Leaving the tropics: The successful colonization of cold temperate regions by *Dolicheremaeus dorni* (Acari, Oribatida)

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**Abstract**

Species diversity is generally higher in the tropics compared to the temperate zones. The phenomenon that one species of an almost exclusively tropical living genus was able to adapt successfully to the cold northern regions is rather rare. However, the oribatid mite *Dolicheremaeus dorni* represents such a species and is in the focus of this study. While 180 *Dolicheremaeus* species are confined to the tropics and subtropics, only five species are known to occur in temperate climates and *D. dorni* represents the only species with a wider distribution in this climatic region. This species is distributed in Central and Southern Europe and was now recorded for the first time in Austria. A morphological and molecular genetic investigation of specimens from Austria, Poland and Croatia confirmed this distribution pattern and revealed specific geographic clades and haplotypes for each population and hence indicate low gene flow between populations. A further molecular genetic analysis of the 18S rRNA gene sequence of *D. dorni* confirmed its phylogenetic position within Carabodoidea. Based on record information, this species is associated with trees or tree habitats and seems to be rather a generalist than a specialist for a specific substrate (e.g., tree species) or food source.

**KEYWORDS**

Carabodoidea, cytochrome oxidase I, first Austrian record, haplotype network, tree-living

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1 | **INTRODUCTION**

Species diversity is not homogeneous across the Earth. There are regions, such as the tropics or macrohabitats such as coral reefs, which particularly favor the life of organisms leading to high biological diversity (e.g., Brown, 2014), whereas other areas with rather harsh environmental conditions doubtlessly limit the existence of species (e.g., arctic regions or deserts); however, most others fall somewhere in between (Gaston, 2000). Despite long-standing studies, causes and/or factors for this increase in species diversity occurring from the poles to the tropics, also known as “latitudinal diversity gradient,” are still unresolved and a universally accepted explanation seems to be a challenging task for the future (Brown, 2014; Condamine, Sperling, Wahlberg, Rasplus, & Kergoat, 2012; Mittelbach et al., 2007; Rohde, 1992). So far, higher species richness in tropical regions could be detected in several groups, for example, in mammals (Rolland, Condamine, Jiguet, & Morlon, 2014), in birds (Ricklefs, 2006), in amphibians (Pyron & Wiens, 2013), in insects (Novotny et al., 2006), and, as shown recently, in oribatid mites too (Pachl et al., 2017). However, in a former study, Maraun, Schatz, and Scheu (2007) demonstrated a non-linear latitude-diversity pattern of oribatid mite species diversity as species richness increased from high latitudes to the warm temperate regions but not further to the tropics. In oribatid mites, a good example for high tropic species diversity can be found in the superfamily Carabodoidae which includes five families: the speciose Carabodidae and Otocephidae,
the smaller Nippobodidae and Dampfiellidae (each with two genera), and the monogenic Tokunocephaeidae—a classification scheme based on Norton and Behan-Pelletier (2009). Most genera have an exclusive tropical distribution excepting a few, as for example, the caraboid Austrocarabodes, Carabodes and Odontocephaeus, or the dampfiellid Dampfiella which all are distributed across several climate zones (Norton & Behan-Pelletier, 2009).

With more than 180 species, Dolicheremaeus is the most diverse genus of the family Otocephaeidae, which includes 39 described genera (Norton & Behan-Pelletier, 2009). The preferred habitats of these taxa are wet decaying, spongy woods in tropical regions. As a possible evolutionary adaptation to the high moisture and heavy rainfall present in the tropics, adults of this genus have a special feature allowing to breathe under flooded conditions, namely respiratory taenia of a type more commonly found in (semi-)aquatic oribatid mites (Norton & Behan-Pelletier, 2009; Travé, 1986). Given the large variety of Dolicheremaeus species and their more or less exclusive occurrence in tropic areas of the world, cold temperate European biota seem to be unfavorable for these organisms. However, there is one species, namely Dolicheremaeus dorni (Balogh, 1937), which has been found sporadically in some, mainly more southern, European countries, for example, Greece, Montenegro, Southern Romania, and Southern France (Balogh, 1937; Mahunka, 1982; Tarman, 1977; Travé, 1986). Additionally, Bulanova-Zachvatkina (1967) described a species, Dolicheremaeus georgii, from the Trans-Carpathians which is morphologically clearly distinct from D. dorni, but since its original description, there were no more findings of this species. Accordingly, D. dorni represents the only species of this genus showing a wider distribution in European regions.

Despite there is a huge number of otocephid species described (more than 400, following the classification of Norton & Behan-Pelletier, 2009), no barcoding sequences of the mitochondrial cytochrome c oxidase subunit I gene (COI) are available. However, there are seven sequences of different nuclear markers representing four species of Otocephaeidae recorded in GenBank.

In this study, we investigate the geographic distribution and the population structure of D. dorni and discuss the unusual occurrence of this species in non-tropical areas. As there is a limit of genetic data in the Otocephaeidae, we additionally provide the first COI sequences of D. dorni and a second otocephid species Spinotocephaeus sp., and present their phylogenetic placement within the Oribatida by the use of the standard nuclear small subunit rRNA (18S rRNA) gene. Furthermore, we integrate a short redescription including leg drawings to the manuscript.

2 | MATERIAL AND METHODS

2.1 | Sampling

In total, 49 individuals of D. dorni were assayed in this study, whereof all were firstly used for a (at least rough) morphological investigation including body size measurements. Afterward, 14 individuals were used for genetic analyses. All of them were analyzed for a fragment of the COI gene for intraspecific studies. Furthermore, one single individual of an undetermined Spinotocephaeus species was analyzed with the same methods as mentioned before for D. dorni individuals. To study the phylogenetic placement, we sequenced part of the 18S rRNA gene (18S) of one D. dorni and the Spinotocephaeus individual too. These were then aligned together with 54 oribatid mite 18S sequences from GenBank, including all available sequences of possible sister taxa/groups according to the classification scheme of Norton and Behan-Pelletier (2009). Species of the supercohort Palaeosomatidae are generally considered as the most primitive Oribatida group; therefore, we decided to use them as outgroup taxa.

Detailed information on herein investigated individuals is shown in Table 1. Individual data obtained from GenBank are given in the Table A1.

Specimens were found in five Norway spruce (Picea abies (L) Karst) bark samples, damaged by bark beetles, collected from Mantscha (Styria) and Lavamünd (Carinthia) in Austria, from Błatowięża in Poland (leg. Dr. Nuria Selva), and from Litorić in Croatia (leg. Dr. Milan Pernek) (see also Figure 1a). Spinotocephaeus sp. was extracted from leaf litter collected in Trang (Southern Thailand).

For morphological comparisons, we used the specimens described by Weigmann (2014), some specimens collected in a former study from Peggau (preserved in 70% ethanol) and further two individuals deposited in the Senckenberg Museum für Naturkunde Goerlitz [collection numbers: 01/42007 Biê Karpaty Mts., Sidonia Nature Reserve (CZ) and 07/44662 Cerová vrchovina Mts., Hajnácka (SK)].

Mites were extracted from bark samples using Berlese–Tullgren funnels and then preserved in 100% ethanol for molecular genetic analyses.

2.2 | Genetic analysis

2.2.1 | DNA extraction, amplification, and sequencing

Total genomic DNA of single individuals was extracted by means of the rapid Chelex 100 resin protocol described in Richlen and Barber (2005). Body remnants (cuticle structures) of all investigated specimens were kept and frozen for a later preparation of permanent slides serving as vouchers. All voucher specimens are deposited in the mite collection at the Institute of Zoology, University of Graz (voucher IDs are same as sample IDs; see Table 1).

A 1258-bp segment of the COI gene (including the barcoding region) was amplified in two overlapping fragments using our newly designed primer pairs MiteCOI_fwd1 (5′-GNTCAACNAAATCWWAGATATTGG-3′) and MiteCOI_rev2 (5′-CNTCNGGNNTGNCCAAAAATC-3′) for the barcoding region (amplicon length 704 bp) and the previously published primers Mite COI-2F and Mite COI-2R (Otto & Wilson, 2001) for the subsequent second COI region (amplicon length 574 bp). PCR conditions were same as in Schäffer, Krisper, Pfingstl, and Sturmbauer (2008).

Also, PCR amplification of the 18S sequences was performed in two overlapping fragments of approximately 950 and 1500 bp
length each, using the same protocol and primer pairs (18Sfwd/rev960 and fw1230/rev18S) as described in Dabert, Witalinski, Kazmierski, Olszanowski, and Dabert (2010).

Purification of all PCR products and DNA sequencing followed standard protocols as described in Schäffer et al. (2008) using same primers as for PCR amplification. In case of 18S sequences, two additional internal sequencing primers were used (fw390 and fw770; Dabert et al., 2010). DNA fragments were purified with Sephadex™ G-50 (Amersham Biosciences) following the manufacturer’s instruction and visualized on an ABI PRISM 3130xl automated sequencer (Applied Biosystems). All sequences are available from GenBank with the accession numbers MG719346 to MG719360 for COI and MG719344 and MG719345 for 18S (see also Table 1 & Table A1).

### 2.2.2 | Data analysis

All COI sequences were verified by comparisons with known oribatid mite sequences from GenBank and aligned by eye in MEGA version 6 (Tamura, Stecher, Peterson, Filipski, & Kumar, 2013). To infer and visualize the genealogical relationships among the D. dorni individuals, the COI data were used for a TCS network reconstruction (Clement, Snell, Walker, Posada, & Crandall, 2002) using the program PopART (http://popart.otago.ac.nz).

For 18S sequence alignment, the R-Coffee web server (Moretti, Wilm, Higgins, Xenarios, & Notredame, 2008; available at http://www.tcoffee.org) which takes into account the predicted secondary structures, was used. To eliminate poorly aligned positions/regions of the resulted RNA alignment, the program Gblocks v0.91b (Castresana, 2000) was applied under default parameters, except "Minimum Length of A Block" was set to a smaller value (5 instead of 10) as recommended by the authors for rDNA-like alignments. The final 18S alignment had a total length of 1375 bp. All alignments are provided as Supporting Information.

Phylogenetic inference was based on maximum likelihood (ML) and Bayesian inference (BI) for the 18S set, conducted in RAxML v8.2.4 (Stamatakis 2014) and MrBayes 3.1.2 (Ronquist & Huelsenbeck, 2003). For ML, the best-fit substitution model selected by the corrected Akaike information criterion (AICc) implemented in MEGA was GTR+G+I. Nodes were supported by bootstrapping (1000 replicates). For BI inference, number of substitution types was set to six (GTR model) for each data partition and among-site rate variation was drawn from a gamma distribution. Posterior probabilities were obtained from a Metropolis-coupled Markov chain Monte Carlo simulation (two independent runs, eight chains with 15 million generations each, chain temperature 0.2, and trees sampled every 1000 generations). After checking parameter values of the sampled chains in Tracer v1.6 (Rambaut & Drummond, 2007; available at http://tree.bio.ed.ac.uk/software/tracer/), the first 10% of the sampled trees were excluded as burn-in. From the remaining trees, a majority rule consensus tree was calculated.

### 2.3 | Morphological analysis

In general, mite specimens were mounted in Berlese medium (a mixture of arabic gum, aqua dest., glucose, chloral hydrate, and glacial ethanoic acid) as permanent slides.

### Table 1

| Sampling locality | Coordinates (North/East) | Sample ID = Voucher ID | GenBank Acc. No.  |
|-------------------|--------------------------|-----------------------|------------------|
| Mantscha1 Styria/Austria | 47.031403 15.366568 | DdR2_1 DdR2_2 DdR2_3 | MG719354 MG719355 MG719356 |
| Mantscha2 Styria/Austria | 47.025242 15.365272 | DdR14_1 | MG719349 |
| Mantscha3 Styria/Austria | 47.025240 15.365269 | DdR15_1 | MG719350 |
| Lavamund Carinthia/Austria | 46.614942 14.986607 | DdR53_1 DdR53_2 | MG719348 MG719347 |
| Litori Croatia | 45.412936 15.077517 | DdR55_1 DdR55_3 DdR55_4 DdR55_6 | MG719351 MG719352 MG719353 MG719357 |
| Biawowieza Poland | 52.739825 23.774201 | DdR88_1 DdR88_2 DdR88_3 | MG719358 MG719359 MG719360 |
| Trang Thailand | 7.460046 99.612081 | Spin_sp | MG719346 MG719345 |
For scanning electron microscopy, the specimens were dehydrated in ascending ethanol concentrations, air-dried, mounted on aluminum stubs with double-sided adhesive tape, and coated with gold. Scanning electron microscopy (SEM) micrographs were taken at the Institute of Plant Sciences with a Philips XL30 ESEM.

3 | RESULTS

3.1 | Genetic analyses

3.1.1 | COI sequences

In total, six haplotypes were identified in the 14 studied D. dorni individuals. Pairwise sequence divergence (uncorrected p-distance) within the species ranged from 0.2% to 5.8%. According to the TCS network, there was no haplotype sharing between the populations with the exception of individuals from two different trees in the region of Mantscha, which had the same haplotype (yellow and blue colored circle in Figure 1b). Furthermore, the analysis revealed a clear signal for a subdivision of the studied populations into four geographically distinct clades (Figure 1b): one included individuals from Styria/Mantscha (yellow and blue colored), one from Poland (orange colored), one from Carinthia/Lavamünd (red colored), and one from Croatia (green colored). As the uncorrected pairwise differences between the two studied otocepheid species ranged from 22.3% to 23.2%, we avoided it to include the Spinotocepheus sp. haplotype in the network reconstruction.

3.1.2 | 18S sequences

The results of both methods, BI and ML, yielded highly similar topologies (Figure 2 & Figure S1). Differences were either due to unresolved parts in the ML tree compared to the BI analysis (there, however, nodes were poorly supported) or in lower node supports of some taxa. In general, Parhyposomatides and Enarthronotides formed one clade at the basis of the phylogeny with Desmonomatides as sister group which is congruent with previously published data (Dabert et al., 2010; Pachl et al., 2012, 2017). Also within Desmonomatides, the topology went quite along with the morphology-based system after Norton and Behan-Pelletier (2009). Nearly all included superfamilies were resolved as monophyletic entities excepting Ceratozetoidea and Crotonioidea—in latter case, however, only weakly supported by both analyses (Figure 2 & Figure S1). Hermannielloidea and Crotonioidea were at the basis of the Desmonomatides, while Licneremaioidea, Achipterioidea, and Oripodoidea were inferred as the most derived ones. Furthermore, BI analysis revealed, with good to high statistical support, monophyly of all included species and/or genera of the Carabodoidea, but paraphyly of one of the three studied families, namely of the Otocepheidae. Moreover, data showed that Cepheoidea [represented by
**Epieremulus granulatus** (Balogh & Mahunka, 1979)] were the sister group of Carabodoidea and both together the sister clade of Oppioidea.

### 3.2 | Morphology of Austrian Dolicheremaeus dorni specimens

Adult. Body length 406–672 μm (mean 558 μm), width 179–312 μm (mean 250 μm). Specimens investigated: females (n = 12), length: 488–672 μm (mean 580 μm), width: 209–312 μm (mean 257 μm); males (n = 6), length: 469–594 μm (mean 512 μm), width: 209–269 μm (mean 236 μm).

Prodorsum (Figures 3a and 4a). Cerotegument finely granular, except for area between costulae showing large granules. All prodorsal setae robust and slightly barbed; rostral setae (lm), curved inwards, lamellar setae (le) same length, interlamellar setae (in) slightly shorter (approx. 55 μm), and exobothridial setae (ex) the shortest (approx. 20 μm). Posterior edge of prodorsum with two rounded median (co.pm) and two rounded lateral condyles (co.pl) opposing lateral condyles of notogaster (co.nl). Respiratory taenidia present, typical for the genus (see Travé, 1986 p. 88; Figure 1).

Gastronotic region (Figures 3a and 4a). Cerotegument finely granular, granules loosely distributed. Lateral condyles of notogaster (co.nl) triangular in shape and tips slightly covered by prodorsal lateral condyles (co.pl) in dorsal view. Ten pairs of robust, long (length 55–75 μm), and slightly barbed notogastral setae, c, la, lm, lp, h₁₋₃, p₁₋₃. Lateral aspect (Figures 3b and 4b). Cerotegument granular, large granules on pedotectum I and II and in lateral sejugal furrow. Pedotectum I (ptcl) well developed, reaching lateral edge of bothridium, pedotectum II (ptcll) also well developed, triangular in lateral and ventral view. Discidium (dis) triangular.

Ventral region of idiosoma (Figures 3c and 4c). Epimeral setation 3-1-3-3, all setae thin and of medium length (approx. 30 μm), except for longer seta 1b (approx. 40 μm). Four pairs of genital setae, one pair of longer aggenital setae. Median (Vm) and posterior genital papillae (Vp) normally shaped, whereas anterior papilla (Va) smaller and laterally displaced and hence difficult to observe. Posterior median borders of anal valves with interlocking tooth-like cuticular projection. Two pairs of long anal setae an₁₋₂ (approx. 20 μm). Anterior and posterior median borders of anal valves with interlocking tooth-like cuticular projections. Three pairs of long anal setae ad₁₋₃ (approx. 55 μm). Seta ad₂ slightly anterior of anterior border of anal opening, ad₃ and ad₄ laterad of anal valves. Lyrifissure iad orientated longitudinally, flanking anterior part of anal orifice.

Legs (Figure 5). Monodactylous. Broad smooth claws. Cerotegument finely granular. Femora with long but slender ventral carinae. Large porose areas on dorsal face of all femora. All setae barbed except for dorsal tarsal setae. Solenidion q₂ inserted on small apophysis. Tibia of leg IV very slender and nearly a third longer than other tibiae. Chaetome and solenidia see Table S1.

### 4 | DISCUSSION

#### 4.1 | Genetics

All herein investigated *D. dorni* specimens, originating from six European countries, represent one and the same species. This is in contrast to other studies on mites, insects, or other invertebrates, which have shown that presumed widespread taxa often represent complexes of cryptic species (Cicconardi, Fanciulli, & Emerson, 2013; Navia et al., 2013; Pérez-Portela, Arranz, Rius, & Turon, 2013; Schäffer et al., 2010). However, a clear geographic pattern can be seen in the haplotypes, which means that populations from different geographic locations do not show extensive gene flow between each other and dispersal may be limited. Accordingly, geographic distance is the main isolating factor shaping the population structure of European *D. dorni* populations.

Furthermore, our results revealed similar topologies as already published phylogenies (e.g., Iseki & Karasawa, 2014; Pachl et al., 2012, 2017), aside from the different taxa and taxonomic classification used. According to the system provided by Norton and Behan-Pelletier (2009), Oppioidea and Gustavioidea might be closely related to the Carabodoidea, which in fact is supported by our phylogenetic data. However, the resulted sister grouping of Carabodoidea and Cepheoidea is questionable, with the reason that the accommodation of the family Anderemaeidae, represented by *E. granulatus* in this study, to the Cepheoidea is still under discussion and therefore might be wrong (Norton & Behan-Pelletier, 2009; Woas, 2002). Moreover, we call the result of paraphyly of Ceratozetoidae, which is based on the clustering of the ceratozetoid *Euzetes globulus* (Nicolet, 1855) together with species of Gustavioidea, into question as there is no plausible explanation supporting such a grouping. It is more likely that this specimen was originally erroneously identified. Unfortunately, there was no individual of *E. globulus* available for this study, to confirm our suspicion but of course, it has to be checked in the future.

#### 4.2 | Ecology

Basicallly all tropical Dolicheremaeus species can be found in soil and litter of wet decaying, spongy wood (Norton & Behan-Pelletier, 2009; Aoki, 1965, 1967; etc.). The temperate *D. dorni* was originally described from decaying leaves in the area of Baile Herculane (Meridional Carpathians) (Balogh, 1937) and Mahunka (1982) examined individuals from soil samples under *Abies cephalonica* Loud. on Mountain Panachaikon (Peloponnese, Greece). However, there are other records documenting individuals of this species collected from bark samples of a beech grove in Massane (Travé, 1978) or from *Fomitopsis pinicola* (Fr.) Karst., a mushroom which colonizes all kind of trees beginning from living to dying or dead ones, in Germany (Maraun, Müller, Bässler, & Scheu, 2014; Weigmann, 2014). Moreover, Murvanidze, Mumladze, Arabili, Barjadze, and Salakaia (2016) obtained their specimens from dead wood in Georgia and all but one population of the present study were found in bark samples of
FIGURE 2  Bayesian inference tree based on the 18S rRNA gene of oribatid mites. Numbers at nodes represent Bayesian posterior probability values. Only support >0.5 is shown. The families of Carabodoidea are written in different colors: Carabodidae in green, Dampfiellidae in blue, and Otocepheidae in red. Tropic taxa of Carabodoidea are underlined; all others have a temperate distribution. *=sequences are generated in this study
P. abies trees, which were infested by different bark beetle species. In this context, another record of this species seems to be quite interesting, namely those from a study of Pernek, Wirth, Blomquist, Avtzis, and Moser (2012) who detected specimens in samples of the fir bark beetle Pityokteines curvidens Germ. caught in pheromone traps in Croatia. However, as this is the only known case of such an association, it would be highly speculative to suggest phoretic behavior for D. dorni. Pernek et al. (2012) also stated that the finding of this taxon is more likely the result of accidental dispersal than an active phoretic behavior of the mite (see also Norton, 1980). Moreover, phoresy increases the dispersal ability of individuals leading to positive effects on population demography, evolution, and community success of a species (Clobert, Danchin, Dhondt, & Nichols, 2001). Given the rare and accidental records in Europe (Figure 1a) but also the clear signal of four geographically distinct clades in our network reconstruction (Figure 1b), phoresy seems not to be a common phenomenon in the studied species.

However, as D. dorni was found in litter, on bark, and tree-associated mushrooms, this species clearly seems to be associated with tree habitats but at the same time seems to be a generalist within these habitats. Maybe this generalistic nature is one of the reasons why D. dorni could colonize a larger area within cold temperate regions.

4.3 | Diversity and distributions

Presently, there are 185 species and nine subspecies of the genus Dolicheremaeus known worldwide (Subias, 2004). Five species occur in temperate climates, Dolicheremaeus absolon (Balogh & Csizsár, 1963), D. dorni, Dolicheremaeus georgii (Bulanova-Zachvatkina, 1967), Dolicheremaeus longipilus (Higgins & Woolley, 1963), and Dolicheremaeus montanus (Krivolutsky, 1971), and eight species in subtropical areas and 178 dwell in the tropics. Four species are distributed across subtropical and tropical climate zones [Dolicheremaeus...
distinctus (Aoki, 1982), Dolicheremaenus elongatus (Aoki, 1967), Dolicheremaenus infrequens (Aoki, 1967), and Dolicheremaenus orientalis (Aoki, 1955)]. Accordingly, there is a clear latitudinal gradient with the lowest species number in temperate regions and the highest number in tropical areas which may be explained by the tropical conservatism hypothesis (Wiens & Donoghue, 2004). This general concept suggests that (i) species richness is higher in tropical biomes because most taxa originated in the tropics, (ii) tropic taxa had more time and area available for speciation, and (iii) species are specialized for tropical climates and only few were able to disperse out of the tropics and adapt to the cold (often freezing) temperatures of middle- and high-latitude regions. These three points are also met by the hypothesis of Pachl et al. (2017) stating that the desmonomatan radiation started on the super continent Pangaea where mites were mainly exposed to tropical climatic conditions.

From a geographical point of view, South-East Asia is the species-richest area of the world, more than two-thirds of all Dolicheremaenus species are occurring within this region (Figure 6). The reason for this higher number of species is unclear, but this area contains thousands of islands showing a tropical or subtropical climate and hence the high speciation rates may be due to the tremendous amount of ecological niches present within this region (e.g., Hammer & Wallwork, 1979). However, sampling activity has been quite unbalanced across the tropics and large regions of South America and Africa remain uncharted in terms of mite occurrence, and therefore, presently known distribution patterns may not reflect the real distribution of Dolicheremaenus in the tropics.

Actually, D. dorni has a relatively wide distribution range known within Europe, with Greece as the southernmost point and Poland as the northernmost. Based on the numerous records located in the

**FIGURE 4** SEM photographs of adult D. dorni. Scale bars 200 μm. (a)—dorsal view; (b)—lateral view; (c)—ventral view

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*From Schäffer et al., Journal of Zoological Systematics and Evolutionary Research.*
south of Europe (Figure 1), it may be assumed that *D. dorni* originally dispersed out of the warmer tropical regions into the cold temperate, more northern European areas. However, to infer this colonization pattern and to support the tropical conservatism hypothesis, it is necessary to perform detailed phylogenetic studies of the genus *Dolicherematidae*, necessarily with various tropical species.

4.4 | Morphology

The present specimens are well in accordance with the original description of *D. dorni* given by Balogh (1937), but the information Balogh provided lacked important details. Therefore, Weigmann (2014) redescribed this species more extensively based on specimens.
collected in South-East Germany. The presently investigated specimens also conform to the latter description except for one morphological feature, namely the size of the epimeral setae. Weigmann stated that the epimeral setae of his individuals were short to moderately long ranging in size from 6 to 25 μm, but the same setae of all presently investigated European populations range from 30 to even 40 μm. Especially, the setae on epimeron I and II are conspicuously shorter in the depicted South-East German individuals. However, we were able to investigate one of the latter specimens, kindly provided to us by Weigmann, and could not find any conspicuous difference in the length of epimeral setae. The different indication of size given by Weigmann (2014) hence may have been caused by a smaller inclination angle of the setae in his preparation which may result in a shorter appearance. The investigated D. dorni specimens clearly possess the same taenidia as shown in the tropical Dolicheremaeus africanus (Wallwork, 1962) (Travé, 1986) which is an indication that they may also be able to withstand longer periods of inundation. This ability may facilitate the colonization of rain-soaked dead wood and other similar wet microhabitats.

A comparison of overall body sizes (Table S2) of different European D. dorni individuals revealed no obvious deviations, whereas large- and small-sized animals of each population even show the same haplotype. Interestingly, Weigmann (2014) already demonstrated large intraspecific size differences in the German individuals (more than 100 μm between smallest and largest, equaling a fifth of overall body size), and this unusual variation is also present in Austrian and Croatian populations (Table S2). Oribatid mites are known to show a size-dependent sexual dimorphism with females being basically larger than males (e.g., Behan-Pelletier, 2015) and the same kind of dimorphism can be found in D. dorni. However, males are only by trend smaller and body sizes of both sexes do largely overlap so that the found large variation cannot be explained by such a sexual dimorphism. Jacot described Dolicheremaeus rubripedes (Jacot, 1938) and stated ”size quite variable” (Jacot, 1938: p.51), which indicates that large intraspecific variation can also be found in other Dolicheremaeus species and hence variable body size may simply be a generic trait.

Other possible generic traits which have been neglected so far by most authors may be the presence of porose areas on the legs and the reduced anterior genital papilla. The existence of porose areas on the legs of D. dorni is shown here for the first time, but most of the descriptions of Dolicheremaeus species are lacking detailed information about the legs and their features and hence an appropriate assessment in terms of distribution and systematic relevance of these structures is not feasible. The same applies to the modified anterior genital papillae which are also mentioned here for the first time in Dolicheremaeus. The type of reduction in the anterior genital papillae is similar to that shown in Oppiidae (Behan-Pelletier, 1991), whereas in the latter, these structures are completely reduced. The similarity in this trait may reflect the close relationship of Carabodoidea and Oppioidea shown in the phylogenetic tree (Figure 2).

However, a comparison with the other two non-tropical Dolicheremaeus species, namely D. georgii from Trans-Carpathians and D. montanus from Eastern-Kirghizia (Ghilarov, 1975), shows that they are quite similar in terms of morphology, and they mainly differ in the shape of notogastral setae and the length of prodorsal lamellae from each other.
5 | CONCLUSIONS

Morphological and molecular genetic analyses clearly demonstrate that D. dorni shows a wider distribution in Central Europe. Nearly all investigated populations show specific haplotypes indicating that there is actually no or low gene flow between the populations. Based on all the records of the temperate D. dorni, we suggest that this species is basically associated with tree habitats, whereas preferences for specific tree species or specific microhabitats on the trees could not be detected.

Presently, D. dorni represents the only species of this genus that was able to colonize a wider region within the cold temperate climate zone.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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### TABLE A1  Species list of included 18S rRNA sequences obtained from GenBank

| Species                     | Superfamily         | Family          | GenBank Acc.no. | References                        |
|-----------------------------|---------------------|-----------------|-----------------|-----------------------------------|
| *Achipteria coleoptrata*    | Achipteroidea       | Achipteridae    | EF091418        | Domes, Norton, Maraun, and Scheu (2007) |
| *Adoristes poppei*          | Gustavioidea        | Liacaridae      | EU432202        | Maraun et al. (2009)              |
| *Aeroppha sp.*              | Oppioidea           | Oppiidae        | HM070344        | Pepato, da Rocha, and Dunlop (2010) |
| *Alysnobates reticulatus*   | Ameronothroidea     | Fortuyniidae    | AB818526        | Iseki and Karasawa (2014)         |
| *Beckiaella arctica* Perez-Itigo & Baggio, 1986 | Caraboidoidea | Dampfiellidae   | KX397628        | Krause et al. (2016)              |
| *Beckiaella capitulum* Balogh & Mahunka, 1978 | Caraboidoidea   | Dampfiellidae   | KR081602        | Pachl et al. (2017)               |
| *Camisia spinifer* (Koch, 1836) | Crotonioidea   | Camisiidae      | EF091420        | Domes et al. (2007)               |
| *Carabodes coriaceus* Koch, 1835 | Caraboidoidea   | Carabodidae     | EF093787        | Laumann et al. (2007)             |
| *Carabodes labrynthicus* (Michael, 1879) | Caraboidoidea   | Carabodidae     | KX397629        | Krause et al. (2016)              |
| *Carabodes sp.*             | Caraboidoidea       | Carabodidae     | GQ864283        | Dabert et al. (2010)              |
| *Carabodes subarcticus* Tragardh, 1902 | Caraboidoidea | Carabodidae     | EF091429        | Domes et al. (2007)               |
| *Ceratoppia bipilis* (Hermann, 1804) | Gustavioidea   | Ceratoppiidae   | EU432204        | Maraun et al. (2009)              |
| *Eniochthonius minutissimus* (Berlese, 1903) | Hypochthonoidea | Eniochthoniidae | EF091428        | Domes et al. (2007)               |
| *Eohypochthonius sp.*       | Hypochthonoidea     | Hypochthoniidae | JQ000037        | Klimov and O'Connor (2013)        |
| *Eomeremus granulatus* (Balogh & Mahunka, 1979) | Oppioidea / Cepheoidea | Caleremaeidae / Anderemaeida | KR081610 | Pachl et al. (2017) |
| *Eurremaeus oblongus* (Koch, 1835) | Eremaeoidea | Eremaeidae      | GQ864287        | Dabert et al. (2010)              |
| *Eupelops plicatus* (Koch, 1835) | Phenopeloidea | Phenopelopidae  | EF091419        | Domes et al. (2007)               |
| *Euzetes globulus* (Nicolet, 1855) | Ceratzoetoidea | Euzetidae       | AF022030        | Thomas (unpublished)              |
| *Fortunyia rotunda* Marshall & Pugh, 2002 | Ameronothroidea | Fortuyniidae    | AB818525        | Iseki and Karasawa (2014)         |
| *Gehypochothion urticinus* (Berlese, 1910) | Parhypochothionioida | Gehypochothioniidae | AF022031 | Thomas (unpublished) |
| *Gittella variabilis* Ermilov, Sandmann, Marian & Maraun, 2013 | Oppioidea | Oppiidae        | KR081612        | Pachl et al. (2017)               |
| *Globehypochthonia maior* Hammer, 1962 | Oppioidea | Oppiidae        | KR081613        | Pachl et al. (2017)               |
| *Gymnodaemoidea bicostatus* (Koch, 1835) | Gymnodaemoidea / Plateremaeoidea | Gymnodaemeidae | GQ864285 | Dabert et al. (2010) |
| *Hemileius singularis* Sellnick, 1930 | Oripioidea | Hemileiidae     | AB818531        | Iseki and Karasawa (2014)         |
| *Heminothrus paolius* (Berlese, 1913) | Crotonioidea | Camisiidae      | EF091423        | Domes et al. (2007)               |
| *Hermannia gibba* (Koch, 1839) | Hermannioidea / Hermannielloidea | Hermanniidae | EF091426        | Domes et al. (2007)               |
| *Hydrozetes convereae* Schrank, 1781 | Hydrozoetoidea | Hydrozetidae   | AB818523        | Iseki and Karasawa (2014)         |
| *Hydrozetes lacustris* Michael, 1882 | Hydrozoetoidea | Hydrozetidae   | EU433987        | Schaefer, Norton, Scheu, and Maraun (2010) |
| *Liacorus coracinus* Koch, 1841 | Gustavioidea | Liacaridae      | KR081619        | Pachl et al. (2017)               |
| *Lioidea sp.*               | Lioidea* / Neolioidea | Lioidea | AF022035 | Thomas (unpublished) |
| *Lohmannia banksi* Norton, Metz & Sharma, 1978 | Lohmannioidea / Hypochthonioidea | Lohmanniidae | AF022036 | Thomas (unpublished) |
| *Maculobates bruneiensis* Ermilov, Chatterjee & Marshall, 2013 | Oripioidea | Liebstidiidae   | AB818522        | Iseki and Karasawa (2014)         |
| *Nothrus silvestris* Nicolet, 1855 | Crotonioidea | Nothridae       | EF091425        | Domes et al. (2007)               |
| *Odontocephus oblongus* Banks, 1895 | Caraboidoidea | Carabodidae     | KP325065        | Pepato & Klimov (2015)            |
| *Oppiella nova* (Oudemans, 1902) | Oppioidea | Oppiidae        | KR081626        | Pachl et al. (2017)               |
| *Oripoda sp.*               | Oripioidea          | Oripodida       | AB818532        | Iseki and Karasawa (2014)         |

(Continues)
| Species                      | Superfamily               | Family                | GenBank Acc.no. | References                      |
|------------------------------|---------------------------|                      |                 |                                |
| *Palaeacarus hystricinus*    | Palaeacoidea              | Palaeacaridae        | EF204472       | Schaefer et al. (unpublished)  |
| *Peloribates acutus* Aoki, 1961 | Oripoidea               | Haplozetidae         | AB818529       | Iseki and Karasawa (2014)      |
| *Platynothrus peltifer* (Koch, 1839) | Crotonioidea          | Camisiidae           | EF091422       | Domes et al. (2007)            |
| *Plenotocepheus neotropicus* Ermilov, Sandmann, Marian & Maraun, 2013 | Carabodoidea         | Tetracondylidae*     | KR081631       | Pachl et al. (2017)            |
| *Protoribates hakonensis* Aoki, 1994 | Oripoidea               | Protoribatidae       | AB818528       | Iseki and Karasawa (2014)      |
| *Pseudotocepheus amonstruosus* Mahunka, 1973 | Carabodoidea       | Otocephidae          | HM070341       | Pepato et al. (2010)           |
| *Rostrazetes ovulum* Berlese, 1908 | Oripoidea               | Haplozetidae         | HM070342       | Pepato et al. (2010)           |
| *Scheloribates pallidulus* (Koch, 1841) | Oripoidea               | Scheloribatidae      | AB818527       | Iseki and Karasawa (2014)      |
| *Schusteria littorea* Grandjean, 1968 | Ameronothroidea    | Selenoribatidae      | HM070345       | Pepato et al. (2010)           |
| *Scutovertex sculptus* Michael, 1879 | Licneremaeoidea    | Scutoverticidae      | GQ864305       | Dabert et al. (2010)           |
| *Tectocepheus minor* Berlese, 1903 | Tectocepheoidea       | Tectocepheidae       | EF093776       | Laumann et al. (2007)          |
| *Tectocepheus sarekensis* Tragärth, 1910 | Tectocepheoidea       | Tectocepheidae       | EF093781       | Laumann et al. (2007)          |
| *Tectocepheus velatus* (Michael, 1880) | Tectocepheoidea       | Tectocepheidae       | EF093778       | Laumann et al. (2007)          |
| *Thalassozetes shimojanai* (Karasawa & Aoki, 2005) | Ameronothroidea     | Selenoribatidae      | AB818524       | Iseki and Karasawa (2014)      |
| *Trhypochthonius cladonicola* (Willmann, 1919) | Trhypochthonioidea*/  | Trhypochthoniidae    | JQ000047       | Klimov and OConnor (2013)      |
| *Trichocephus trimaculatus* (Koch, 1835) | Ceratozetoidea       | Ceratozetidae        | EU432195       | Maraun et al. (2009)           |
| *Xenillus discrepans* Grandjean, 1936 | Gustavioidea        | Xenilliidae          | EU432203       | Maraun et al. (2009)           |
| *Zachvatkinella_sp*         | Acaronychoidea       | Archeoonothridae     | EF203776       | Domes, Althammer, Norton, Scheu, and Maraun (2007) |

*Classification according to GenBank; classification used in the present study following Norton & Behan-Pelletier (2009).*