Evolutionary Systematics. 10 2026, 275–281 | DOI 10.3897/evolsyst.10.205134

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EVOLUTIONARY SYSTEMATICS

Origins of the northern microrefugial populations of the giant centipede *Scolopendra cingulata* Latreille, 1829 revealed (Chilopoda, Scolopendromorpha, Scolopendridae)

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https://zoobank.org/41C822C2-338E-42AB-B270-90B5E493D5D2

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Academic editor: Danilo Harms ♦ **Received** 23 June 2026 ♦ **Accepted** 15 July 2026 ♦ **Published** 24 July 2026

Abstract

Catastrophic events like climatic changes can lead to a drastic decline and loss of populations in widespread species. Small refugia can shield relict populations from extinction and are of great importance for maintaining genetic diversity and for recolonization events. In the giant centipede *Scolopendra cingulata* Latreille, 1829, widely distributed along the Mediterranean Sea, the northern-most populations occur in isolated microrefugia in Austria and Hungary. The origin and relationships of these populations remain largely unknown. Here we describe a second, previously unknown, microrefugial population of *S. cingulata* from Austria and provide insights into the evolutionary history of the northern-most populations of the species based on molecular analyses (COI) of 16 populations. Our results show that the Austrian and Croatian populations are closely related, while genetically distinct from the Hungarian and Romanian representatives. Therefore, we conclude that the northern-most populations of *S. cingulata* are relicts from multiple independent post-glacial recolonization events from southern refugia.

Key Words

DNA barcoding, microrefugia, relict species, soil arthropods

Introduction

The thermophilous centipede *Scolopendra cingulata* Latreille, 1829 is one of the largest, most widely distributed, and best studied European centipedes (e.g. Simaiakis et al. 2011; Simaiakis et al. 2012; Oeyen et al. 2014; Faraone et al. 2025). The species is famous for large intraspecific variations in the color pattern of different populations (Faraone et al. 2025), and infamous for its painful bite. Species of the genus *Scolopendra* are the only European myriapods which can harm (e.g. Yao et al. 2013) or even cause the death of humans (Serinken et al. 2005; Voigtländer 2011).

S. cingulata shows a widespread distribution along the Mediterranean Sea (Lewis 2010), with isolated population at its northern limit of distribution in Romania, Hungary and Austria. These populations are surviving in microrefugia, which are interpreted as relicts from a previous wider distribution during the times following the post-glacial climatic optimum (Attems 1930; Franz 1936, 1938; Rabitsch and Essl 2009). In contrast to the main area of occurrence, where the species can be very

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common, these relict populations are small in the number of individual specimens present and occupy only a very limited area. These relict populations of *S. cingulata* are often considered to be locally endangered, especially by habitat alteration (e.g. for Hungary see Dányi 2006; Korsós et al. 2006). The recent rediscovery of a single Austrian population prompted molecular analyses which revealed that the isolated populations in Romania, Hungary and Austria likely have independent origins (Oeyen et al. 2014). However, no clear hypothesis could be proposed regarding the origin of the Austrian population specifically.

As Austria, for such a small country, has a very large and active community of Naturalists and Zoologists, we hoped that our initial publication would lead to reports of additional populations of this conspicuous large invertebrate. This was indeed the case, as Prof. E. Christian (University of Natural Resources and Life Sciences, Vienna, Austria) reported a second locality (Christian, pers. comm.), 5 km distant from the previously described population (Fig. 1). This second locality was visited in the company of Dr. Andreas Ranner from the "Amt für Natur- und Umweltschutz der Burgenländischen Landesregierung" in 2015 and the presence of *S. cingulata* was confirmed. Permission was given to remove two juvenile specimens from the population, deposited as vouchers at the ZFMK, for which their genetic barcode could be sequenced (Hebert et al. 2003).

Figure 1. Second previously unknown population of *Scolopendra cingulata* in Austria. **A.** Adult; **B.** Juvenile, showing its typical coloration; **C.** Refugial habitat in Austria.

Table 1. Material studied. Asterisk (*) marks specimens newly sequenced for this study. ZFMK = Zoological Research Museum A. Koenig, Bonn, Myriapoda collection; GBMYR = Zoological State Collection Bavaria, Munich, Myriapoda collection.

Map #	Sample ID	Voucher #	Species	Locality	Accession numbers
1	Austria 1	ZFMK-Sco-1	*S. cingulata*	Austria, Burgenland, Leitha Mts.	KJ812067
1	Austria 2	ZFMK-Sco-2	*S. cingulata*	Austria, Burgenland, Leitha Mts.	KJ812068
1	Austria 3	ZFMK-Sco-3	*S. cingulata*	Austria, Burgenland, Leitha Mts.	KJ812069
1	Austria 4	ZFMK-Sco-4	*S. cingulata*	Austria, Burgenland, Leitha Mts.	KJ812070
1	Austria 5	ZFMK-Sco-5	*S. cingulata*	Austria, Burgenland, Leitha Mts.	KJ812071
1	Austria 6	ZFMK-Sco-6	*S. cingulata*	Austria, Burgenland, Leitha Mts.	KJ812072
1	Austria 7	ZFMK-Sco-7	*S. cingulata*	Austria, Burgenland, Leitha Mts.	KJ812073
1	Austria 8	ZFMK-Sco-8	*S. cingulata*	Austria, Burgenland, Leitha Mts.	KJ812074
1	Austria 9	ZFMK-Sco-9	*S. cingulata*	Austria, Burgenland, Leitha Mts.	KJ812075
1	Austria 10	ZFMK-Sco-10	*S. cingulata*	Austria, Burgenland, Leitha Mts.	KJ812076
2	Hungary 1	ZFMK MYR 01559	*S. cingulata*	Hungary, Vértes Mts., Csákberény, Bucka	KJ812077
2	Hungary 2	ZFMK MYR 01560	*S. cingulata*	Hungary, Vértes Mts., Csákberény, Bucka	KJ812078
2	Hungary 3	ZFMK MYR 01561	*S. cingulata*	Hungary, Vértes Mts., Csákvár, Szólókő	KJ812079
3	Greece Kavala 1	ZFMK-Sco-14	*S. cingulata*	Greece, Kavala	KJ812080
3	Greece Kavala 2	ZFMK MYR	*S. cingulata*	Greece, Kavala	KJ812081
4	Greece Port Lagos 1	ZFMK-Sco-13	*S. cingulata*	Greece, Nestos Delta, Port Lagos	KJ812082
5	Greece_Port Lagos 2	ZFMK-Sco-15	*S. cingulata*	Greece, Nestos Delta, Port Lagos	KJ812083
6	Greece Nisyros	-	*S. cingulata*	Greece, Nisyros	JN688421
7	Greece Koufonisi	-	*S. cingulata*	Greece, Koufonisi	JN688413
8	Greece Paros	-	*S. cingulata*	Greece, Paros	JN688427
9	Greece Anafi	-	*S. cingulata*	Greece, Anafi	JN688398
10	Greece Amorgos	-	*S. cingulata*	Greece, Amorgos	JN688397
11	Romania	ZFMK-Sco-11	*S. cingulata*	Romania, Anina	KJ812086
12	Turkey Troy	ZFMK-Sco-12	*S. cingulata*	Turkey, Troy	KJ812084
13	Turkey Izmir	ZFMK MYR 583	*S. cingulata*	Turkey, Izmir	KJ812085
14	France	ZFMK MYR 1593	*S. cingulata*	France, Banyuls-sur-mer	KJ812087
X	Austria New 1*	ZFMK MYR 4832	*S. cingulata*	Austria, Burgenland, N. Lake Neusiedl	MN447232
X	Austria New 2*	ZFMK MYR 4833	*S. cingulata*	Austria, Burgenland, N. Lake Neusiedl	MN447233
17	S. canidens 1	-	*S. canidens*	Greece, Serifos	JN688441
18	S. canidens 2	-	*S. canidens*	Greece, Sifnos	JN688442
19	Croatia	GBMYR072-13	*S. cingulata*	Croatia: Istra, Stella Maris 2 km N Umag	KU497147

Here we report a second locality of *S. cingulata* in Austria (Fig. 1) and a comparative analysis of barcode sequences (COI) derived from this population and previously published sequence data from Austria, Croatia, Hungary, Romania, Greece, Turkey, and France (Simaiakis et al. 2011; Oeyen et al. 2014; Wesener et al. 2016; Table 1) to provide new insights into the origin of the microrefugial northern populations of the Giant Centipede.

Material and methods

Collecting

Two juvenile specimens of the second Austrian population, near Lake Neusiedl, Burgenland, were collected by hand and preserved in 96% ethanol by W. Böhme et al. on 19.viii.2015. Both specimens are stored as vouchers in the collections of the ZFMK (Table 1). The exact localities of *S. cingulata* in Austria are not disclosed in this publication due to the fact that wild caught specimens are commonly offered for sale in the pet trade and that private collectors could potentially severely deplete the small populations of this long-living charismatic invertebrate.

Sequencing

DNA extraction from the two specimens of the second Austrian population, amplification of the COI gene fragment, and sequencing was conducted under identical conditions to those of earlier studies (Oeyen et al. 2014; Moritz and Wesener 2017; Wesener 2019). The COI JJ primer (Astrin and Stüben 2008) was used for both PCR and sequencing. Sequences were uploaded to GenBank and are publicly available under the accession numbers MN447232 (ZFMK-MYR4832) and MN447233 (ZFMK-MYR4833).

Taxon sampling

In addition to the two newly sequenced *S. cingulata* sequences, we included a published sequence from a Croatian *S. cingulata* (Wesener et al. 2016), as well as the

dataset from Oeyen et al. (2014). Two *S. canidens* sequences were included as outgroup. The final dataset consisted of 31 sequences (Table 1), 29 of which were *S. cingulata* from 16 different populations from France, Croatia, Austria, Hungary, Romania, Greece, and Turkey (Table 1).

Alignment

Sequences were aligned using the MUSCLE algorithm (Edgar 2004) under default settings as implemented in Geneious (Biomatters). Missing ends were filled with N's. There were a total of 647 positions in the final dataset, of which 442 sites were invariant.

Distance analyses

Genetic distances were analyzed in MEGA X (version 10.1; Kumar et al. 2018). The absolute number of differences as well as individual and mean group uncorrected pairwise genetic distances were computed considering $1^{st}+2^{nd}+3^{rd}$ codon positions. All ambiguous positions were removed for each sequence pair.

Tree reconstruction

The best fitting maximum likelihood model was selected based on the BIC criterion using ModelFinder (Kalyaanamoorthy et al. 2017) as implemented in IQ-TREE (version 1.6.8; Nguyen et al. 2015). Tree reconstruction was conducted in IQ-TREE (version 1.6.8) under the maximum likelihood criterion, using the selected model (TIM2+F+G4; BIC: 6046.58), and branch support was estimated using 1000 non-parametric bootstrap replicates.

Results

The second Austrian population of *Scolopendra cingulata*

Similar to the first population, the adults (Fig. 1A) and juveniles (Fig. 1B) of the second population of *S. cingulata* were found on an exposed south-facing slope with smaller rocks and shrubs (Fig. 1C). The adult and juvenile coloration is identical to what was described for the first Austrian population (Oeyen et al. 2014). The adults are amber colored, with yellow legs, and a dark longitudinal dorsal stripe (Fig. 1A). The juveniles are greyish-blueish, with an orange head and last tergite, blue legs, and a black longitudinal dorsal stripe (Fig. 1B). Genetically, the two specimens of the second Austrian population show different haplotypes in the COI sequence, with substitutions at 11 positions (1.7%; Suppl. material 1: tables S1, S2). Haplotype 1 is identical to some of those found in specimens of the first Austrian population (max. p-distance: 1.4%, Fig. 2). Haplotype 2 differs from the first Austrian population in 4–19 positions (max. p-distance: 3.0%). The Austrian population differs from the Croatian specimen by just 2.0% (mean between group p-distance), while the distances to the more eastern populations are higher: 6.0% to Romania and 7.6% to Hungary (Suppl. material 1: table S1).

Evolutionary history of Austrian *S. cingulata*

The observed genetic distances are mirrored in the phylogenetic tree. The Croatian *S. cingulata* specimen and the haplotype 1 of the second Austrian population are recovered in a monophyletic clade including the members of the first Austrian population (Fig. 3). The second, more distinct haplotype, of the second Austrian

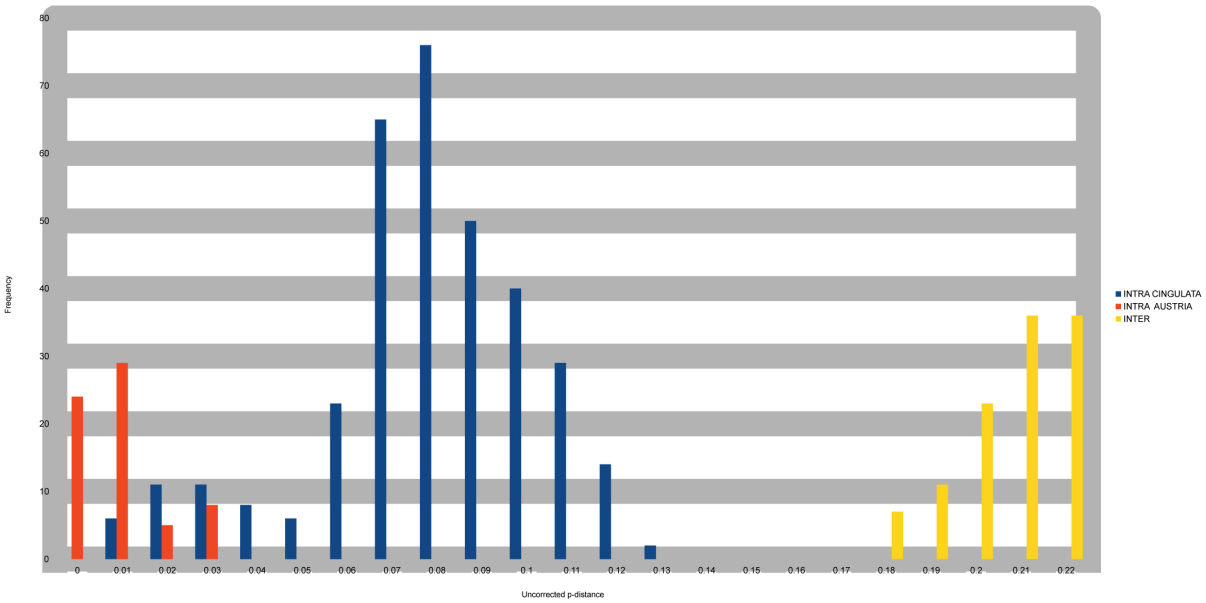

Figure 2. Genetic variability within all studied *Scolopendra cingulata* (blue), within the Austrian *S. cingulata* (red) and genetic distance to *S. canidens* (yellow). Frequency of uncorrected P-Distances considering $1^{st}+2^{nd}+3^{rd}$ codon positions (see also Suppl. material 1: table S1).

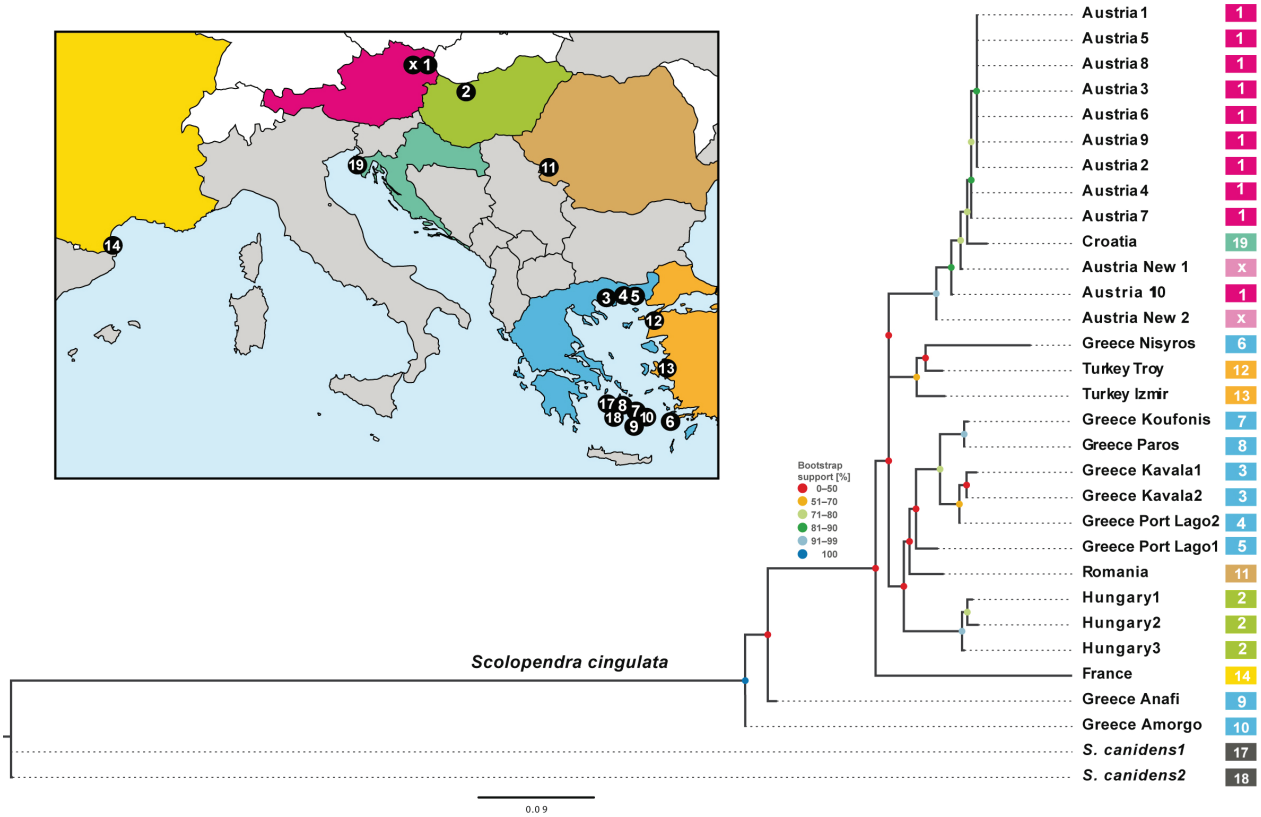

Figure 3. Location and phylogenetic relationship (ML) of the studied populations of *Scolopendra cingulata*. Numbers in circles correspond to localities in Table 1. X indicates the second, previously unknown population in Austria.

population is recovered as the earliest branching member of the well-supported Croatian-Austrian clade (Fig. 3). The Hungarian and Romanian *S. cingulata* specimens are recovered in a separate clade, together with the Greek mainland populations, as well as specimens from the Greek islands Koufonisi and Paros (Fig. 3). This group, however, does not receive very strong branch support.

Discussion

A previous study on the first rediscovered population of the Austrian *S. cingulata* showed that the current distribution and observed relationships of the northern-most populations could neither be explained by the speciation-by-distance scenario proposed by Attems (1930), nor could it propose a clear alternative hypothesis (Oeyen et al. 2014). The inclusion of specimens of the second Austrian population, but especially of the *S. cingulata* specimen from Croatia provides further evidence for the origins of the isolated Austrian populations of *S. cingulata*. The close relationship of the Austrian and Croatian *S. cingulata* indicates that the northern-most populations of the species were independently colonized, possibly from separate refugia, after the last glacial period. At the very least, two separate recolonization routes must be hypothesized. One from the west, via Croatia to Austria, and one from the east, via Greece or the Balkans to Hungary and Romania. This hypothesis is in agreement with what has been suggested for multiple groups of insects (Varga 2010). However, a denser geographic sampling, as well as population genetic markers with a higher resolution are necessary to fully unravel the phylogeographic history of the species in the region.

Relict populations of widespread species have been shown to harbor unique genetic information (Cassel-Lundhagen 2010). This was found to be true for the first rediscovered population of *S. cingulata* in Austria. Here, the observed genetic distances within the population were low (max. uncorrected p-distance: 1.3%), but constituted a unique haplotype within the species (Oeyen et al. 2014). The second locality expands the genetic diversity found within Austria notably and highlights the importance of these small and likely fragile populations in the context of the overall genetic diversity of a species. The maximum intraspecific p-distance of 11.9% (Austria5-France) is in line with earlier studies which found an average p-distance of 11% between clades in of *S. cingulata* in southern Italy (Faraone et al. 2025).

Although to our knowledge, no attempts have been made to quantify and monitor the populations of *S. cingulata* in Austria, some insights can be gained from the yearly excursion reports of the same team of researchers. While a large number of adults and sub-adults were found in 2015 and 2016 (Koch and Böhme 2016; Koch and Böhme 2017), the report from 2017 showed an unexpected rarity of the species (Böhme et al. 2018). This was again the case when one of us (LM) visited the site in 2018 and only juveniles could be found. It is therefore possible that the populations are overall small and subject to fluctuations in population sizes.

Given the unique genetic information found in these likely small and fragile populations, their habitats should be seen as important targets for protection and conservation measures. This notion is reinforced by the presence of other thermophilic and potentially endangered species in the same habitat (Koch and Böhme 2016). Amongst others, the first population of *S. cingulata* in Austria shares its habitat with the only known Austrian population of the centipede *Cryptops croaticus* (Wesener et al. 2016) as well as the endangered ground beetle *Carabus hungaricus* (Müller-Motzfeld 2004; Böhme et al. 2014; Koch and Böhme 2016).

Acknowledgements

We thank the GBOL-Team in Munich (ZSM) and Bonn (ZFMK) for their collecting and sequencing efforts and Claudia Etzbauer (ZFMK) for assistance in the molecular lab. The Landesregierung Burgenland is thanked for collection permits and we especially thank Dr. Andreas Ranner from the "Amt für Natur- und Umweltschutz der Burgenländischen Landesregierung" who personally visited the site in 2015. Furthermore, we express our gratitude to Prof. Dr. Christian who reported the new locality and to Prof. Dr. Böhme and all participants of the Neusiedl Lake expedition.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

Artificial Intelligence (AI) use

The authors accept full responsibility for the content of the manuscript, including the disclosure of any use of AI.
No AI tools were used in the preparation of this manuscript.

Funding

No funding was reported.

Author contributions

Conceived and designed the experiments: JPO LM TW. Performed the experiments: JPO. Analyzed the data: JPO TW. Contributed reagents/materials/analysis tools: JPO LM TW. Wrote the paper: JPO, LM, TW.

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Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

Supplementary material 1

Supplementary information

Authors: Jan Philip Oeyen, Leif Moritz, Thomas Wesener
Data type: docx
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