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FOSSIL RECORDS OF *MARSTONIOPSIS INSUBRICA* (KÜSTER, 1853) SUGGEST ITS WIDE DISTRIBUTION IN CENTRAL EUROPE DURING THE EARLY HOLOCENE

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INTRODUCTION

The rare and endangered freshwater snail *Marstoniopsis insubrica* (Küster, 1853) (Gastropoda: Amnicolidae) today has a highly disjunct distribution in Europe (Fig. 1). It is more or less continuously distributed throughout the northern part of Europe (Glöer, 2002), where it inhabits alkaline lakes and stagnant parts of large rivers. Its status in Britain is equivocal, but some occurrences there are clearly modern introductions (Preece & Wilmot, 1979; Kerney, 1999). Isolated records are known from northern Italy (Cossignani & Cossignani, 1995) and Switzerland, but the Swiss site has now been destroyed (Turner et al., 1998). The great distance between the main and continuous range of the species and the Alpine outlier (more than 500 km away) led to the description of two distinct species: *Marstoniopsis scholtzi* (Schmidt, 1856) living in the north of Europe and *M. insubrica* (Küster, 1853), from the Alps. Recent work based on mitochondrial COI gene of these two species showed that they belong to a single species (Falniowski & Wilke, 2001), with the latter name having priority. Falniowski & Wilke (2001) suggested several scenarios of postglacial dispersal that may have resulted in this allopatric distribution. They suggested that the modern distribution did not indicate dispersal along waterways or other corridors linking northern Europe and the Alps. They also claimed that a lack of Pleistocene evidence makes it difficult to reconstruct population history and historical pathways of dispersal. A new Holocene record from Slovakia, described here, has been radiocarbon-dated to the early Holocene adding to the short list of other records from central Europe, all of which were hitherto poorly dated. These records can shed new light on the origin of its present disjunct distribution. Although rare fossil records are known in central Europe from the Eemian interglacial (Alexandrowicz & Alexandrowicz, 2010; V. Ložek pers. comm.), the critical evidence

for understanding the recent distribution are needed from the time period after the end of the last glaciation.

METHODS AND FOSSIL RECORDS

We abstracted all known published Holocene fossil records of *Marstoniopsis insubrica*, previously reported as *M. scholtzi*. The earliest Holocene record close to the modern distribution has been reported from central-east Germany by Fuhrmann (1973). Ten years later, Krolopp & Vörös (1982) published the first Holocene fossil find for Hungary, and subsequently several more records have been made throughout the western part of Hungary (Krolopp, 1986; Fűköh, 1988, 2000, 2001, 2008). Although none of these other records have been radiocarbon-dated, they appear to be early Holocene, mostly Boreal or around the Boreal/Atlantic transition (Krolopp, 1986). These ages are consistent with the new record from southern Slovakia, which is also the first for this country. The studied Parížske močiare deposits represent a full Holocene succession through a calcareous marsh, located NE of the village of Nová Vieska (47°52'25"N, 18°27'44"E) in Slovakian Danube Lowland. The age was determined using radiocarbon dating of *Carex* sp. seeds associated with the two shells of *Marstoniopsis insubrica* (Fig. 2) from 495–500 cm in the profile, the only level yielding this species. The uncalibrated date was 9760 ± 30 yrs BP (lab code UGAMS 10035), which gave a calibrated age (95.4% probability) between 11240–11165 cal. yrs BP using the IntCal09 calibration curve (Reimer et al., 2009) in the OxCal 4.1 program (Bronk Ramsey, 2009).

RESULTS AND DISCUSSION

The early Holocene records from Hungary together with the new record from southern Slo-

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FIG. 1. Distribution of *Marstoniopsis insubrica* in Europe based on available literature data: Great Britain (Kerney, 1999), Switzerland (Turner et al., 1998), Italy (Boeters, 1973; Giusti & Pezzoli, 1980; Dalfredo & Maiolini, 2003), northern and central Europe (Falniowski, 1987; Fückoh, 1988, 2000; Glöer, 2002; Glöer & Meier-Brook, 2003; Krolopp, 1986). Distribution of other three species of the genus *Marstoniopsis* in Europe is shown: MA, *M. armoricana* (Paladilhe, 1869) known from western France (Pasco, 2005; Gargominy et al., 2011); MC, *M. croatica* Schütt, 1974, recorded at few sites in Slovenia (Schütt, 1974); and MV, *M. vrbasi* Bole & Velkovrh, 1987, known only from the type locality in Bosnia and Herzegovina (Bole & Velkovrh, 1987), which has been probably destroyed.

vakia fill a distribution gap between northern and southern present populations (Fig. 1). Because of the presence of continental ice sheet that covered much of northwestern Europe during the last cold stage, it is likely that the modern distribution of *M. insubrica* in most of northern Europe is of postglacial origin. These fossil records can therefore suggest a possible dispersal pathway of postglacial spreading from southern refugia to the north, in a southeastwards direction along the Alps, though the location of its glacial refugia are unknown. Although they cannot identify the location of refugia, they enable us to exclude some speculations about the origin of northern populations and also explain the surprisingly low genetic differentiation between northern and southern populations reported by Falniowski & Wilke (2001). Their hypothesis of passive long-distance dispersal by birds does not seem to be parsimonious. During the early Holocene, possibly up to the beginning of the Atlantic period (Krolopp, 1986), the species may have continuously occupied a large area from Italy into northeastern Europe. The age of these

records, close to the end of the last glaciation, might further support the hypothesis of periglacial survival in the Pleistocene periglacial zone of central Europe (Falniowski & Wilke, 2001). Interestingly, the southernmost fossil record from Hungary is located only 150 km from an isolated population of *Marstoniopsis* in Slovenia, originally described as a distinct species, *M. croatica* Schütt, 1974. This raises a question on the status of that species, a resolution that must await further molecular data. In this respect, another endemic species, *M. vrbasi* Bole & Velkovrh, 1987, described from a single site in Bosnia and Herzegovina (Bole & Velkovrh, 1987) also requires taxonomic reconsideration. The same is true for the fourth member of the genus, *M. armoricana* (Paladilhe, 1869), known from western France (Pasco, 2005; Gargominy et al., 2011).

In conclusion, the records of *Marstoniopsis insubrica* from the early Holocene suggest an alternative model of postglacial dispersal. It is possible, that this cold adapted species (data in Falniowski & Wilke, 2001) survived the last glacial maximum in the periglacial zone of temperate Europe and also possibly south of the Alps. After the deglaciation it might have spread northwards, but left several isolated populations in southern interglacial refugia behind (Stewart et al., 2010). Similar postglacial scenarios have been suggested for some cold tolerant *Vertigo* species that display remarkably similar distribution patterns in Europe (Kerney et al., 1983; Schenková & Horsák, 2013). As these four recently isolated southern populations of *Marstoniopsis* were originally described as distinct species, further molecular research is needed to resolve the question of their refugial character. We should test a hypothesis that these geographically limited species might have originated from much wider distribution of *M. insubrica* in central and southern Europe during the Late Glacial and early Holocene.



FIG. 2. Shell of *Marstoniopsis insubrica* (Küster, 1853) from the Parížske močiare Holocene succession (SE Slovakia); the material is deposited in M. Horsák's personal collection (Brno). Shell height/width: 1.80/1.25 mm. Photo by M. Horsák.

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