

**Research Article****First documented record of the neotropical ant  
*Brachymyrmex cordemoyi* Forel, 1895 (Formicidae: Formicinae) in Germany**Martin Husemann<sup>1,\*</sup> and Claudia M. Ortiz-Sepulveda<sup>2</sup><sup>1</sup>University of Hamburg, Centrum für Naturkunde, Martin-Luther-King Platz 3, 20146 Hamburg, Germany<sup>2</sup>Univ. Lille, CNRS, UMR8198 - Evo-Eco-Paleo, F-59000 Lille, FranceAuthor e-mails: [Martin.Husemann@uni-hamburg.de](mailto:Martin.Husemann@uni-hamburg.de) (MH), [claudiamarcelao@gmail.com](mailto:claudiamarcelao@gmail.com) (CMOS)*\*Corresponding author*

**Citation:** Husemann M, Ortiz-Sepulveda CM (2019) First documented record of the neotropical ant *Brachymyrmex cordemoyi* Forel, 1895 (Formicidae: Formicinae) in Germany. *BioInvasions Records* 8(4): 764–773, <https://doi.org/10.3391/bir.2019.8.4.04>

**Received:** 12 February 2019**Accepted:** 10 July 2019**Published:** 18 September 2019**Handling editor:** Ben Hoffmann**Thematic editor:** Stelios Katsanevakis**Copyright:** © Husemann and Ortiz-SepulvedaThis is an open access article distributed under terms of the Creative Commons Attribution License ([Attribution 4.0 International - CC BY 4.0](https://creativecommons.org/licenses/by/4.0/)).**OPEN ACCESS****Abstract**

*Brachymyrmex cordemoyi* Forel, 1895 is a small ant species native to the Neotropics, but it has been introduced into Africa, Madagascar, the Arabian Peninsula and some tropical oceanic islands. We report on a non-native *Brachymyrmex* population that has been discovered indoors in the vicinity of Euskirchen (Germany). Specimens were identified morphologically and subjected to DNA barcoding; molecular data of the new population was analyzed jointly with morphologically verified GenBank entries. Morphological identification and phylogenetic inference based on a fragment of the mitochondrial gene Cytochrome Oxidase subunit 1 gave congruent results. The population was clearly assigned to *B. cordemoyi* and represents the second report of this species from Europe, with a recent record from the Netherlands. In Germany the species has only been found indoors, and the here reported population has been exterminated. This new record represents one of many indoor introductions of the genus *Brachymyrmex*, likely via tropical plants. We present a diagnosis of the species and additionally review all known introductions of the genus which have been identified to the species level.

**Key words:** rover ant, Europe, indoor introduction, tropical plants, anthropogenic**Introduction**

Global trade in general, and of plants and plant materials in particular, can lead to the anthropogenic dispersal of animals that upon establishment in new regions outside of their native range may constitute a first step towards biological invasion (Hulme 2009; Simberloff and Rejmanek 2011). Especially small and stress-resistant species may survive long-distance transport and may establish in new environments. Such new environments may have a special micro-climate, such as houses, greenhouses or swimming pools, where the invader may thrive locally, without escaping into natural environments (Kenis et al. 2007).

Insects and arachnids contain various species that are commonly dispersed via plants or plant products (Hulme et al. 2008; Roques 2010). The most publically known invaders are perhaps banana spiders (Blick et al. 2006), but a large number of small insects from various taxonomic

groups are commonly imported (Malumphy 2012). Another group containing various common invaders are ants, which may become pests upon colonization (e.g. MacGown et al. 2007; Klotz et al. 2008; Gotzek et al. 2015). Whereas most non-native species cause little harm, some others may pose direct threats to biodiversity or economy and may be considered pests. Prominent examples are the fire ant *Solenopsis invicta* and the Argentinian ant *Linepithema humile*, which cause severe ecological problems as they replace the local fauna (Kenis et al. 2009). Another example is the pharaoh ant (*Monomorium pharaonis*), which represents an important household pest (Wetterer 2010).

In Germany 25 species of non-native ants have been recorded (Geiter et al. 2002). Several of these have become established and some are now considered to be pests, whereas others have a more restricted impact. Several species of the genus *Brachymyrmex* belong to such invaders. The genus *Brachymyrmex* is originally distributed in the Neotropics and consists of 40 valid species, subspecies and varieties (Ortiz-Sepulveda et al. 2019). Several species of *Brachymyrmex* have been recorded outside of their native ranges and *B. patagonicus* is even considered to be a pest (e.g. MacGown et al. 2007; Klotz et al. 2008; [www.antmaps.org](http://www.antmaps.org) summarizes these records). In their native habitat most *Brachymyrmex* species nest in soil or rotten wood, but in urban areas they also may nest in flower pots (Dash et al. 2005) and in this way they have invaded greenhouses (Forel 1907).

Currently, *Brachymyrmex patagonicus* Mayr, 1868 appears to be the most successful invader of the genus; it has successfully settled in the United States and has been introduced to Japan, Madagascar, Mauritius, the Netherlands and Germany (Ortiz and Fernandez 2014; Terayama et al. 2014; Boer and Vierbergen 2008; MacGown et al. 2007; Geiter et al. 2002; Smith and Fischer 2009). Other species of the genus recorded outside their native ranges are *Brachymyrmex heeri* Forel, 1874 (e.g. Eichler 1952), *B. obscurior* Forel, 1893 (e.g. Klotz et al. 2008; Boer and Vierbergen 2008), *B. longicornis* Forel, 1907 (Weidner 1972), *B. minutus* Forel, 1893 (e.g. Clouse 1999) and *B. cordemoyi* Forel, 1895 (e.g. Sharaf et al. 2016), the latter of which has been described from Réunion (Forel 1895) (see Table 1). Yet, many records may need to be re-evaluated in the future, as *Brachymyrmex* species are often misidentified (Boer et al. 2018). A recent example is the record of *B. patagonicus* from Hong Kong (Guénard 2019), which displays the diagnostic features of *B. cordemoyi* (Ortiz-Sepulveda, pers. obs.).

Three species of the genus have so far been recorded in Germany (*B. longicornis*, *B. patagonicus* and *B. heeri*). Here, we present the first record of *B. cordemoyi* from Germany. Specimens of this species were identified using diagnostic morphological features and the identification was subsequently verified with DNA barcoding. We also summarize all literature records of *Brachymyrmex* introductions where a species-level

**Table 1.** Records of invasive *Brachymyrmex* species with indication of the country and year of introduction, and the respective reference. Most records were obtained from <http://antmaps.org>.

Genus	Species	Country	Reference
<i>Brachymyrmex</i>	<i>cordemoyi</i>	Germany	this study
<i>Brachymyrmex</i>	<i>cordemoyi</i>	Netherlands	Boer et al. 2018
<i>Brachymyrmex</i>	<i>cordemoyi</i>	Comoros	Fisher 2014a
<i>Brachymyrmex</i>	<i>cordemoyi</i>	Comoros	Forel 1907
<i>Brachymyrmex</i>	<i>cordemoyi</i>	Comoros	Wheeler 1922
<i>Brachymyrmex</i>	<i>cordemoyi</i>	Madagascar	Fisher 1997
<i>Brachymyrmex</i>	<i>cordemoyi</i>	Madagascar	Fisher 2003
<i>Brachymyrmex</i>	<i>cordemoyi</i>	Madagascar	Fisher 2014b
<i>Brachymyrmex</i>	<i>cordemoyi</i>	Mascarene Islands	Donisthorpe 1949
<i>Brachymyrmex</i>	<i>cordemoyi</i>	Mascarene Islands	Emery 1895
<i>Brachymyrmex</i>	<i>cordemoyi</i>	Mascarene Islands	Fisher and Blard 2014
<i>Brachymyrmex</i>	<i>cordemoyi</i>	Mascarene Islands	Fisher 1997
<i>Brachymyrmex</i>	<i>cordemoyi</i>	Mascarene Islands	Fisher and Suarez 2014
<i>Brachymyrmex</i>	<i>cordemoyi</i>	Mascarene Islands	Forel 1895
<i>Brachymyrmex</i>	<i>cordemoyi</i>	Mascarene Islands	Mamet 1954
<i>Brachymyrmex</i>	<i>cordemoyi</i>	Mascarene Islands	Santschi 1923
<i>Brachymyrmex</i>	<i>cordemoyi</i>	Mascarene Islands	Wheeler 1922
<i>Brachymyrmex</i>	<i>cordemoyi</i>	Seychelles	Dorow 1996
<i>Brachymyrmex</i>	<i>cordemoyi</i>	Seychelles	Fisher 1997
<i>Brachymyrmex</i>	<i>cordemoyi</i>	Seychelles	Fisher 2014c
<i>Brachymyrmex</i>	<i>cordemoyi</i>	Seychelles	Forel 1912a
<i>Brachymyrmex</i>	<i>cordemoyi</i>	Seychelles	Forel 1912b
<i>Brachymyrmex</i>	<i>cordemoyi</i>	Seychelles	Gaigher et al. 2012
<i>Brachymyrmex</i>	<i>cordemoyi</i>	Seychelles	Gerlach 2004
<i>Brachymyrmex</i>	<i>cordemoyi</i>	Seychelles	Santschi 1923
<i>Brachymyrmex</i>	<i>cordemoyi</i>	Seychelles	Wheeler 1922
<i>Brachymyrmex</i>	<i>cordemoyi</i>	Tanzania	Pape and Swenningsen 2014
<i>Brachymyrmex</i>	<i>cordemoyi</i>	Saudi Arabia	Sharaf et al. 2016
<i>Brachymyrmex</i>	<i>heeri</i>	Azores	Borowiec 2014
<i>Brachymyrmex</i>	<i>heeri</i>	France	Bernard 1967
<i>Brachymyrmex</i>	<i>heeri</i>	France	Borowiec 2014
<i>Brachymyrmex</i>	<i>heeri</i>	Germany	Eichler 1952
<i>Brachymyrmex</i>	<i>heeri</i>	Switzerland	Emery 1878
<i>Brachymyrmex</i>	<i>heeri</i>	Ukraine	Bernard 1967
<i>Brachymyrmex</i>	<i>heeri</i>	Ukraine	Borowiec 2014
<i>Brachymyrmex</i>	<i>longicornis</i>	Germany	Weidner 1972
<i>Brachymyrmex</i>	<i>minutus</i>	USA: FL	Clouse et al. 1999
<i>Brachymyrmex</i>	<i>minutus</i>	USA: FL	Deyrup 2003
<i>Brachymyrmex</i>	<i>minutus</i>	USA: FL	Deyrup 2016
<i>Brachymyrmex</i>	<i>minutus</i>	USA: FL	Deyrup and Davis 2000
<i>Brachymyrmex</i>	<i>minutus</i>	USA: FL	Deyrup et al. 2014
<i>Brachymyrmex</i>	<i>minutus</i>	USA: FL	Ferster and Prusak 1994
<i>Brachymyrmex</i>	<i>minutus</i>	USA: FL	Moreau et al. 2014
<i>Brachymyrmex</i>	<i>obscurior</i>	Netherlands	Boer and Vierbergen 2008
<i>Brachymyrmex</i>	<i>patagonicus</i>	Great Britain	Donisthorpe 1915
<i>Brachymyrmex</i>	<i>patagonicus</i>	Germany	Eichler 1952
<i>Brachymyrmex</i>	<i>patagonicus</i>	Japan	Terayama et al. 2014
<i>Brachymyrmex</i>	<i>patagonicus</i>	Netherlands	Boer and Vierbergen 2008
<i>Brachymyrmex</i>	<i>patagonicus</i>	Spain	Espadaler and Pradera 2016
<i>Brachymyrmex</i>	<i>cordemoyi</i>	Hong Kong	Guénard 2019

identification was made, although we have not been able to confirm the identifications for some of these records.

## Materials and methods

Specimens were collected indoors by an insect exterminator in the vicinity of Euskirchen ( $50^{\circ}40'02.3''N$ ;  $6^{\circ}48'10.7''E$ ) in Germany (the population was exterminated after sampling). Voucher specimens are deposited in the collection of the Zoological Museum Hamburg (ZMH) under accession number ZMH 2018/7. Individuals were morphologically identified by CMOS following the identification key of Ortiz-Sepulveda et al. (2019).

Genomic DNA was extracted from one specimen using a standard Chelex protocol (Walsh et al. 1991). PCR was performed using the general barcoding primers (HCO-LCO, Folmer et al. 1994), DreamTaq Polymerase (Thermo Fisher Scientific, Bremen, Germany) and a standard protocol with an annealing temperature of  $50^{\circ}C$  in a  $10\ \mu l$  volume. PCR products were checked on a 1% agarose gel stained with GelRed (Biotium, Fremont, Ca, USA), purified with a mix of Exonuclease and Shrimp Alkaline Phosphatase before sequencing by Macrogen Europe (Amsterdam, Netherlands).

The obtained sequence was inspected, aligned with species level data from public databases (see below) and subjected to phylogenetic analysis with Bayesian Inference (BI). We only included GenBank specimens for which voucher images are available that allow unambiguous identification (Table 2). In total, the analysis was performed with 28 specimens covering seven *Brachymyrmex* species and one specimen of *Myrmelachista* (the sister-genus of *Brachymyrmex* (Blaimer et al. 2015; Ortiz-Sepulveda et al. 2019)) as outgroup taxon. Several of these sequences are currently unpublished although they are available in GenBank (provided by the International Barcode of Life Consortium and P. E. Hanish).

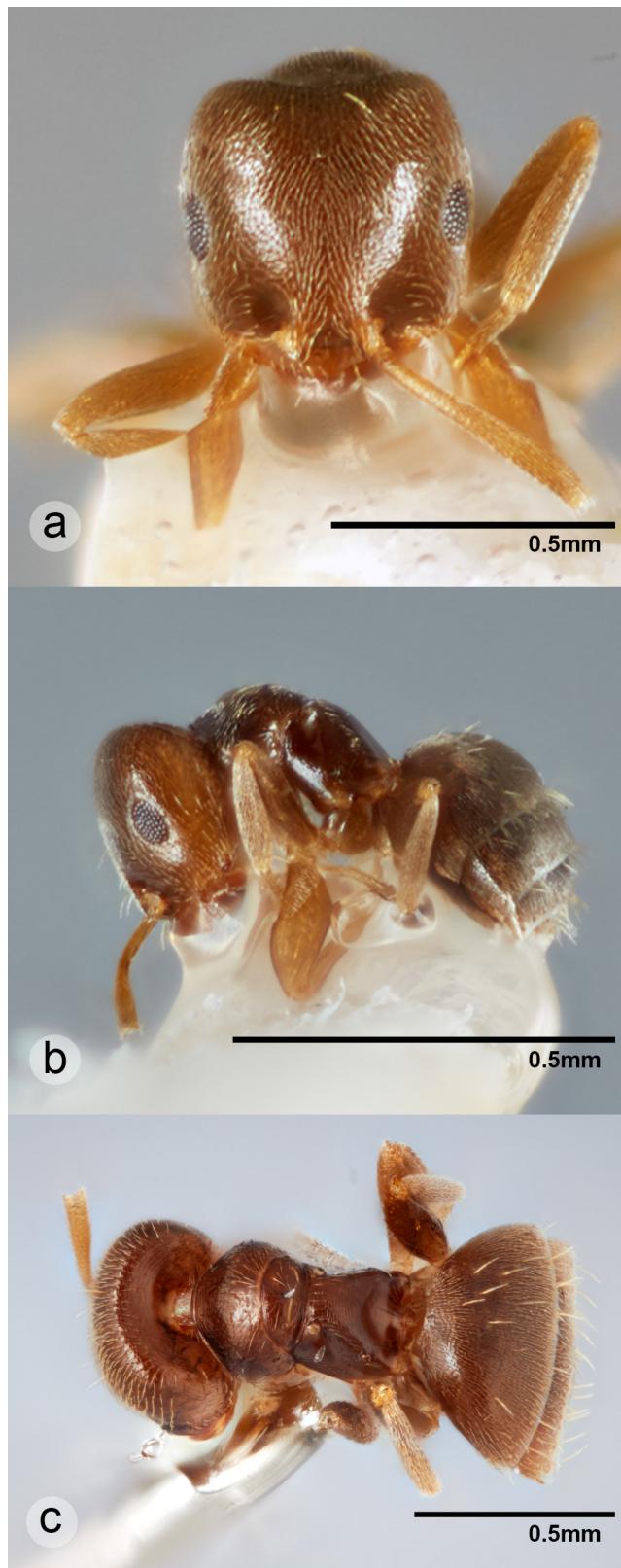
Sequences were aligned using MAFFT v. 7 (Katoh and Standley 2013); the alignment was inspected in MESQUITE v. 2.10 (Maddison and Maddison 2017) to determine codon positions. Models of sequence evolution were fit with PartitionFinder v. 1.1.1 (Lanfear et al. 2012) taking into account potential differences in substitution models for the various codon positions. The fit of the various models was evaluated with a Bayesian Information Criterion (BIC). Subsequently, the data was phylogenetically analyzed with Bayesian Inference (BI) in MrBayes v. 3.2.6 (Ronquist et al. 2012) using the CIPRES Science Gateway v. 3.3 (Miller et al. 2010). Two independent Markov chain Monte Carlo (MCMC) runs were conducted for 30 million generations sampling every 1,000 generations. Each run was distributed across four chains with a heating parameter of 0.2 and 25% of the samples were discarded as burn-in. Convergence was checked by average split frequencies being below 0.01 and by checking the effective sample sizes (ESS) in Tracer v. 1.6. (Rambaut et al. 2013). As all ESS values were above 200, the maximum clade credibility tree was visualized with FigTree v. 1.4.2 (Rambaut 2012).

**Table 2.** Species identification, locality and NCBI Genbank accession numbers for the COI sequences of the taxa studied in the phylogenetic analysis. GenBank sequences generated by the International Barcode of Life consortium (iBoL) were only included if voucher images allowed unambiguous identification. One GenBank sequence from P.E. Hanish of a specimen of *B. cordemoyi* was also included in our phylogenetic analysis. Note that these sequences have been publicly deposited, but that the current study is their first report in the scientific literature.

Collection code	Specimen code	Taxon	Country	COI	From
ACGAD611_10	10COSTA-0610	<i>B. heeri</i>	Costa Rica	HQ545883	iBoL
ACGAB032_09	08COSTA-0544	<i>B. heeri</i>	Costa Rica	GU708679	iBoL
PBA0605	BCPBA0605	<i>B. patagonicus</i>	Ecuador	KU985505	iBoL
Wm-C-07-1-10	CASENT0613756	<i>B. cavernicola</i>	Honduras	JN270706	iBoL
Wa-C-04-2-06	CASENT0617100	<i>B. cavernicola</i>	Honduras	JN270709	iBoL
ACGAB179_09	08COSTA-0691	<i>B. cavernicola</i>	Costa Rica	GU709009	iBoL
ACGAB340_09	08COSTA-0852	<i>B. cavernicola</i>	Costa Rica	GU709019	iBoL
ASPNA1434-10	PKSP5218	<i>B. bruchi</i>	United States	HQ551103	iBoL
ASANE612_10	CASENT0191351-D01	<i>B. bruchi</i>	United States	HQ925273	iBoL
ASMA067_05	CASENT0057422-D01	<i>B. cordemoyi</i>	Mauritius	EF609727	iBoL
ASMA136_05	CASENT0059705-D01	<i>B. cordemoyi</i>	Mauritius	EF609722	iBoL
ASMA288_05	CASENT0060378-D01	<i>B. cordemoyi</i>	Mauritius	EF609763	iBoL
ASANP101_09	CASENT0146383-D01	<i>B. cordemoyi</i>	Comoros	GU710679	iBoL
n.a.	MACN-Bar-Ins-ct02961	<i>B. cordemoyi</i>	Argentina	MF925900	P. E. Hanish
MEKOU_024319	MEKOU_024319	<i>B. minutus</i>	Panama	KM224720	iBoL
MEKOU011361	MEKOU011361	<i>B. minutus</i>	Panama	JF863683	iBoL
BYT391	YT391	<i>B. minutus</i>	Ecuador	KY442006	iBoL
ACGAB608_09	08COSTA-1120	<i>B. minutus</i>	Costa Rica	GU709339	iBoL
ACGAD507_10	10COSTA-0506	<i>B. minutus</i>	Costa Rica	HQ545796	iBoL
ACGAD050_10	10COSTA-0050	<i>B. minutus</i>	Costa Rica	HM919664	iBoL
ACGAH028_11	BIOUG01155-C04	<i>B. minutus</i>	Costa Rica	KC418964	iBoL
SMTPJ4104_14	BIOUG16155-F11	<i>B. depilis</i>	Canada	KR884779	iBoL
SMTPB3340_13	BIOUG0536-B03	<i>B. depilis</i>	Canada	KR873789	iBoL
BBHYA3116_12	BIOUG02686-B02	<i>B. depilis</i>	United States	KM996564	iBoL
USFOR340_10	BIOUG_09BBUSA0340	<i>B. depilis</i>	United States	HQ984902	iBoL
CNKJP241_14	BIOUG12967-H07	<i>B. depilis</i>	Canada	KR402540	iBoL
JTL6972	CX-06	<i>Myrmelachista zeledoni</i>	Honduras	MK992402	Ortiz-Sepulveda et al. (2019)
ZMH 2018/7	ZMH 2018/7	<i>B. cordemoyi</i>	Germany	MK803279	this study

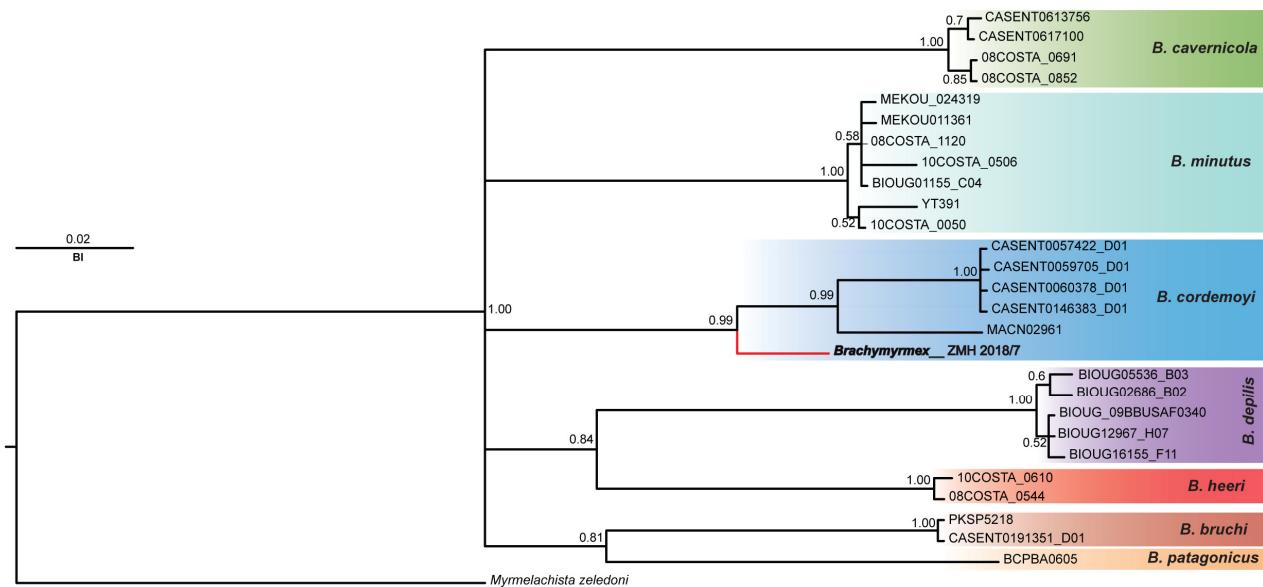
## Results and discussion

The *Brachymyrmex* population from Germany was morphologically identified as *B. cordemoyi* (Figure 1). *Brachymyrmex cordemoyi* strongly resembles *B. obscurior* and to lesser extent also *B. patagonicus*. These three species have scapes that touch the posterior cephalic margin, or extend beyond it, but by a distance that is smaller than the maximal diameter of the eye; in lateral view their mesonotum does not bulge out dorsally above the pronotum, and the metanotal groove is narrower than the diameter of the methathoracic spiracles. However, *B. cordemoyi* has a longer pronotum and mesonotum than *B. obscurior*, more ommatidia along the maximal diameter of the eye, and lighter-colored pubescence, which is denser on the dorsum of the entire body and appressed on the gaster (instead of decumbent in *B. obscurior*); the gaster also bears several scattered and sub-erect hairs mainly, but not exclusively along the edges of the segments. *Brachymyrmex cordemoyi* differs from *B. patagonicus* by having considerably denser pubescence on the gaster. It can also be confused with *B. termitophilus*, from which it differs in the body color (*B. cordemoyi* is dark brownish, whereas *B. termitophilus* is yellowish – Ortiz-Sepulveda et al. 2019).



**Figure 1.** Head (a), lateral (b) and dorsal (c) habitus of *B. cordemoyi* from Germany.

The phylogenetic analysis supports the morphological identification. The individual from Germany constitutes a well-supported monophyletic clade with other specimens of *B. cordemoyi* (BPP = 0.99, Figure 2). However, the deep split between the specimens of *B. cordemoyi* from the



**Figure 2.** Maximum clade credibility phylogeny obtained from analyzing COI sequences of 28 *Brachymyrmex* individuals, including one specimen from the population captured at a public swimming pool in Germany.

Comoros, Mauritius and Argentina and that from Germany, as well as the long branch-length towards the German specimen are noteworthy. In this respect it is important to highlight that *B. cordemoyi* has several diagnostic features, but also considerable intraspecific variation in various traits and that our current concept of *B. cordemoyi* may include several biological species (Ortiz-Sepulveda et al. 2019). Our data shows the value of DNA barcodes to identify species of *Brachymyrmex* as long as comparative sequences are available for well-identified individuals. Genetic resources are especially important considering the uncertain taxonomy of this genus and the ambiguity that long existed on putatively diagnostic morphological traits (Ortiz and Fernández 2014; Creighton 1950; Ortiz-Sepulveda et al. 2019). However, studies with additional genetic markers are required to better understand phylogenetic relationships within *Brachymyrmex*.

In Germany only *Brachymyrmex heeri*, *B. patagonicus* and *B. longicornis* have previously been reported (Table 1). The specimens of *B. longicornis* held at the ZMH are poorly preserved, however, they have been reported as syntypes in the past (Weidner 1972). *Brachymyrmex longicornis* is now considered to be a junior synonym of *B. australis* (Ortiz-Sepulveda et al. 2019).

Our new record of *B. cordemoyi* raises the number of exotic *Brachymyrmex* species in Germany to four, i.e. one species less than for Europe altogether (*B. obscurior* has been reported from the Netherlands). It is likely that additional species have been reported under other names or have just been overlooked or misidentified (Boer et al. 2018). Furthermore, considering the ease with which species of the genus *Brachymyrmex* can be transported, i.e. given their small size and their nesting habits, we can expect additional introductions in the future. The rise in global temperatures may even result in the establishment of perennial populations in natural environments in the future, at least in southern and central Europe.

## Acknowledgements

We thank Christopher Wilson (University of Texas, El Paso, Texas, USA) for comments on the morphological identification of the species, Bert Van Bocxlaer for discussion on the manuscript and two anonymous reviewers for valuable comments on a previous version of this manuscript. Further, we are grateful to André Pauquet for providing samples, to Thure Dalsgaard for imaging the specimen and to Kerstin Dreczko for help with sequencing. CMOS holds a PhD fellowship co-funded by Lille University and ANR project JCJC-EVOLINK of the French Agence Nationale de la Recherche and was further supported by CPER research project CLIMIBIO funded by the Hauts-de-France Region and the European Funds for Regional Economical Development.

## References

- Bernard F (1967) Faune de l'Europe et du Bassin Méditerranéen. 3. Les fourmis (Hymenoptera Formicidae) d'Europe occidentale et septentrionale. Paris: Masson, 411 pp
- Blaimer BB, Brady SG, Schultz TR, Lloyd MW, Ward PS (2015) Phylogenomic methods outperform traditional multi-locus approaches in resolving deep evolutionary history: a case study of formicine ants. *BMC Evolutionary Biology* 15: 1–14, <https://doi.org/10.1186/s12862-015-0552-5>
- Blick T, Haengii A, Wittenberg R (2006) Spiders and Allies - Arachnida. In: Wittenberg R (ed), Invasive alien species in Switzerland. An inventory of alien species and their threat to biodiversity and economy in Switzerland, Federal Office for the Environment FOEN, Bern, pp 91–97
- Boer P, Vierbergen B (2008) Exotic ants in The Netherlands (Hymenoptera: Formicidae). *Entomologische Berichten* 68(4): 121–129
- Boer P, Noordijk J, Loon AJ van (2018) Ecologische atlas van Nederlandse mieren (Hymenoptera: Formicidae). EIS Kenniscentrum Insecten en andere ongewervelden. Leiden, 123 pp
- Borowiec L (2014) Catalogue of ants of Europe, the Mediterranean Basin and adjacent regions (Hymenoptera: Formicidae). *Genus (Wroclaw)* 25(1–2): 1–340
- Clouse R (1999) Leaf-litter inhabitants of a Brazilian Pepper stand in Everglades National Park. *The Florida Entomologist* 82: 388–403, <https://doi.org/10.2307/3496866>
- Creighton WS (1950). The ants of North America. *Bulletin of the Museum of Comparative Zoology* 104: 1–585
- Dash ST, Hooper-Bùri LM, Seymour MA (2005) The pest ants of Louisiana: a guide to their identification, biology and control. Louisiana State University AgCenter Publ. 2915, 24 pp
- Deyrup M (2003) An updated list of Florida ants (Hymenoptera: Formicidae). *Florida Entomologist* 86: 43–48, [https://doi.org/10.1653/0015-4040\(2003\)086\[0043:AULOFA\]2.0.CO;2](https://doi.org/10.1653/0015-4040(2003)086[0043:AULOFA]2.0.CO;2)
- Deyrup M (2016) Ants of Florida: identification and natural history. CRC Press, 423 pp, <https://doi.org/10.1201/9781315368023>
- Deyrup M, Davis S (2000) Exotic ants in Florida. *Transactions of the American Entomological Society* 126(3+4): 293–326
- Deyrup M, Prusak Z, Davis L (2014) Florida ants. Antweb. <http://www.antweb.org/page.do?name=florida> (accessed 27 April 2014)
- Donisthorpe H (1949) A new *Camponotus* from Madagascar and a small collection of ants from Mauritius. *Annals and Magazine of Natural History* (12): 271–275, <https://doi.org/10.1080/0022934908653987>
- Donisthorpe H (1915) British ants, their life-history and classification. Plymouth: Brendon & Son Ltd. CRC Press, 423 pp
- Dorow WHO (1996) Review and bibliography of the ants of the Seychelles. *Journal of African Zoology* 110(2): 73–95
- Eichler W (1952) Die Tierwelt der Gewächshäuser. Akademische Verlagsgesellschaft Geest & Portig, Leipzig, 93 pp
- Emery C (1878) Catalogo delle formiche esistenti nelle collezioni del Museo Civico di Genova. Parte seconda. Formiche dell'Europa e delle regioni limitrofe in Africa e in Asia. *Annali del Museo Civico di Storia Naturale* 12: 43–59
- Emery C (1895) Mission scientifique de M. Ch. Alluaud dans le territoire de Diego-Suarez (Madagascar-nord) (Avril-août 1893). Formicides. *Annales de la Société Entomologique de Belgique* 39: 336–345
- Espadaler X, Pradera C (2016) *Brachymyrmex patagonicus* and *Pheidole megacephala*, two new exotic ants in Spain (Hymenoptera, Formicidae). *Iberomyrmex* 8: 4–10
- Ferster B, Prusak Z (1994) A preliminary checklist of the ants (Hymenoptera: Formicidae) of Everglades National Park. *Florida Entomologist* 77: 508–512, <https://doi.org/10.2307/3495707>
- Fisher BL (1997) Biogeography and ecology of the ant fauna of Madagascar (Hymenoptera: Formicidae). *Journal of Natural History* 31: 269–302, <https://doi.org/10.1080/00222939700770141>

- Fisher BL (2003) Formicidae, ants. In: Goodman SM, Benstead JP (eds), *The natural history of Madagascar*. Chicago: University of Chicago Press, pp 811–819
- Fisher BL (2014a) Comoros Islands. Antweb. <http://www.antweb.org/page.do?name=comoros> (accessed 07 February 2019)
- Fisher BL (2014b) Madagascar Ants. Antweb. <http://www.antweb.org/page.do?name=madagascar> (accessed 07 February 2019)
- Fisher BL (2014c) Seychelles Ants. Antweb. <http://www.antweb.org/page.do?name=seychelles> (accessed 07 February 2019)
- Fisher BL, Blard F (2014) Reunion Ants. Antweb. <http://www.antweb.org/page.do?name=reunion> (accessed 07 February 2019)
- Fisher BL, Suarez A (2014) Mauritius Ants. Antweb. <http://www.antweb.org/page.do?name=mauritius> (accessed 07 February 2019)
- Forel A (1893) Formicides de l'Antille St. Vincent, récoltées par Mons. H. H. Smith. *Transactions of the Entomological Society of London* 41: 333–418
- Forel A (1874) Les fourmis de la Suisse. Systématique, notices anatomiques et physiologiques, architecture, distribution géographique, nouvelles expériences et observations de moeurs. *Neue Denkschriften der Allgemeinen Schweizerischen Gesellschaft für die Gesammten Naturwissenschaften* 26: 1–452, <https://doi.org/10.5962/bhl.title.125537>
- Forel A (1895) Nouvelles fourmis de diverses provenances, surtout d'Australie. *Annales de la Société Entomologique de Belgique* 39: 41–49
- Forel A (1907) Ameisen von Madagaskar, den Comoren und Ostafrika. Wissenschaftliche Ergebnisse. *Reise in Ostafrika* 2: 75–92
- Forel A (1912a) Formicides néotropiques. Part VI. 5me sous-famille Camponotinae Forel. *Mémoires de la Société Entomologique de Belgique* 20: 59–92, <https://doi.org/10.5962/bhl.part.19251>
- Forel A (1912b) The Percy Sladen Trust Expedition to the Indian Ocean in 1905, under the leadership of Mr. J. Stanley Gardiner, M.A. Volume 4. No. XI. Fourmis des Seychelles et des Aldabras, reçues de M. Hugh Scott. *Transactions of the Linnean Society of London. 2nd Series. Zoology* 15: 159–167, <https://doi.org/10.1111/j.1096-3642.1912.tb00096.x>
- Gaigher R, Samways MJ, Jolliffe KG, Jolliffe S (2012) Precision control of an invasive ant on an ecologically sensitive tropical island: a principle with wide applicability. *Ecological Applications* 22: 1405–1412, <https://doi.org/10.1890/11-2002.1>
- Geiter O, Homma S, Kinzelbach R (2002) Bestandsaufnahme der Neozoen in Deutschland. *Forschungsbericht* 296 89 901/01 Umweltforschungsplan des Bundesministeriums für Umwelt, Naturschutz und Reaktorsicherheit, 308 pp
- Gerlach J (2004) Impact of the invasive crazy ant *Anoplolepis gracilipes* on Bird Island, Seychelles. *Journal of Insect Conservation* 8: 15–25, <https://doi.org/10.1023/B:JICO.0000027454.78591.97>
- Gotzek D, Axen HJ, Suarez AV, Helms Cahan S, Shoemaker D (2015) Global invasion history of the tropical fire ant: a stowaway on the first global trade routes. *Molecular Ecology* 24: 374–388, <https://doi.org/10.1111/mec.13040>
- Guénard B (2019) First record of *Brachymyrmex patagonicus* Mayr 1868 (Hymenoptera: Formicidae) from continental Asia. *Asian Myrmecology* 10: e010012
- Hulme P (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology* 46: 10–18, <https://doi.org/10.1111/j.1365-2664.2008.01600.x>
- Hulme PE, Bacher S, Kenis M, Klotz S, Kühn I, Minchin D, Nentwig W, Olenin S, Panov V, Pergl J, Pysek P, Roques A, Sol D, Solarz W, Vilà M (2008) Grasping at the routes of biological invasions: a framework for integrating pathways into policies. *Journal of Applied Ecology* 45: 403–414, <https://doi.org/10.1111/j.1365-2664.2007.01442.x>
- Katoh K, Standley DM (2013) MAFFT Multiple Sequence Alignment Software Version 7: Improvements in Performance and Usability. *Molecular Biology and Evolution* 30: 778–780, <https://doi.org/10.1093/molbev/mst010>
- Kenis M, Rabitsch W, Auger-Rozenberg MA, Roques A (2007) How can alien species inventories and interception data help us prevent insect invasions. *Bulletin of Entomological Research* 97: 489–502, <https://doi.org/10.1017/S0007485307005184>
- Kenis M, Auger-Rozenberg M-A, Roques A, Timms L, Pérez C, Cock MJW, Settele J, Augustin S, Lopez-Vaamonde (2009) Ecological effects of invasive alien insects. *Biological Invasions* 11: 21–45, <https://doi.org/10.1007/s10530-008-9318-y>
- Klotz J, Hansen L, Pospischil R, Rust M (2008) Urban ants of North America and Europe. Identification, biology and management. Cornell University Press, Ithaca and London, 224 pp
- Lanfear R, Calcott B, Ho SYW, Guindon S (2012) PartitionFinder: combined selection of partitioning schemes and substitution models for phylogenetic analyses. *Molecular Biology and Evolution* 29: 1695–1701, <https://doi.org/10.1093/molbev/mss020>
- MacGown JA, Hill JG, Deyrup MA (2007) *Brachymyrmex patagonicus* (Hymenoptera: Formicidae), an emerging pest species in the southeastern United States. *Florida Entomologist* 90: 457–464, [https://doi.org/10.1653/0015-4040\(2007\)90\[457:BPAE\]2.0.CO;2](https://doi.org/10.1653/0015-4040(2007)90[457:BPAE]2.0.CO;2)

- Maddison WP, Maddison DR (2017) Mesquite: a modular system for evolutionary analysis. 2.10
- Malumphy C (2012) Arthropods intercepted on air plants (*Tillandsia* spp.) imported from Guatemala into England and Wales. *Entomologist's Gazette* 63: 54–62
- Mamet R (1954) The ants (Hymenoptera Formicidae) of the Mascarene Islands. *Mauritius Institute Bulletin* 3: 249–259
- Mayr G (1868) Formicidae novae Americanae collectae a Prof. P. de Strobel. *Atti della Societa dei Naturalisti e Matematici di Modena* 3: 161–178
- Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In: Proceedings of the Gateway Computing Environments Workshop (GCE), New Orleans, LA, 14 Nov. 2010, pp 1–8, <https://doi.org/10.1109/GCE.2010.5676129>
- Moreau CS, Deyrup MA, David Jr. LR (2014) Ants of the Florida Keys: species accounts, biogeography, and conservation (Hymenoptera: Formicidae). *Journal of Insect Science* 14: 295, <https://doi.org/10.1093/jisesa/ieu157>
- Ortiz CM, Fernández F (2014) *Brachymyrmex* species with tumuliform metathoracic spiracles: description of three new species and discussion of dimorphism in the genus (Hymenoptera, Formicidae). *ZooKeys* 371: 13–33, <https://doi.org/10.3897/zookeys.371.6568>
- Ortiz-Sepulveda CM, Van Boclaer B, Meneses AD, Fernández F (2019) Molecular and morphological recognition of species boundaries in the neglected ant genus *Brachymyrmex* (Hymenoptera: Formicidae): towards a taxonomic revision. *Organisms Diversity & Evolution* 19: 447–542, <https://doi.org/10.1007/s13127-019-00406-2>
- Pape T, Svennningsen C (2014) Tanzania ants. Antweb. <https://www.antweb.org/> (accessed 24 December 2014)
- Rambaut A (2012) FigTree. Version 1.4.0. a graphical viewer of phylogenetic trees. <http://tree.bio.ed.ac.uk/software/figtree/>
- Rambaut A, Suchard MA, Xie D, Drummond AJ (2013) Tracer. Version 1.6. <http://beast.bio.ed.ac.uk/Tracer>
- Roques A (2010) Alien forest insects in a warmer world and a globalised economy: impacts of changes in trade, tourism and climate on forest biosecurity. *New Zealand Journal of Forestry Science* 20 suppl.: S77–S94
- Ronquist F, Teslenko M, Van der Mark P, Ayres D, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* 61: 539–542, <https://doi.org/10.1093/sysbio/sys029>
- Santschi F (1923) Revue des fourmis du genre *Brachymyrmex* Mayr. *Anales del Museo Nacional de Historia Natural de Buenos Aires* 31: 650–678
- Sharaf MR, Salman S, Aldahafer HM, Yousef AFA, Aldawood AS (2016) First occurrence of the ant genus *Brachymyrmex* Mayr, 1868 (Hymenoptera: Formicidae) from the Kingdom of Saudi Arabia. *Sociobiology* 63: 800–803, <https://doi.org/10.13102/sociobiology.v63i2.981>
- Simberloff D, Rejmanek M (2011) Encyclopedia of Biological Invasions. University of California Press, Berkeley, USA, 792 pp
- Smith MA, Fisher BL (2009) Invasions, DNA barcoding, and rapid biodiversity assessment using ants of Mauritius. *Frontiers in Zoology* 6: 1–12, <https://doi.org/10.1186/1742-9994-6-31>
- Terayama M, Kubota A, Eguchi K (2014) Encyclopedia of Japanese ants. Asakura Shoten: Tokyo, 278 pp
- Weidner H (1972) Die Entomologischen Sammlungen des Zoologischen Instituts und Museums der Universität Hamburg. VIII. Teil. Insecta V. *Mitteilungen aus dem Hamburgischen Zoologischen Museum und Institut* 68: 107–134
- Wetterer JK (2010) Worldwide spread of the pharaoh ant, *Monomorium pharaonis* (Hymenoptera: Formicidae). *Myrmecological News* 13: 115–129
- Wheeler WM (1922) Ants of the American Museum Congo expedition. A contribution to the myrmecology of Africa. IX. A synonymic list of the ants of the Malagasy region. *Bulletin of the American Museum of Natural History* 45: 1005–1055