 1829, Coluber viperinus Rafinesque, 1814, Vipera vissena Rafinesque, 1814, Natrix torquata var. Senescens Minà Palumbo, 1863, Tropidonotus natrix var. nigri-torquata Ninni, 1880, and Natrix natrix calabra Vanni & Lanza in Lanza, 1983 correspond to mtDNA lineage A of Kindler et al. (2013).

Natrix natrix lanzai Kramer, 1970 corresponds to mtDNA lineage F of Kindler et al. (2013).

All five mtDNA lineages from mainland Italy and Sicily (A, C, D, F, G) represent the same microsatellite cluster, which is why SCHULTZE *et al.* (2020) lumped together all grass snakes from mainland Italy in the subspecies *Natrix helvetica sicula*.

Distribution: Mainland Italy, across the Alps to southernmost Bavaria (Germany).

Natrix natrix (Linnaeus, 1758)

- 1832 Tropidonotus Natrix var. minax Fitzinger. Type material: perhaps in the Naturhistorisches Museum Wien. Type locality: Archduchy of Austria (approximately matching Upper and Lower Austria).
- 1832 Tropidonotus Natrix var. murorum Fitzinger. Type material: perhaps in the Naturhistorisches Museum Wien. Type locality: Archduchy of Austria (approximately matching Upper and Lower Austria).
- 1833 Coluber natrix var. dalmatina Schinz. Type material: unknown. Type locality: Dalmatia.
- 1864 Tropidonotus natrix var. bilineata Jan (permanently invalid name; junior primary homonym of Tropidonotus viperinus var. bilineata Jan, 1863 = Natrix maura [Linnaeus, 1758]).
 Type material: Museo Civico di Storia Naturale di Milano, destroyed. Type locality: Dalmatia and other southern European countries.
- 1864 Tropidonotus natrix var. subbilineata Jan. Type material: Museo Civico di Storia Naturale di Milano, destroyed. Type locality: Dalmatia and other southern European countries.
- 1875 *Coluber sparsus* Schreiber (*partim*). Syntypes: material from Spain in the Naturhistorisches Museum Wien (NMW 20515:1, 2; NMW 21960:1; NMW 21978:1). Type locality: southern Illyria, Salzburg, Spain.
- 1880 Tropidonotus natrix var. lineata Ninni (pertains most likely to admixed population). Type material: possibly in the Museo di Storia Naturale di Venezia. Type locality: Venetia (Veneto)?
- 1930 Tropidonotus natrix dystiensis Hecht (pertains most likely to admixed population). Holotype: Museum für Naturkunde Berlin, ZMB 13594. Type locality: Δύστος, Εύβοια (Dystos, Euboea), Greece.
- 1930 Tropidonotus natrix syrae Hecht (pertains most likely to admixed population). Holotype: Museum für Naturkunde Berlin, ZMB 13533. Type locality: Σύρος (Syros), Cyclades, Greece
- 1932 Natrix natrix schweizeri Müller (pertains to admixed population). Syntypes: Zoologische Staatssammlung München, destroyed; further syntypes could be in the Senckenberg Museum Frankfurt. Type locality: Μήλος (Milos), Cyclades, Greece.
- 1981 Natrix natrix gotlandica Nilson & Andrén (pertains to admixed population). Holotype: Göteborg Natural History Museum, GNM-Ba.Re.Su 1031. Type locality: Muske mire, 1.5 km east-northeast of Sundre church, southern Gotland, Sweden.
- 1990 Natrix natrix fusca Cattaneo (pertains most likely to admixed population). Holotype: private collection A. Cattaneo, Roma, NN/KEA 10[2]. Type locality: Οτζιάς, Κέα (Otsias, Kea), Greece.

Remarks: The names listed above refer to the species Natrix natrix (Linnaeus, 1758) but cannot be identified with any particular subspecies or genetic lineage. In some cases, the composite type localities correspond to more than one subspecies or mtDNA lineage. In other cases, the respective source population of the type material is evidently admixed and belongs to a unimodal hybrid zone without pure parental genotypes. Thus, these names cannot be assigned to any subspecies, and the names must not be used as valid for either of the parental taxa, even if they should be the oldest ones (ICZN, 1999: Article 23.8).

For *Tropidonotus natrix* var. *lineata* Ninni, 1880, *Tropidonotus natrix dystiensis* Hecht, 1930, *Tropidonotus natrix syrae* Hecht, 1930, and *Natrix natrix fusca* Cattaneo, 1990 no genetic data are available. However, the

broader genetic evidence (KINDLER *et al.*, 2017; SCHULTZE *et al.*, 2020) and geographic context suggest that these taxa also represent admixed populations.

Natrix natrix (Linnaeus, 1758)

1758 Coluber Natrix Linnaeus. Neotype: Swedish Museum of Natural History, Stockholm, NRM 8260. Type locality: Fada mill pond, approximately two kilometres southeast of the Berga-Tuna Estate, Nyköping, Sweden.

Remarks: This subspecies corresponds to the 'yellow mtDNA lineage' (lineage 3) and the 'yellow microsatellite cluster' of KINDLER *et al.* (2013, 2017).

Distribution: Scandinavia including Åland Islands (Finland), Central Europe. Hybridizes in southern Central Europe with *Natrix natrix vulgaris*.

Natrix natrix persa (Pallas, 1814)

- 1814 Coluber persa Pallas (precedence over Coluber minutus Pallas, 1814 established by Eichwald, 1841). Holotype: putatively lost. Type locality: Gilan and Mazandaran, Iran.
- 1814 *Coluber minutus* Pallas. Holotype: putatively lost. Type locality: "Persia."
- 1831 *Tropidonotus persicus* Eichwald (incorrect subsequent spelling of *Coluber persa* Pallas).
- 1930 Tropidonotus natrix schirvânae Hecht. Holotype: Museum für Naturkunde Berlin, ZMB 1938. Type locality: Şirvan, Azerbaijan.

Remarks: This subspecies is tentatively identified with populations characterized by mtDNA lineage 1 of KINDLER et al. (2013). Further research is needed to disentangle the nuclear genomic identity of Natrix natrix persa, in particular whether further mtDNA lineages have to be identified with this taxon.

Distribution: Azerbaijan, northern Iran.

Natrix natrix scutata (Pallas, 1771)

- 1771 Coluber scutatus Pallas. Type specimens neither designated in original description nor known to exist. Type locality: lower Ural River near Atyrau, Kazakhstan.
- 1831 Tropidonotus ater Eichwald. Type material: perhaps in the Zoological Institute of the Russian Academy of Sciences, St. Petersburg. Type locality: islands in the Volga River near Astrakhan, Russia.
- 1842 Tropidonotus Natrix var. colchica Nordmann in Démidoff. No type specimens designated in original description; a syntype is shown in plate 12, figure 1 (Nordmann in Démidoff, 1842). Type locality: Crimea and Transcaucasian Black Sea coast between Anapa (Russia) and Anaklia (Georgia).
- 1842 Tropidonotus Natrix var. nigra Nordmann in Démidoff (potentially invalid name; primary homonym of Tropidonotus niger Holbrook, 1842 = Nerodia sipedon [Linnaeus, 1758]). No type specimens designated in original description; a syntype is shown in plate 11, figure 1 (Nordmann in Démidoff, 1842). Type locality: Transcaucasian Black Sea coast between Anapa (Russia) and Anaklia (Georgia).
- 1925 Natrix vibakari continentalis Nikolsky. Originally two syntypes in the Zoological Institute of the Russian Academy

- of Sciences, St. Petersburg; ЗИСП 14236 (lost) and ЗИСП 16073. Type locality: Троицкосавск, Кяхта, Бурятия [Troitskosavsk, Kyakhta, Buryatia], Russia.
- 1930 *Tropidonotus natrix bucharensis* Hecht. Holotype: Museum für Naturkunde Berlin, ZMB 1943. Type locality: 'Mountains of Mugosarsk,' Kazakh steppe east of the Aral Sea.
- 1987 *Natrix megalocephala* Orlov & Tuniyev. Holotype: Zoological Institute of the Russian Academy of Sciences, St. Petersburg, ЗИСП 11846. Type locality: Пицунда, Абхазия [Pitsunda, Abkhazia].

Remarks: This subspecies corresponds to the 'green mtDNA lineage' (lineage 8 of KINDLER et al. 2013, 2017) that also represents another microsatellite cluster compared to the nominotypical subspecies and Natrix natrix vulgaris.

Distribution: From eastern Polish border region eastward to Lake Baikal, northern Anatolia (Turkey) and western Transcaucasus.

Natrix natrix syriaca (Hecht, 1930)

1930 *Tropidonotus natrix syriacus* Hecht. Holotype: Museum für Naturkunde Berlin, ZMB 13768. Type locality: Zincirli, İslahiye/Gaziantep, Turkey.

Remarks: This subspecies was identified with mtDNA lineage 6 by Kindler et al. (2013), and we tentatively accept this. However, it is unclear whether this lineage occurs indeed in the region of the type locality Zincirli because the sequenced samples originated from the other side of the Amanus Mountains (Nur Dağları). Additional research is also needed to determine the nuclear genomic identity of grass snakes with mtDNA lineage 6.

Distribution: Gulf of İskenderun (Turkey) and adjacent region east of the Nur Dağları.

Natrix natrix vulgaris Laurenti, 1768

1768 Natrix vulgaris Laurenti. Neotype: Naturhistorisches Museum Wien, NMW 36405:2. Type locality: Oberedlitz, Gemeinde Thaya, Niederösterreich (Lower Austria), Austria.

Remarks: This subspecies corresponds to the 'red mtDNA lineage' (lineage 4) and the 'red microsatellite cluster' of Kindler et al. (2013, 2017). This subspecies invaded Central Europe from the Balkans (Kindler et al., 2018b). In its former glacial refuge, it admixed later with other genetic lineages, so that pure populations are now restricted to southern Central Europe.

Distribution: Southern Central Europe. To the north, *Natrix natrix vulgaris* hybridizes with the nominotypical subspecies and to the south and southeast, with genetic lineages from the Balkans of unclear taxonomy. Some genotypically pure populations of *N. n. vulgaris* in southern Central Europe show cytonuclear discordance (introgressed mtDNA of the nominotypical subspecies; see maps in Kindler *et al.*, 2017; Schultze *et al.*, 2020).

Names of unresolved taxonomic identity corresponding to mtDNA lineages of *Natrix natrix*

mtDNA lineage 5

- 1833 Coluber bilineatus Bibron & Bory de Saint-Vincent (permanently invalid name; junior primary homonym of Coluber bilineatus Latreille in Sonnini & Latreille, 1801 = Amphiesma stolatum [Linnaeus, 1758]). Syntype: Muséum national d'Histoire naturelle, Paris, MNHN-RA-0.3468. Type locality: Peloponnesus, Greece.
- 1882 Tropidonotus natrix var. moreoticus Bedriaga. Type material: Natural History Museum of Athens University, Greece. Type locality: northern Peloponnesus, Greece.
- 1930 *Tropidonotus natrix bithynius* Hecht. Holotype: Museum für Naturkunde Berlin, ZMB 31425. Type locality: Alem Dagh (hill), approx. 30 km from Shkodër, Albania.
- 1930 Tropidonotus natrix cephallonicus Hecht. Holotype: Museum für Naturkunde Berlin, ZMB 18422. Type locality: Αργοστόλι, Κεφαλονιά (Argostoli, Kefalonia), Greece.

Remarks: Tropidonotus natrix var. moreoticus Bedriaga, 1833 represents the oldest name that can be applied to grass snakes with mtDNA lineage 5, if such populations should be deemed as a distinct subspecies in future. MtDNA lineage 5 is distributed on the Peloponnesus and the adjacent southwestern Balkan Peninsula, and ranges northward approximately to the Pelješac Peninsula, Croatia (Kindler et al., 2013, 2017).

mtDNA lineage 7

1930 Tropidonotus natrix cypriacus Hecht. Holotype: Museum für Naturkunde Berlin, ZMB 16122. Type locality: Cyprus.

Remarks: MtDNA lineage 7 has been recorded from the southeastern Balkans (Bulgaria, eastern Greece, Turkish Thrace), western Anatolia (Turkey), and Cyprus.

Nomina dubia that have been erroneously identified with grass snakes:

Natrix Gronoviana Laurenti, 1768

Coluber arabicus Gmelin, 1789

Coluber Capite-triangulatus Lacepède, 1789 (unavailable name; ICZN, 1987: Opinion 1463)

Coluber Semimonile Lacepède, 1789 (unavailable name; ICZN, 1987: Opinion 1463)

Coluber Torquatus Lacepède, 1789 (unavailable name; ICZN, 1987: Opinion 1463)

Coluber decorus Gravenhorst, 1807 (permanently invalid name; junior primary homonym of Coluber decorus Shaw, 1802 = Dendrelaphis pictus [Gmelin, 1789])

Coluber irroratus Gravenhorst, 1807

Natrix hybridus Merrem, 1820

Tropidonotus Oppelii Boie, 1827

Coluber niger Dvigubsky, 1832

Tropidonotus natrix var. nigra Jan, 1864 (permanently invalid name; junior primary homonym of Tropidonotus Natrix var. nigra Nordmann in Démidoff, 1842 = Natrix natrix scutata [Pallas, 1771], Tropidonotus niger Holbrook, 1842 = Nerodia sipedon [Linnaeus, 1758], and Tropidonotus tessellatus var. nigra de Betta, 1857 = Natrix tessellata [Laurenti, 1768])

Tropidonotus natrix var. picturata Jan, 1864 Tropidonotus fallax Fatio, 1872

Tropidonotus natrix var. concolor Ninni, 1880 (permanently invalid name; junior primary homonym of Tropidonotus tessellatus var. concolor Jan, 1864 = Natrix tessellata [Laurenti, 1768])
Tropidonotus natrix var. albo-torquata Camerano, 1891
Tropidonotus natrix var. albiventris Dürigen, 1897
Tropidonotus natrix var. fasciatus Dürigen, 1897
Tropidonotus natrix var. subfasciatus Boulenger, 1913

Nomina nuda:

Coluber Natrix minax Fitzinger, 1826 Coluber Natrix murorum Fitzinger, 1826 Natrix viperina var. bilineata Bonaparte, 1840 Coluber bicephalus Sachse, 1825

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