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New records and an updated overview of the distribution of *Acantholycosa norvegica sudetica* (L. Koch, 1875) in Germany, with notes on DNA barcodes and its taxonomic status

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Abstract

The wolf spider *Acantholycosa norvegica sudetica* (L. Koch, 1875) is a relict species in central Europe, exclusively restricted to screes. Knowledge about the species is limited due to the challenging sampling conditions in its restricted habitat. Here, we present new records for the species based on a large field campaign, literature and database research and provide an updated distribution map for Germany. We provide new records for the federal states of Saxony and Thuringia. With this, the species has now been reported for seven federal states in Germany and most low mountain ranges therein. Additionally, we analyzed DNA barcodes to determine whether local isolated populations exhibit genetic differentiation. Our analysis found no evidence of differentiation among the populations, suggesting that gene flow possibly remains prevalent despite pronounced geographic isolation. Yet, our genetic data suggests that *A. norvegica sudetica* deserves species status as it is diverged from the nominal form. It is clearly distinct from the nominal form *A. norvegica* (Thorell, 1872), both genetically and by its exclusiveness to screes. Accordingly, we propose raising it to species status, *A. sudetica* (L. Koch, 1875) **stat. nov.** It is a characteristic spider species of threatened EU habitat types and deserves protection of its populations and their unique habitats.

Keywords: block screes • COI • faunistics • low mountain ranges • Lycosidae • specialist species • wolf spiders

Introduction

Wolf spiders (Lycosidae) are a common group of spiders in most parts of the world, with many rather generalistic species, most abundant in open habitats with low vegetation and therefore sometimes called grassland spiders (Jocqué & Alderweireldt 2005). In turn, most species of the lycosid genus *Acantholycosa* are specialized scree dwellers (Fomichev & Marusik 2018). We currently know 38 species and one subspecies (World Spider Catalog 2026), which can only be found in the northern hemisphere. Most of them populate montane or boreo-alpine regions (Dahl & Dahl 1927; Buchar & Thaler 1993), with many endemic species in the Altai Mountains in Southern Siberia and the Sikhote-Alin Range in the Russian Far East (Marusik, Azarkina & Koponen 2004; Fomichev & Omelko 2020), where they live in screes and stony tundra (Buchar & Thaler 1993; Fomichev & Marusik 2018). In Europe, only three species are known: *Acantholycosa lignaria* (Clerck, 1757), which is linked to dead wood and is very rare in Germany, *A. pedestris* (Simon, 1876), which is only known from screes over 2000 m (Thaler & Buchar 1994), and *A. norvegica* (Thorell, 1872), which includes the nominate species *A. norvegica* (Thorell, 1872) and the subspecies *A. norvegica sudetica* (L. Koch, 1875), which was defined as the type species of *Acantholycosa* by Dahl, (1908: 197).

Acantholycosa norvegica sudetica is a highly specialized subspecies (Fig. 1A), which is also reflected in its distribution: it is only known from Central Europe, France, Italy, Romania (World Spider Catalog 2026) and is strictly confined to screes, which act as cold glacial refugia in low mountain ranges. Screes are characterized by a very special geomorphology and microclimate. They are composed of rocks without any soil substrate in between, generating a unique micro-cave system (Fig. 1B–E). The widely open surface allows a special airflow, creating a kind of natural air conditioning. In the winter period, warm air escapes from the openings of screes, leading to an inflow of cold air at their feet. This, in turn, enables conservation of ice cores in the depth. In summer, cold air flows out at the scree's lower parts, locally leading to a cold microclimate

(Molenda 1996; Möseler & Wunder 1999). It has even been suggested, that some screes in low mountain ranges may even have permafrost cores inside (Möseler & Molenda 1999; Gude *et al*. 2003). In contrast to stable cold conditions in the deep hollow parts, the surface of the screes can be heated strongly by the sun, even in cold periods, especially in south-exposed slopes. Screes in the Black Forest (Schwarzwald) reached maximum surface temperatures up to 60°C (Kastner *et al*. 2018). This explains the presence of thermophilous species (Molenda 1996; Fritze & Blick 2010; Růžička & Zacharda 2010). Due to their unique climatic conditions under the surface, screes represent important refuge areas for cold-adapted species and are therefore home to a very specialized fauna composed of periglacial relicts. Hence, screes represent extra-alpine and extra-boreal relic habitats for several species, potentially since ten thousands of years (Blick & Fritze 2010; Höfer *et al*. 2019).

The species assemblages of screes are highly specialized and are composed of species that are exclusively living in the specific micro-habitats of the screes; others have boreo-alpine or alpine distributions. Hence, screes represent structures of high conservation concern due to the uniqueness of their species community and the potential high threat from climate change. Arthropod communities of screes include: cold-adapted carabid species (e.g. *Leistus montanus* Stephens, 1827, *Leistus piceus* Frolich, 1799, and *Pterostichus negligens* Sturm, 1824) (Fritze & Blick 2010; Klesser, Fritze & Husemann 2022), snow flies (*Chionea* spp.) (Blick & Fritze 2009; Bellstedt *et al*. 2014; Klesser *et al*. 2024), *Choleva* (Leiodidae) beetles (Ružicka & Zacharda 1994; Fritze & Blick 2010; Hadulla & Wagner 2016) and rare spiders like *Clubiona alpicola* Kulczyński, 1882, *Attulus rupicola* C. L. Koch, 1837, *Pardosa nigra* C. L. Koch, 1834, *Bathyphantes eumenis buchari* Růžička, 1988, *Wubanoides uralensis lithodytes* Schikora, 2004, and *A. norvegica sudetica* L. Koch, 1875 (see Schikora 2001, 2015; Růžička & Zacharda 2010; Höfer *et al*. 2019).

However, these habitats are nowadays threatened by a combination of ecological succession, changes in anthropogenic land use, and climate change. Although screes are protected habitats by the European Habitats Directive (codes 8110, 8150, 8160) and *A. norvegica sudetica* is known as a characteristic species for this habitat type, little

Mountain Range	Location	2018–2019		2020		Altitude
		A. l.	*A. s.*	*A. l.*	*A. s.*	
Bavarian Forest	Summer-Road to Lusen	6				1200
Bavarian Forest	Farrenberg			2	34	1081
Bavarian Forest	Gr. Rachel			3	2	1348
Bavarian Forest	Lusen		2	1	28	1362
Bavarian Forest	Road to Steinfleckberg			3		1280
Bavarian Forest	Steinfleckberg			1	39	1305
Black Forest	Melkereikopf				13	946
Black Forest	Ochsenkopf				2	920
Erz Mts	Kahleberg		61		33	897
Fichtel Mts	Backöfele		89		29	1027
Fichtel Mts	Haberstein		5		32	907
Fichtel Mts	Platte		6		31	867
Fichtel Mts	Schneeberg2				29	998
Fichtel Mts	Schneeberg3				1	957
Harz	Achtermann				29	922
Harz	Goldenkerklippe				41	813
Harz	Hammersteinklippe		77		39	748
Harz	Mönchskappe		20		29	660
Harz	Odertal		31		31	587
Harz	Wartenberg				9	556
Harz	Wolfswarte		38		41	900
Oberpfalz	Rauher Kulm		71			633
Osthessisches Bergland	Hoher Meissner		18			679
Rhoen Mts	Schafstein		40		35	762
Thuringian Highland	Steinheid		10			695
Thuringian Forest	Jüschnitz		75			559
Thuringian Forest	Lütsche		11		20	550

Table 1: All records, locations, and sampling periods of *Acantholycosa* spp. in this study. *A. l.* = *A. lignaria*; *A. s.* = *A. sudetica*.

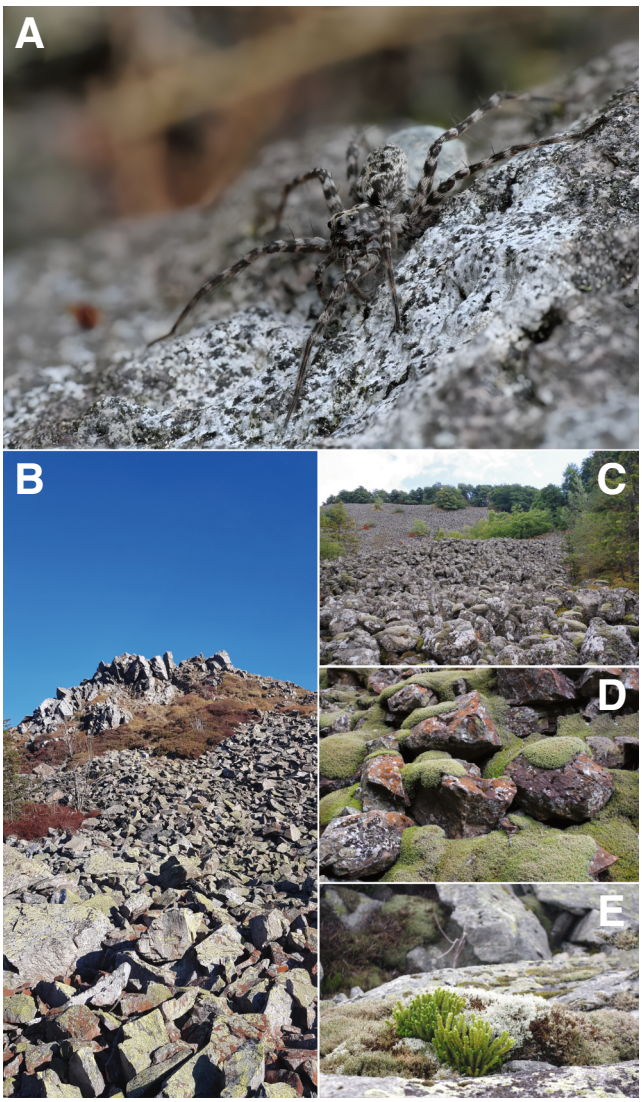


Fig. 1: **A** *Acantholycosa sudetica* stat. nov. female on sunny spot on scree surface carrying a cocoon; colouration provides a perfect camouflage on rocks and lichens; typical habitat in lower mountain ranges: **B** Harz; **C** Rhoen mountains; **D** thousands of entrances to the micro-cave system characterize the surface; **E** plant composition resembles alpine vegetation with *Huperzia selago*, *Racomitrium lanuginosum*, and lichens.



Fig. 2: Hand catches were made with a home-made exhauster constructed of an USB-keyboard vac-cleaner, cut falcon tubes, an acrylic glass pipe, and hot glue. Falcon tubes can be easily replaced.

is known about its distribution, ecology and the condition of the German populations. Its distribution is restricted to central Europe, the Alps, the Swiss Jura, and the Giant Mountains in Poland and the Czech Republic (Kropf 1999; Blick & Fritze 2010; World Spider Catalog 2026). These spiders are perfectly adapted to their habitat with long legs, which allow jumping and very fast hiding in the micro-cave system, and a color which makes them almost invisible on the stones of the scree, which are often covered with lichens (Blick & Fritze 2010; Kastner *et al*. 2018); the colour also presumably helps rapidly warming in the sun. Past studies of screes in Germany revealed the presence of *A. norvegica sudetica* in several low mountain ranges (500–1500 m) in Bavaria (Blick & Fritze 2010; Fritze & Blick 2010), Baden-Württemberg (Molenda 1996; Loch 2002; Kastner *et al*. 2018), Rhineland-Palatinate (Buse *et al*. 2021), Hessen (Homann 1951), and Lower Saxony (Molenda 1996; Schikora 2015). Yet, there is no complete review of the distribution and conservation status of this rare wolf spider.

Hence, we here summarize previously known records for *A. norvegica sudetica* and present several new findings based on a large field campaign, improving our knowledge about its distribution in Germany. Further, we provide extensive barcoding data from different populations from most parts of Germany to test for geographic isolation and we give some insights into the phylogeography and taxonomic status of *A. norvegica sudetica*. We find that *A. norvegica sudetica* is ecologically and genetically clearly distinct from the nominate form and hence raise it to species status (*Acantholycosa sudetica* **stat. nov.** from here on).

Material and methods

Sampling

In 2018–2019, more than 250 pitfall traps (up to 21 at each location, depending on the size of the screes) were deployed in screes at 16 locations in seven lower mountain ranges across Germany (Table 1). Between 14 and 21 traps were placed at each site, aiming at an equal distribution across the habitat (this study focused on molecular work to figure out genetic variation at each locality, not on ecological questions). Clearly structured screes consisting of source rock, scree body, and base of the scree, vegetated and bare areas, including basal areas overgrown by forest, received the same number of traps in each area. In 2019–2020, 18 traps were placed under the same conditions in a further scree at Rauher Kulm in Upper Palatinate/Bavaria.

The pitfall traps each consisted of a plastic cup with a volume of 0.3 L or 0.5 L, which was inserted in substrate between blocks whenever possible or inserted in a proper hole, cut in small wooden boards and placed on and between the blocks at the scree surface (Klesser *et al*. 2024). This construction was used to bridge deeper lacunas and provide a plain runway to the spiders leading to the trap. The cups were filled with 99% propylene glycol (BayWa AG, Munich, Germany) and some drops of detergent. Propylene glycol has been suggested as good DNA conservation fluid for pitfall traps in the past (Höfer *et al*. 2015; Weigand *et al*. 2021), also providing the advantage of lower evaporation compared to ethanol and water-based conservation fluids. Sampling was performed between April 2018 and October 2020. All traps were employed for at least one continuous year in the screes. Material was collected and conservation liquid changed every two to three months. Traps were active for the whole winter season under snow and emptied, as soon as the snow melt allowed safe access to the locality.

If trapping was not successful for *A. sudetica* stat. nov. in a sampling site, observation-based hand sampling was done in 2019 and 2020 using self-built exhausters (Fig. 2). At a few sites, sampling was only done by hand. To catch the wolf spiders, we used modified micro-vacuum cleaners, which received 3D-printed adapters of 20–40 cm long transparent acrylic glass tubes with diameters of 1–1.5 cm. In 2019–2020, we also received hand-collected spiders from collaboration partners from the locations Lütschetalsperre, Schafstein, and Kahleberg, where we had performed the sampling in the year before. Overall, we caught spiders in six federal states in Germany from 10 mountain ranges and 27 locations by hand or by trap (Table 1). Specimens from southern Siberia, eastern Kazakhstan, and the Russian Far East were used as comparative material. A total of seven species of Asian *Acantholycosa* were included. All these spiders were hand collected from screes between 2015 and 2019. Collecting localities of Asian *Acantholycosa* are situated in alpine zones of high mountain ranges (altitude range: 1440–2600 m). The spiders were preserved in 75% ethanol. In total, we collected 1101 specimens of *Acantholycosa sudetica* stat. nov. in Germany for this and further studies. Here, we analysed 90 of these specimens by DNA barcoding and added eight specimens of Russian species as reference, in addition to 21 previously published sequences from BOLD (Tab. S1, 10.5281/zenodo.22922849).

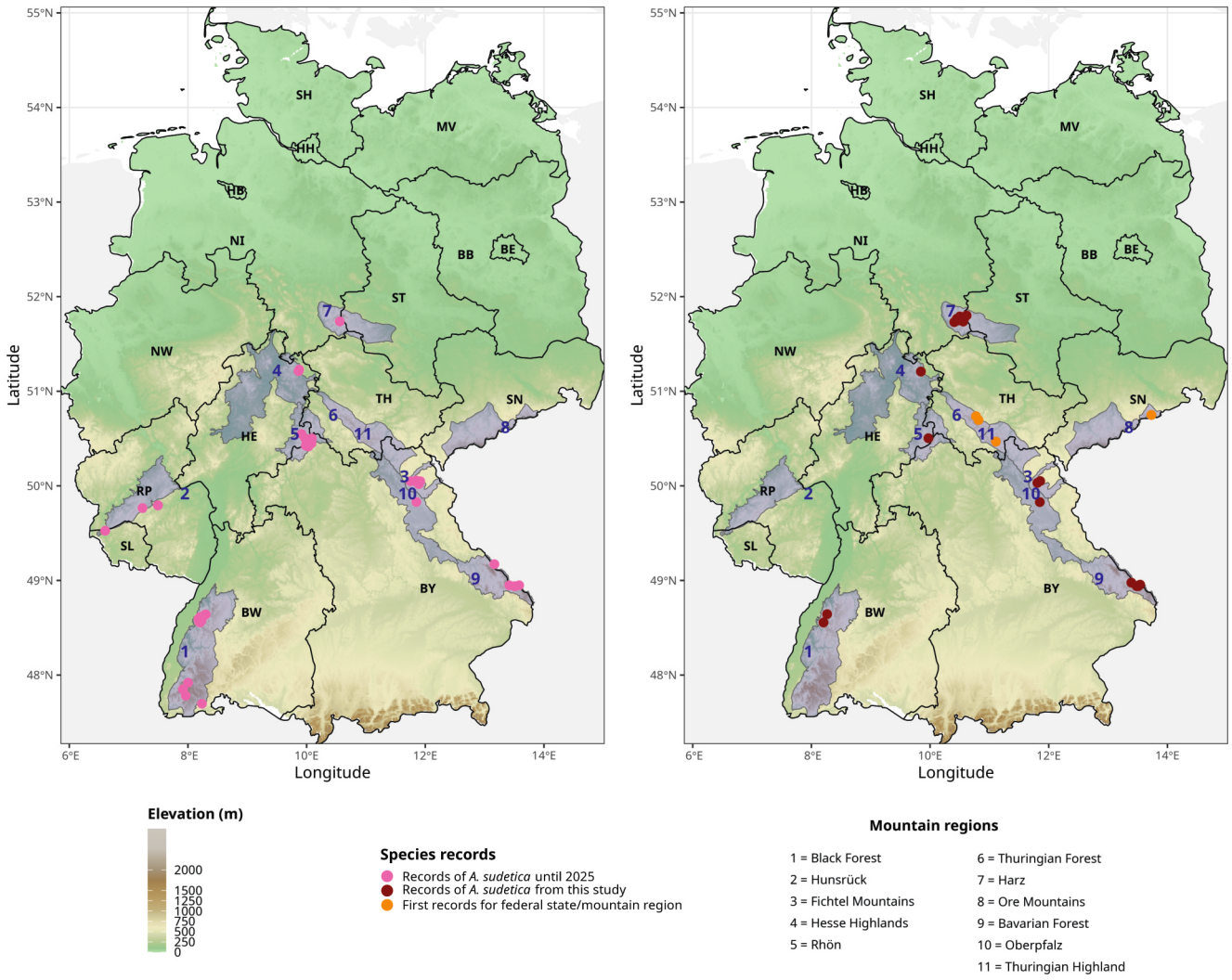


Fig. 3: Distributions of *A. sudetica* stat. nov. known from AraGes Atlas (https://atlas.arages.de/) until 2025 and distribution of confirmed and new records of *A. sudetica* stat. nov. in Germany. The study reports first records from Ore Mountains (Saxony), Thuringian Forest and Thuringian Highland.

Morphological determination was performed in most cases by studying the general habitus and, in locations with sympatric occurrence of other *Acantholycosa* species by dissecting the copulatory organs. Especially in the Bavarian forest, confusion with *A. lignaria* may happen.

Records of *A. sudetica* stat. nov. were mapped in R version 4.6.1 (R Core Team 2026). Administrative boundaries of Germany were obtained from Natural Earth using the R package rnaturalearth (Massicotte *et al*. 2026). Elevation data for Germany were retrieved using elevatr (Hollister *et al*. 2025) and displayed as a hypsometric-tint background. Mountain regions were delineated from the Bundesamt für Naturschutz (BfN) dataset "Naturräumliche Gliederung" Deutschlands.

Further, we added records from published and unpublished former studies (Fritze & Blick 2010; Schikora 2015; Kastner *et al*. 2018) and from communications with other arachnologists. In addition, the database of the *Atlas of the European Arachnids* (Arachnologische Gesellschaft 2025) was checked for missing records.

DNA barcoding

In addition, we performed DNA barcoding for more than 90 specimens. We took one leg of each specimen and used a standard CTAB extraction protocol (Borges *et al*. 2009). The barcoding fragment of the COI gene was amplified using standard PCR procedures with the primers LCO-1490 and HCO-2198 (Folmer *et al*. 1994). PCR was performed with the following setup: 5.7 µl PCR grade water, 2 µl 5x buffer, 0.5 µl of each primer, 0.2 µl dNTPs, 0.1 µl Dream-TaqTM polymerase and 1 µl template. PCR conditions were as follows: activation at 95°C for 5 min, followed by 35 cycles of 30 s denaturation at 95°C, 1 min annealing at 50°C and 1 min elongation at 72°C. Finally, a 10 min elongation step was performed. PCR success was checked on 1.5 % agarose gels stained with GelGreen. Successful products were purified with an enzyme mix consisting of Exonuclease I and Shrimp-Alkaline Phosphatase (ExoSap). Products were sent to Macrogen (Amsterdam, Netherlands) for sequencing.

Analyses

All chromatograms were checked, trimmed and proofread in GENEIOUS v.9 (Kearse *et al*. 2012). MUSCLE (Edgar 2004), as implemented in GENEIOUS, was used to align all sequences. We added eight sequences from Russian specimens, we previously barcoded, two sequences from BOLD (Ratnasingham & Hebert 2007) corresponding to *Acantholycosa solituda* (H. W. Levi & L. R. Levi, 1951), three *Acantholycosa lignaria* (Clerck, 1757) and several lycosid species from other genera to get an outgroup rooting (Supporting Information, Table S1, 10.5281/zenodo.22922849). The resulting alignments were trimmed to a similar length. Overall, we submitted 100 (including eight specimen from Russia) new sequences to BOLD (Supporting Information, Table S2, 10.5281/zenodo.22922849). The final alignment had a length of 569 bp.

We performed tree reconstruction with BEAST v.2.6.2 (Bouckaert *et al*. 2014). The best substitution model, TIM3 + Gamma, was determined using the R package PHANGORN (Schliep *et al*. 2017) in mran v.3.4 (Microsoft 2017) with RStudio v.1.0.143 (RStudio Team 2015). BEAST input files were generated in BEAUti v.2.6.2 (Bouckaert *et al*. 2014) for 100 million generations. The MCMC tree file was checked with Tracer v.1.7 (Rambaut *et al*. 2018) for convergence and ESS (Effective Sample Size) values > 200. The consensus tree was calculated by TreeAnnotator v.2.6.2 (Bouckaert *et al*. 2014) after excluding a burn-in of 10 %.

In a further step, the alignment was reduced to an alignment without outgroups to construct a TCS haplotype network in PopArt v.1.4 (Leigh & Bryant 2015). A traits file, which categorized the different distributions in lower mountain ranges, was generated and mapped on the haplotype network.

Finally, all individuals were grouped by species and p-distances at the species level were calculated using the R package APE (Paradis, Claude & Strimmer 2004).

Results

We recorded *A. sudetica* stat. nov. from ten mountain ranges in 27 out of 32 screes studied from altitudes between 550 m and 1362 m (Fig. 3, Table 1). Our study reports new records from the Ore Mountains (Saxony), Thuringian Forest, and Thuringian Highland (Thuringia).

We could not find the species in stony accumulations without a micro-cave system or in relict screes, which showed a strongly advanced stage of succession and a high degree of closed micro-caves, e.g. at Großer Beerberg in the Thuringian Forest. Further, we were not able to report the species from Rachel Mountain in the Bavarian Forest with certainty: we observed *Acantholycosa* there, but we were not able to catch any individuals and hence cannot exclude *A. lignaria*. In the Bavarian Forest, we found *A. lignaria* sympatric with *A. sudetica* stat. nov. on screes with dead wood present on the surface.

We found both sexes and different generations during the whole year, although in late summer juveniles seemed to be much more common than adults. Even in the winter months, we were able to observe *A. sudetica* stat. nov. on sunny and snowless spots under conditions with air temperature down to 5°C at Wolfswarte and Achtermann (Harz, Lower-Saxony), Lütschetalsperre (Thuringian Forest, Thuringia), and Haberstein (Fichtel Mountains, Bavaria).

Taxa	*A. lignaria*	*A. aborigenica*	*A. sudetica* (stat. nov.)	*A. sayanensis*	*A.* sp.	*A. norvegica* Tyrol	*A. marusiki*	*A. azyuzini*	*A. levinae*	*A. solituda*	*A. norvegica*
A. lignaria	0	4.78	3.21	2.83	3.19	3.19	2.83	2.48	3.01	3.01	3.54
A. aborigenica	4.78	0	3.77	3.36	4.07	3.72	2.65	3.01	3.19	2.48	3.36
A. sudetica	3.21	3.77	0	1.12	1.46	0.14	2.53	2.53	3.04	1.97	2.15
A. sayanensis	2.83	3.36	1.12	0	0.71	1.06	2.48	2.48	3.01	1.95	2.12
A. sp.	3.19	4.07	1.46	0.71	0	1.42	2.83	2.83	3.36	2.3	2.48
A. norvegica Tyrol	3.19	3.72	0.14	1.06	1.42	0	2.48	2.48	3.01	1.95	2.12
A. marusiki	2.83	2.65	2.53	2.48	2.83	2.48	0	1.77	1.59	1.59	2.12
A. azyuzini	2.48	3.01	2.53	2.48	2.83	2.48	1.77	0	1.24	1.95	2.48
A. levinae	3.01	3.19	3.04	3.01	3.36	3.01	1.59	1.24	0	2.12	2.65
A. solituda	3.01	2.48	1.97	1.95	2.3	1.95	1.59	1.95	2.12	0	1.59
A. norvegica	3.54	3.36	2.15	2.12	2.48	2.12	2.12	2.48	2.65	1.59	0

Table 2: p-distances between species of *Acantholycosa*. *Acantholycosa sudetica* stat. nov. shows a high distance (2.15) to *A. norvegica*. *Acantholycosa norvegica* from Tyrol from BOLD most likely is *A. sudetica*, because of its distribution and p-distance.

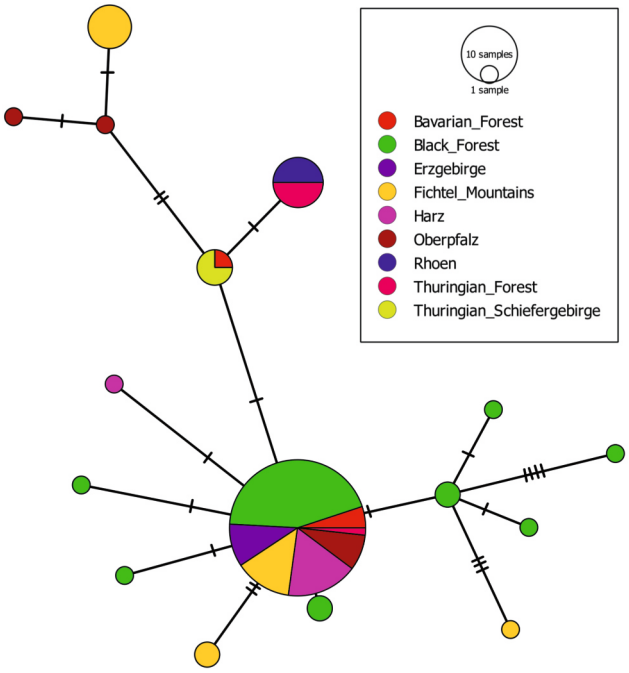


Fig. 4: Haplotype network for all COI sequences generated for *A. sudetica* stat. nov. coloured by the nine lower mountain ranges. The network supports no distinct clades of the phylogeny and a maximum of two mutations between different populations. On the other hand it shows a maximum of six mutations within one population.

DNA barcoding and tree reconstruction

All specimens from Germany were identified by barcoding as *A. sudetica* stat. nov. with high confidence (>99%) in BOLD.

Phylogenies based on COI show no clear signal for differentiation between *A. sudetica* stat. nov. specimens from 24 different sampling locations. The TCS haplotype network shows one common haplotype with some satellites and a maximum of four mutations between haplotypes (Fig. 4). Most populations (7 out of 9) share the common haplotype. No clear patterns are visible, yet, some locations, i.e. Rhoen and Thuringian Highland have unique haplotypes not shared with any other population.

Nevertheless, the tree (Fig. 5) shows a high differentiation between *A. sudetica* stat. nov. and the nominal species *A. norvegica*. Both cluster in distinct clades together with other species from the genus *Acantholycosa*: *Acantholycosa norvegica* from Russia and Norway (BOLD-ID´s: ZMBN779-17; CHEFI1673-18; SPIRU1651-12; SPIRU1652-12; SPIRU1653-12; SPIRU1654-12) clustered with *A. solituda* from Canada (BOLD-ID´s: ARBCM101-13; ARBCM3040-15), *A. aborigenica* (Zyuzin & Marusik, 1988), *A. marusiki* (Fomichev & Omelko, 2020), *A. levinae* (Marusik, Azarkina & Koponen, 2004), and *A. azyuzini* (Marusik, Hippa & Koponen, 1996) from Russia. *A. sudetica* stat. nov. clusters with *A. lignaria* from Norway, Finland, and Germany (FBARB887-14, CHEF|1143-14, ARTRD056-14), *A. sayanensis* (Marusik, Azarkina & Koponen, 2004) and another undetermined species of *Acantholycosa* from Russia (ARU7, ARU8). Both clades are well supported by bootstraps higher than 95%. Outgroups consisting of other lycosid genera cluster at the tree base.

The p-distances of *A. sudetica* stat. nov. to the other species were as follows: *Acantholycosa lignaria* (3.21), *A. aborigenica* (3.77), *A. sayanensis* (1.12), *A.* sp. (1.46), *A. norvegica* (Tyrol, based on location and p-distance *A. sudetica* stat. nov.) (0.14), *A. marusiki* (2.53), *A. azyuzini* (2.53), *A. levinae* (3.04), *A. solituda* (1.97) and *A. norvegica* (2.15) (Table 2).

Discussion

We performed a faunistic review of the specialist spider species *A. sudetica* stat. nov. across Germany and provide new population records for mountain ranges and whole federal states. We found the taxon in all (ten) low mountain ranges in Germany, which we visited for this study. All recorded individuals were found in screes. Genetic analyses showed no differentiation between screes and mountain ranges, suggesting recent (postglacial) connectivity, vicariance or ongoing gene flow. However, the analyses also demonstrated that *A. sudetica* stat. nov. represents an independent lineage with high genetic distance to the nominate form.

New distribution records

We here present the first record of *A. sudetica* stat. nov. for the federal state of Saxony and new records for Thuringia, where it can be found in different mountain ranges (Thuringian Highland, Thuringian Forest, and Ore Mountains) (Fig. 3). Most of our records were uploaded to the *Atlas of the European Arachnids* database (Arachnologische Gesellschaft 2025 under https://atlas.arages.de/source/3744) already in 2020, referring to this paper as in preparation. A different study from 2020 (Gebert 2020) also published the first record of *A. sudetica* stat. nov. for Saxony from the same location, where we found it. This study cited our records from the database. Hence, the specimens referred to here, represent the original first record for Saxony and the Ore Mountains. Our records from the Thuringian Highland and the Thuringian Forest represent the first records for Thuringia. One of these records in the Thuringian Highland was further confirmed by another group one year after we published our original records (Kielhorn 2021).

Ecological observations

This species is known for being exclusive to screes in Germany (Fritze & Blick 2010; Schikora 2015; Kastner *et al*. 2018; Höfer *et al*. 2019; Buse *et al*. 2021); we confirm this, as we never found it around, or apart from this habitat type. In the Bavarian Forest, we found *A. sudetica* stat. nov. in several screes together with *A. lignaria*, especially when large dead wood material or whole dead trees were present



Fig. 5: A phylogenetic tree based on the COI barcoding fragment shows that *A. sudetica* stat. nov represents an independent species distinct from *A. norvegica*.

on the surface. This observation is not unusual, as we found *A. lignaria* in most parts of the Bavarian Forest at higher elevations (>800 m) on dead wood and boardwalks, with wandering males even found on trails and streets during the summer. These observations suggest that several characteristics need to be fulfilled in order for screes to be suitable habitat for *A. sudetica* stat. nov. First, the scree needs to have a three-dimensional character, where the most important dimension is the depth of the rocky outcrops. We found the spiders on very small screes of only a few square metres, if there was a micro-cave system under the surface. If no micro-caves were accessible, and the substrate reached almost the top of the outcrop, the species was not present. Second, succession plays a major role. If the grade of succession reaches high levels and the micro-cave system is filled with debris, the species was not present. Both of these points prohibiting the species from occurring at a site are likely related to the lack of a natural air conditioning system related to the micro-cave system (Blick & Fritze 2010) and to the lack of hiding places. The third characteristic is the presence or absence of sun. The species was only found on sun-exposed southern screes. It seems that *A. sudetica* stat. nov. requires the enormous range of temperatures between the surface and the depth only found in intact screes. Sometimes we found specimens during days after frosty nights until October at sunny spots on the surface, when the temperature was only 5°C. Other factors such as block size, scree size or inclination seem to have much less impact on the occurrence of *A. sudetica* stat. nov. The species was found on a variety of screes with distinct geomorphologies (compare Blick & Fritze 2010 with Kastner *et al*. 2018). Similar ecological observations were made in Central Asia, southern Siberia and the Russian Far East, where *Acantholycosa* species and the related groups prefer three-dimensional large-blocked screes with a micro-cave system under the surface (personal observations of AF).

Further, our findings confirm the idea of winter-activeness. Previous studies already suggested that there could be activity in winter (Kastner *et al*. 2018). On several occasions, active specimens were observed in winter (RK pers. observation) in the Harz Mountains at the Achtermann, Wolfswarte, and Goldenkerklippe screes during a snow fly study (Klesser *et al*. 2024). In several cases between November–February, we observed individuals of *A. sudetica* stat. nov. on sunny and snow-free spots in an air temperature of 5°C on the surface of screes. However, the trap catches decreased strongly during cold periods of the year, suggesting the main activity occurs in warmer months.

DNA barcoding

Analyses based on COI showed no clear signal of intraspecific differentiation between populations of *A. sudetica* stat. nov. Based on the strong isolation and potentially relatively small population sizes, we expected to find some divergence between populations in different mountain ranges, which, however, was not verified. The reason may be the limited resolution of the COI gene and resulting incomplete lineage sorting because of short divergence times. We do not know yet if the colonization of screes by *A. sudetica* stat. nov. took place after the Pleistocene from one to another, or if the species used to be more widely distributed and the current populations only represent relics (Drees *et al*. 2016). A third scenario may be explained by the dispersal ability of the species, as in the Black Forest the species was able to colonize young screes within a few years (HH, unpubl. observation). Those screes have been established after wind throw. Also, migration between neighboring screes, especially of adult males or spiderlings via ballooning or drift are possible. However, so far, no evidence for migration between screes is available despite extensive sampling outside of them. The resolution of our markers does not allow us to distinguish between these three scenarios.

COI has often been criticized as a suboptimal marker for spiders in the past (Maddison *et al*. 2014; Astrin *et al*. 2016; Coddington *et al*. 2016). Hence, it is possible that additional, more fast-diverging markers may provide some signal. In future studies, we will focus on population genetics based on SNPs (single nucleotide polymorphisms), which in addition to resolving biogeography, will also allow us to assess the conservation status of populations and the gene flow between them (Klesser *et al*. in prep.).

On the other hand, we found clearly distinct clades of *A. norvegica* and *A. sudetica* stat. nov. The tree shows a closer relation between *A. solituda* from America, *A. aborigenica*, *A. marusiki*, *A. azyuzini*, and *A. levinae* from Russia to *A. norvegica* than between *A. norvegica* and *A. sudetica* stat. nov. The split between the clades of the nominal species and the former subspecies is rather distinct, which supports the idea of two different species. Further, the clearly distinct distribution and different habitat requirements of both species strengthens this hypothesis. Our analyses demonstrate that *A. sudetica* stat. nov. is most closely related (p-distance 0.14; Table 2) to a specimen identified as *A. norvegica* from Tyrol. This specimen from the database most likely represents *A. sudetica* stat. nov., based on genetic distance, the distribution, and previous records from the region. Hence, we assume that this is a misidentification and both represent the same species. *Acantholycosa sudetica* stat. nov. is significantly more distant from all other species, ranging from 1.12 (to *A. sayanensis*) to 3.77 (to *A. aborigenica*). The distance to the presumed nominal species *A. norvegica* is 2.15 (median of distance to all other species excluding individuals from Tyrol = 2.52, mean = 2.42), which is higher than the distance to three other species (*A. sayanensis*, *A*. sp., *A. solituda*), supporting its status as a distinct species.

Conclusions

Our study showed that *A. sudetica* stat. nov. can be found in a wide range of screes and we were able to record many new populations and first records for two federal states. COI

barcoding showed no differentiation between populations, but it gave prove of a strong differentiation between *A. norvegica* and *A. sudetica* stat. nov. Further, *A. sudetica* stat. nov. is exclusively known from screes.

In a future study, we will focus on the population structure of *A. sudetica* stat. nov. in more detail by using SNP data (Single Nucleotide Polymorphism), which will allow us to understand migration between different populations.

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