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Isolated populations of *Zamenis longissimus* (Reptilia: Squamata) above the northern limit of the continuous range in Europe: origin and conservation status

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Abstract. This paper summarizes the current knowledge about isolated northerly populations of *Zamenis longissimus* (Laurenti, 1768) in Europe. Fossil records outside the present range are reviewed, suggesting a much wider distribution of the species during climatically more favourable periods of Holocene. Due to its geographical position outside of the continuous range, the origin of the isolated populations has long been debated. Despite a number of hypotheses proposed about their origin via human introduction, all evidence suggests that they are relics of the Holocene climatic optimum. Because isolated populations are particularly vulnerable to extinction but may harbour important adaptations to unfavourable conditions, all effort should be made to ensure their survival in the face of the current anthropogenic changes to the environment.

Isolated population, fossil record, origin hypothesis, management, Aesculapian snake, Europe, Palaearctic region

INTRODUCTION

Distribution of many European species has been influenced by Pleistocene climatic changes. The Aesculapian Snake, *Zamenis longissimus* (Laurenti, 1768) is not an exception. Recent isolated populations of the Aesculapian snake above the northern range limit, that are currently considered to be remnants of wider range at climatically more favourable periods, are known from Poland, Germany and Czech Republic (e.g., Böhme 1993, Mikátová & Zavadil 2001, Najbar 2000b, Schultz 1996). The northernmost one survives in the Ohře river valley in the Czech Republic beyond the 50° N. More than 200 km distance separates it from continuous range. This unique position of this population has evoked many hypothesis of its origin since the population was discovered in 1880 (Mikátová & Zavadil 2001). The Aesculapian Snake is undoubtedly most threatened and rarest snake of the Czech Republic as its continuous distribution extends only to the south and southeast of the country. Furthermore, factors as isolation from continuous range, very restricted area limited by microclimate, landscape changes and increasing anthropogenic pressure make the population in northwest Bohemia especially vulnerable (Haleš 1975, 1987, Mikátová & Zavadil 2001). Thus, evaluation of the status of this isolated population in the context of other European populations is a necessary prerequesite for the informed and efficient management.

Zamenis longissimus has a large distribution range extending from southern Spain to northwest Turkey including the following countries – south and central France, south and southwest Switzerland, northern Italy, Austria (thereof slightly expanding to include the Podyjí National Park in the Czech Republic), Slovakia (slightly extending to the Czech Republic in the White Carpathians Protected Landscape Area and Beskydy Protected Landscape Area), Hungary, Slovenia, Croatia, Serbia, Montenegro, Albania, Greece, Romania, Bulgaria, Moldavia and west Ukraine; disjunctive part of the distribution covers the eastern Black Sea coast to the Krasnodar region in Russia as well as parts of Georgia and Turkey (Böhme 1993, Günther & Waitzmann 1996, Schulz 1996).

The formerly recognised subspecies *Elaphe longissima persica* (Werner, 1913) from north Iran and southeast Azerbaijan and *Elaphe longissima romana* (Suckow, 1798) from Sicily and south and central Italy were recently upgraded to the species level [Lenk & Wüster 1999, Nilson & Andrén 1984, Utiger et al. 2002; nowadays *Zamenis persicus* (Werner, 1913) and *Zamenis lineatus* (Camerano, 1891)].

The Aesculapian snake is usually regarded as a thermophile species although this is not completely accurate. Humidity requirements are also important: it prefers moderately humid and warm places, and it avoids especially dry conditions (Gomille 2002). That is why it often occurs

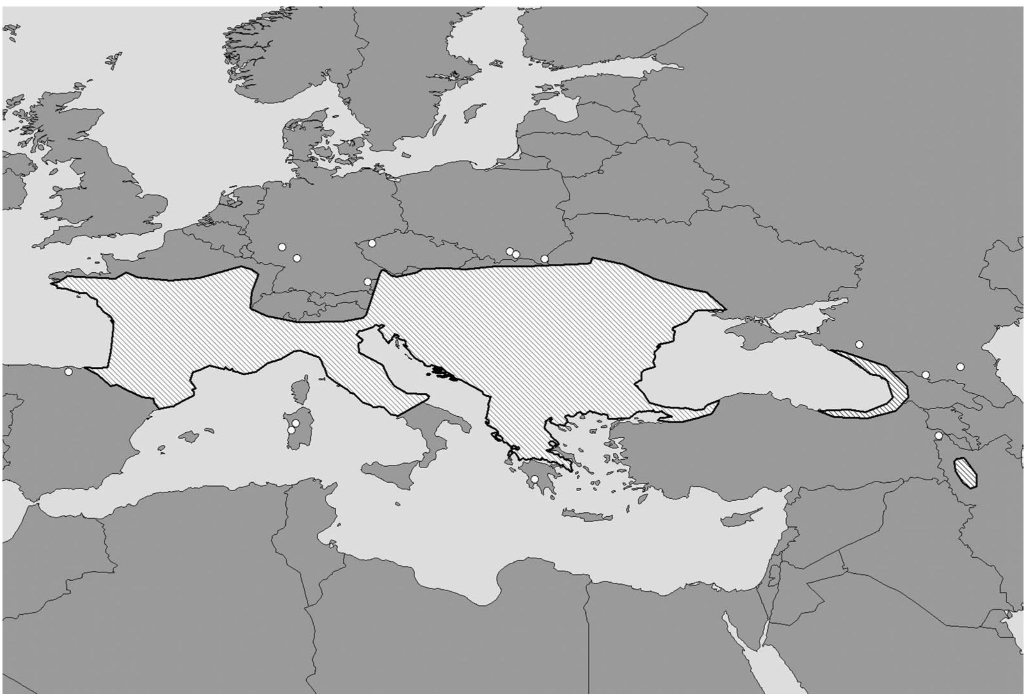

Fig. 1. Distribution of *Zamenis longissimus* (Laurenti) (according to Böhme 1993, Gomille 2002, and Schultz 1996); isolated populations are symbolized by white spots.

sympatrically with the Viviparous lizard, *Zootoca vivipara* (Jacquin, 1787). Nevertheless, higher temperature is necessary for successful egg incubation.

As described by Gomille (2002) the ecological requirements of the Aesculapian snake are reflected by the extent of its continuous range (Fig. 1). The southern, western and eastern limits of the distribution correlate with the range of summer-green deciduous forest that is dependent on precipitation. This type of forest is replaced by an evergreen Mediterranean forest at regions with low precipitation and high temperature, where the Aesculapian snake does not occur (predominant part of the Iberian peninsula, southern part of the Apennine peninsula and southeast Turkey). The northern range limit in central Europe appears to be determined by the temperature (Gomille 2002).

Occurrence at the northern edge of the range seems to be also determined by landscape morphology. Isolated populations are found in river valleys with woody slopes where microclimatic conditions might be of particular significance.

ISOLATED POPULATIONS AND THEIR HISTORY

There are a number of isolated populations of the Aesculapian snake off the limits of the continuous range. There is an isolated populatin near Urmia Lake in Iran, whose taxonomic status remains unclear (Nilson & Andrén 1984, Schultz 1996). Furthermore, isolated populations are known from east Georgia, Russia and Turkey near the eastern Black Sea Coast (Schultz 1996, Schweiger 1994 , Tunijev 1990).

Other isolated populations are located in southwest Spain and Sardinia below the southern range limit (Capocaccia 1965, Meijide 1973, Mellado et al. 1979) and in Germany, Switzerland, Denmark, Czech Republic and Poland above the northern range limit (e.g., Bayer 1894, Böhme 1993, Günther & Waitzmann 1996, Jaeschke 1971, Ljungar 1995, Mertens 1948, 1969, Mikátová & Zavadil 2001, Najbar 2000b, Reinhard 1938, Szyndlar 1984a, Šolcová-Danihelková 1966, Waitzmann 1993). These European populations (Fig. 2) are the focus of the present review.

Some of the isolated populations known from historical time have become extinct. The Danish population became extinct long ago. In the vicinity of Copenhagen, the species was still reported as common at the end of the 18th century (Boulenger 1913). Then three specimens were collected in the Danish island Zealand later in the 19th century, with the last one in 1863 (Hvass 1942). Because almost nothing was known about fossil records at that time they were viewed as introduced exemplars. Discovery of subfossil remains from Lystrup Enge area by Lujngar (1995) brought new light to this case, because now it could have been regarded also as relic of a once wider distribution range.

An isolated population near Basel in Switzerland became extinct quite recently. The last records date from 1971 (Böhme 1993).

Three isolated population are present in Germany today. They are located near Schlangenbad (Taunus Mts, Walluf stream valley, Hessen Province), near Hirschhorn (Odenwald Mts, Neckar valley, border of Hessen and Baden-Württemberg Provinces) and near Burghausen at the lower Salzach river (South Bavaria). The occurrence near Passau in the Danube valley, often described as an isolated population, actually belongs to the western branch of the continuous range extending to Germany from Austria (Waitzmann 1993). A population near Schlangenbad has been known since 1817 (Böhme 1993). Later, in 1905 an occurrence near Burghausen was recorded (Hecht 1928) and a third isolated area near Hirschorn has been discovered quite recently, in 1947–1948 (Mertens 1948).

According to Najbar (2000b, 2004b) there are six localities in Poland where the Aesculapian snake occurred in past and/or present. Złoty potok and Zamojszczyna populations are conside-

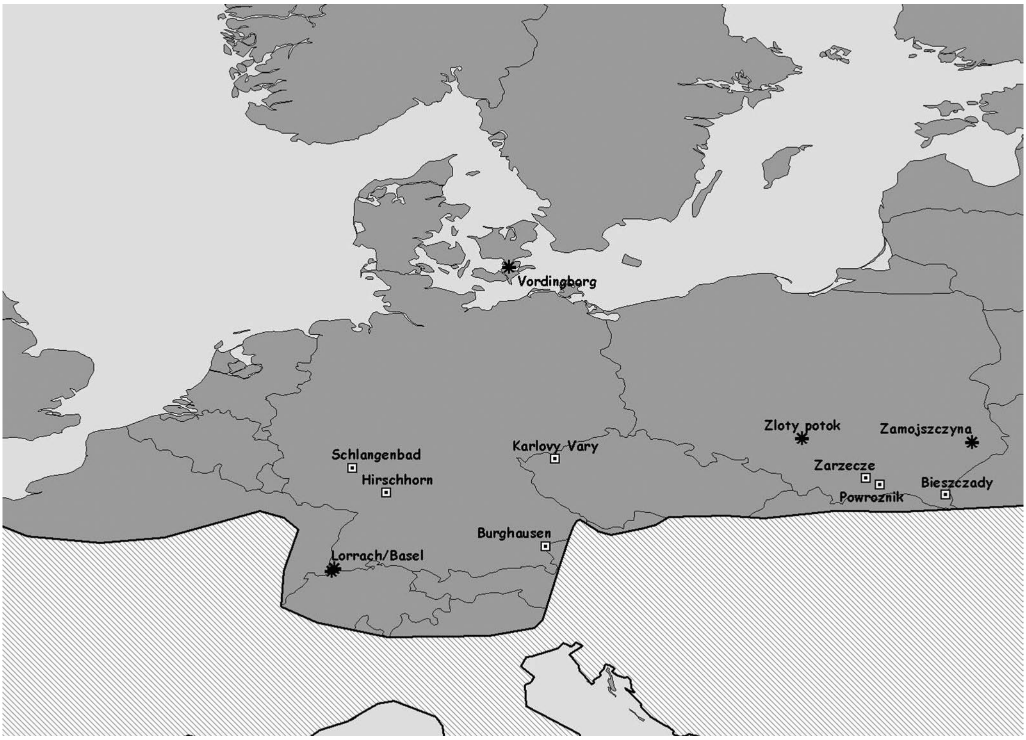

Fig. 2. Isolated populations of *Zamenis longissimus* (Laurenti) in Central Europe (according to Böhme 1993, Gomille 2002, and Schultz 1996), recent isolated populations are symbolized by squares, extinct ones by asterisks.

red to be the extinct, while at other localities (Zarzecze, Powroznik, Bieszczady Mts, Magurski National Park) Aesculapian snakes still occur.

The northern limit of the continuous range of *Zamenis longissimus* runs through southeastern Poland in the Bieszczady Mts, where only one known abundant population occurs. It may have been a peripheral population of the continuous range as described by Szyndlar (1984a), however it has lost contact with the continuous range and today is consider isolated (Najbar 2000a, 2004a). Additional records are recorded from Zarzecze (155 km from the Bieszczady Mts), Powroznik (115 km from Bieszczady Mts) and the Magurski NP (115 km from the Bieszczady Mts). But these are very scarce and of an unclear status.

The first written reference about the Czech isolated population in the Ohře river valley near Karlovy Vary in 1843 comes putatively from a Mr. Döbler, the librarian of the Count of Buquoy. This is reported by Šolcová-Danihelková (1966) as she obtained the information from Mr. Koudelka, the director of the Museum of Karlovy Vary. But this has never been confirmed. The first reliable evidence then comes from 1880 when Mr. Stýbal donated a specimen of the Aesculapian snake from Korunní (formerly Krondorf) to the National Museum in Prague (Bayer 1894, Štěpánek 1949, 1956, Vogel 1952, 1968, Záleský 1922). Vogel (1952, 1968) alleged that since that time nobody has noticed this species in Ohře river valley, however this is obviously not true. During the first half of the 20th century the Aesculapian snake was observed for example by Fieber (1932) and Reinhardt (1937, 1938). Two other specimens are deposited in the Museum of Karlovy Vary. One of them is surely dated before World War II and the second was caught in the mine of Stráž nad Ohří in 1956. Šolcová – Danihelková (1966) was the first to describe the population based on detailed field work. At that time the snake was spotted due to road reconstruction in very narrow part of the Ohře river valley between the villages Stráž nad Ohří and Boč. In the same year an exemplar of *Zamenis longissimus* was killed by a train near the village of Boč and deposited in the Museum of Plzeň (Tišer 1975). During next years the population is often mentioned by Haleš (1969, 1975, 1984 and 1987), Šolcová (1974), Janoušek (1979), Bárta (1983) or Šapovaliv & Zavadil (1990), nevertheless some of these authors intentionally do not specify localities for conservation reasons.

FOSSIL AND SUBFOSSIL RECORD

Fossil and subfossil records are known not only from the present distribution area (for example Italy, Austria, and Slovakia (e.g., Delfino & Bailon 2000, Ivanov 2007)) but also from many places outside the current range (Fig. 3, Table 1). Hence the Aesculapian snake must have occurred far more to the north and east than today in climatically favoured periods. Fossil remains from Pleistocene interglacials and also subfossil records from Holocene in the same localities in south

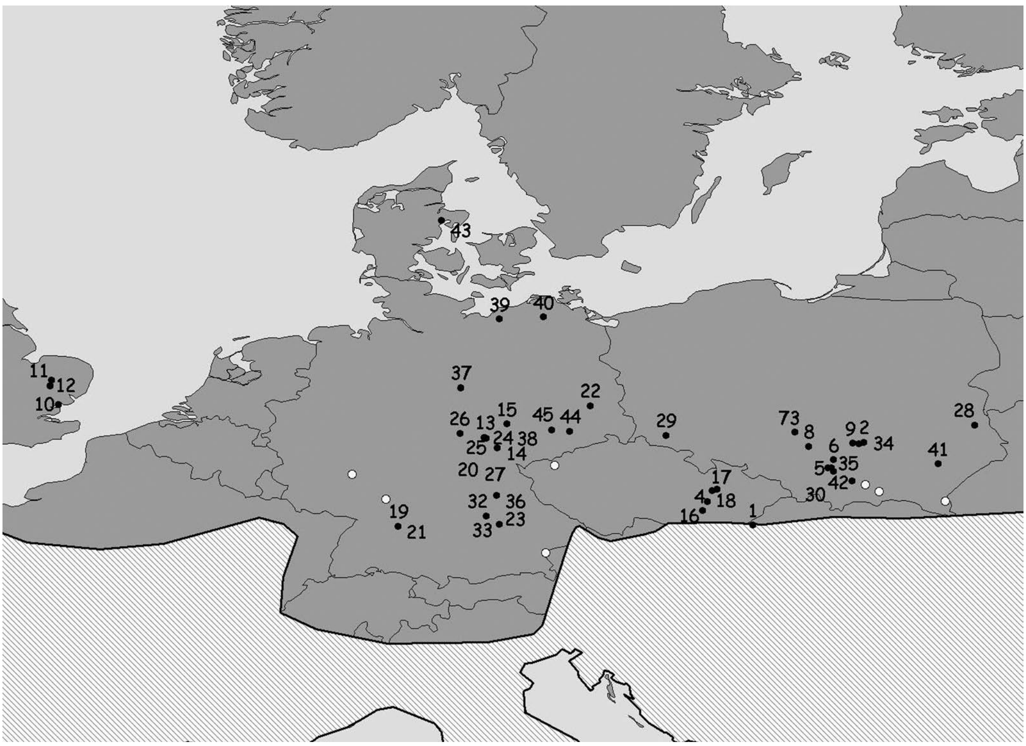

Fig. 3. Fossil record of *Zamenis longissimus* (Laurenti) outside its current range in Central and Northwest Europe (solid circles), numbers refer to Table 1, open circles represent isolated extant populations.

Table 1. Fossil records of the Aesculapian snake (*Zamenis longissimus* (Laurenti)) outside its current range from Central and North- western Europe; L = Lower, M = Middle, U = Upper

No.	locality	country	stage	reference
1	Ivanovce	Slovakia	L Pliocene	Ivanov (2007)
2	Kadzielnia	South Poland	L Pleistocene	Szyndlar (1984b)
3	Zalesiaki B	South Poland	L Pleistocene	Szyndlar (1984b)
4	Malá dohoda Quarry	Czech R., Moravian Karst	L Pleistocene	Ivanov (1996)
5	Kamyk	South Poland	L Pleistocene	Szyndlar (1984b)
6	Zabia Cave	Central Poland	L Pleistocene	Szyndlar (1984b), Ivanov (1997)
7	Zalesiaki A	South Poland	L to M Pleistocene	Szyndlar (1984b)
8	Zamkowa Dolna Cave	South Poland	L to M Pleistocene	Szyndlar (1984b)
9	Kozi Grzbiet	South Poland	L to M Pleistocene	Szyndlar (1984b)
10	Cudmore Grove	England, Essex, Mersea I.	M Pleistocene	Holman et al. (1990)
11	Barnham	England, Suffolk	M Pleistocene	Ashton et al. (1994)
12	Beeches Pit	England, Suffolk	M Pleistocene	Holman (1998 ex Gomille 2002)
13	Weimar-Ehringsdorf	Germany, Thuringia	M Pleistocene	Böhme & Heinrich (1994)
14	Gamsenberg	Germany, Thuringia	M Pleistocene	Böhme (2000)
15	Neumark-Nord	Germany, Saxony	M Pleistocene	Böhme (2001 ex Gomille 2002)
16	Stránská skála Hill	Czech R., Moravia	M Pleistocene	Ivanov (1995)
17	Mladeč Caves	Czech R., Morava	M Pleistocene	Ivanov (2006)
18	Za hájovnou Cave	Czech R., Moravia	M Pleistocene	Ivanov (2005)
19	Stuttgart-Bad Cannstatt	Germany, Baden-Württ.	M Pleistocene	Bottcher (1994)
20	Weimar-Ehringsdorf	Germany, Thuringia	M Pleistocene	Mlynarski & Ulrich (1975)
21	Stuttgart-Bad Cannstatt	Germany, Baden-Württ.	U Pleistocene	Bottcher (1994)
22	Schönfeld-Calau	Germany, Brandenburg	U Pleistocene	Böhme (1991b)
23	Lobsing	Germany, Bavaria	U Pleistocene	Heller (1960), Böhme (1997)
24	Weimar	Germany, Thuringia	U Pleistocene	Böhme G. (1989)
25	Taubach	Germany, Thuringia	U Pleistocene	Böhme G.(1989)
26	Burgtonna	Germany, Thuringia	U Pleistocene	Böhme G.(1989)
27	Gamsenberg	Germany, Thuringia	U Pleistocene	Böhme G. (2000)
28	Wierzbica	Central Poland	U Pleistocene	Szyndlar (1984b)
29	Rzasnik	East Poland	U Pleistocene	Szyndlar (1984b)
30	Zytnia Skala	South Poland	U Pleistocene/Holocene	Szyndlar (1984b)
31	Ciasna Cave	South Poland	U Pleistocene/Holocene	Szyndlar (1984b)
32	Malerfels	Germany, Bavaria	Holocene	Markert (1978 ex Gomille 2002)
33	Euerwanger Bühl	Germany, Bavaria	Holocene	Markert (1975)
34	Raj Cave	South Poland	Holocene	Szyndlar (1984b)
35	Niedostepna Cave	South Poland	Holocene	Szyndlar (1984b)
36	Grundfelsen Hohle	Germany, Bavaria	Holocene	Brunner (1942/3 ex Gomille 2002)
37	Kneitlingen	Germany, Lower Saxony	Holocene	Böhme (1991a)
38	Gamsenberg	Germany, Thuringia	Holocene	Böhme (2000)
39	Neukloster	Germany, Mecklenburg	Holocene	Peters (1977a,b)
40	Pisede	Germany, Mecklenburg	Holocene	Peters (1977a,b)
41	Jozéfow	South Poland	Holocene	Szyndlar (1984b)
42	Giebultow	South Poland	Holocene	Szyndlar (1984b)
43	Lystrup Enge	Denmark	Holocene	Ljungar (1995)
44	Robschütz	Germany, Saxony	Holocene	Böhme (1994)
45	Klosterbuch	Germany, Saxony	Holocene	Böhme (1991a)

Poland and Germany (Gamsenberg) indicate that the range of *Zamenis longissimus* repeatedly contracted and extended again during Quaternary (Szyndlar 1984b, Böhme 2000). Most important in the context of isolated populations are records from central and northwestern Europe (Fig. 3, Table 1).

Subfossil remnants of the Aesculapian snake from the Holocene period were found in northern Germany (Peters 1977a, b), southern Poland (Szyndlar 1984b) and Denmark (Ljungar 1995). The latter is the northernmost fossil record found until today and comes from the Lystrup Enge area. Dating was estimated to 4200–4000 years BC (Ljungar 1995). That corresponds with the Atlantic Period (7100–3750 years BC), climatic optimum of the Holocene, when annual mean temperatures were 2–2.5 °C higher than today (Dahl-Jensen et al. 1998). At that time for example the pond turtle, *Emys orbicularis* (Linnaeus, 1758) occurred even in Sweden close to 59°N (Sommer et al. 2007). Fossil remains have been discovered recently even in the Czech Republic. They come from the Lower or Middle Pleistocene periods and are located in Moravia (Ivanov 1995, 1996, 2005, 2006).

ORIGIN OF THE ISOLATED POPULATIONS

Isolated populations above the northern limit of the continuous range of *Zamenis longissimus* are today mostly regarded as a relic of a wider range in climatically more favourable conditions during the Holocene period (e.g., Gomille 2002, Ljungar 1995). Recent genetic analyses based on protein electrophoresis and mtDNA found no disagreement in the general phylogeografic pattern with this hypothesis for the German isolated populations (Joger et al. 2006, Joger et al. 2007, Lenk et al. 1995).

Nevertheless, their position far from the continuous range has provoked a long debate concerning their origin. The oldest known hypothesis comes from Heyden (1862 ex Böhme 1993), who considered the dispersal of this snake together with the Romans as cult symbol. Purportedly they introduced snakes around thermal spa they had founded. Because no other isolated population or fossil records were known at that time it quickly became a widely accepted explanation for the existence of the geographically isolated population near Schlangenbad (Gomille 2002). It was then cited by many authors, e.g., Brehm (1869) or Dürigen (1897) (both ex Gomille 2002), however soon it has appeared to be unsustainable due to a number of discrepancies. At first, the Aesculapian snake is found also around spas that were founded a hundred years after Roman expansion and also in areas that Romans have never reached (for example Karlovy Vary). Thus many other authors do not support this theory, such as Boulenger (1913), Reinhard (1938), Štěpánek (1949) etc. Moreover, further study has revealed that *Elaphe quatuorlineata* (Lacépède, 1798) rather than *Zamenis longissimus* might have been the cultic snake of Old Romans (Bodson 1981). However this Roman theory is still widespread among people as inferred from numerous web-based references.

Apart from the central Roman theory many local hypotheses attempt to explain the origin of the Bohemian isolated population near Karlovy Vary that are mainly spread by local people. The first theory about introduction by the Count of Buquoy was already mentioned above. This should have been recorded in chronicle by Mr. Döbler but has never been confirmed (Mikátová & Zavadil 2001). The theory has been fist mentioned by Šolcová-Danihelková (1966). Another hypothesis accepted by local people is introduction by the Mathoni family around 1880. However, there is no evidence to support even that assumption. Introduction by Avramides, a Greek merchant who worked in mineral water company in Korunní Kyselka is the last hypothesis. If this were true, the introduction should have happened in first half of the 20th century. The theory is inconsistent with regard to the fact that the first specimen was already captured in 1880. Furthermore, John Bey Avramides several times called specialists attention to the rare occurrence of this snake (e.g., Reinhardt 1938) and hence it is very unlikely that he would have forgotten to mention that he introduced them himself.

The fact that people really tried to introduce Aesculapian snake in many places in Europe might have contributed to formation of various origin hypothesis even of natural populations. The oldest known case of intentional introduction happened close to Schlitz in 1853/1854. Here the Count of Görtzu released circa 40 animals. This population reproduced for the next tens of years but eventually became extinct (Böhme 1993). Jaeschke (1971) was the last one who observed this species at this locality. In the area of the present Czech Republic there were several attempts during the 1980s to introduce the species at localities where it did not occur naturally: for example near Vráž u Berouna and around Slapy Dam (Mikátová & Zavadil 2001), which were unsuccessful in both cases. However, there is an introduced population in north Wales in Great Britain (Edgar & Bird 2005) and in 1994 there was a first announcement about an illegal introduction in Switzerland in a vineyard near the Lac de Bienne (Hofer 2001).

CURRENT STATUS AND FUTURE PROSPECTS

According to Böhme (1991a), herpetofauna of Central Europe is nowadays in withdrawal phase after their maximal expansion in Holocene climatic optimum, so isolated populations are naturally threatened by range contraction caused by climatic deterioration since the Atlantic period of Holocene. The range of the Aesculapian snake has been slowly contracting since this period. However, this natural and gradual process can be made significantly faster with anthropogenic pressure. Habitat alteration and destruction, intensive agriculture or forestry, land consolidation, urbanization, and quarry recultivations are among the most serious threats (Waitzmann 1993). On the other hand, the opposite processes as leaving agricultural land without care and succession leads also to a habitat that is unfavourable for snakes. These factors may have been the reason for the extinction of the Danish population that went extinct in the 19th century, although natural habitat and climatic changes could have also been important. However, an isolated population on the Swiss-German border near Basel and a population near Zloty Potok and Zamojszczyzna in Poland became extinct only a few decades ago. At the latter locality the Aesculapian snake was still described as a frequently met snake in 1910–1912 (Najbar 2000b). The situation of the Polish isolated population is undoubtedly the most critical among recent isolated populations with no chance for recovery. According to Najbar (2000b, 2004a) the territory habited by *Zamenis longissimus* decreased rapidly during the last few decades. Moreover, the territory split to three separate areas that do not appear to communicate with each other. The core area inhabited by Aesculapian snake used to be up to 57 km^2 in post-war term, then 8.5 km^2 later in 1990–1995 and in the years 1999–2003 the area shranked only to 4.0–4.5 km^2 (Najbar 2000b, Najbar 2004a). The same trend can be seen in the numbers of specimens observed in different periods. The first estimations made in the 1990s talked about more than 200 animals, today it is roughly 75 specimens divided into three separated areas Najbar (2000b, 2004a). Even very strict conservation measures that came into effect in 1995 probably will not reverse the decreasing trend.

On the other hand, German isolated populations have been studied intensively since the 1980s. The population near Schlangenbad was studied by Heimes (1988, 1989, 1991), near Hirschhorn by Waitzmann (1989) and Gomille (2002) and the last one near Burghausen is less explored in comparison to them however sufficient study has been completed (Assmann & Drobny 1990). These authors did not feel confident to establish population size estimates and dynamics of German isolated populations due to lack of prior data for comparison. But the abundance can be deduced from the number of captured animals. The number is 190 specimens during seasons 1988 and 1989 (Waitzmann 1989) and 113 animals in 1998 (Gomille 2002) near Hirschhorn and 215 exemplars in 1988 (Heimes 1989) near Schlangenbad. These early studies certainly contribute to management and today's positive status.

The Bohemian population in the Ohře valley has been under some type of study since the 1970s (Haleš 1975, 1984, 1987, Janoušek 1979, Šapovaliv & Zavadil 1990, Zavadil & Šapovaliv 1990). According to Haleš (1987), a rapid decline in abundance has been documented since the 1980s, mainly due to habitat alteration and destruction. Another point worth mentioning is the unusually high degree of synantropism (Haleš 1987). The same was observed in Germany as snakes live alongside people: inhabiting their gardens, outhouses, barns and even garrets (Waitzmann 1993). This synantropism might be consequence of unusually high population density, harsh climatic conditions and progressive succession. Managed dwelling areas can provide enough food and cover and also manmade egg-laying sites that are highly important in these climatically less favourable conditions.

In conclusion, the isolated populations of *Zamenis longissimus* are highly vulnerable to extinction because of their position above the northern range limit. Considering the fate of most other isolated populations in Europe it is evident that the isolated population in the Czech Republic may be close to following the same trend as those in, e.g., Poland. Once the isolated populations become extinct, there is no possibility of immediate natural restoration due to the spatial remoteness and habitat separation from the nearest extant populations. However, the loss of isolated populations may have important consequencies for the entire species. For example, isolated northerly populations may show various types of ecological and physiological adaptations to less favourable climatic and environmental conditions that could be important for the response of the species to changing climate but that would be lost with the extinctions of these populations. Therefore, all effort should be made to preserve these populations and to understand their ecological requirements and evolutionary adaptations to the environment they occupy.

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