



First report of *Wolbachia* in *Damaeus onustus* (Acari: Oribatida)

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Abstract

Purpose: Little is known about the distribution and phylogeny of bacterial endosymbionts in oribatid mites (Acari: Oribatida). Thus, we undertook the issue of occurrence of these microbial symbionts in this arthropod group.

Methods: We used PCR technique for detection of *Wolbachia* in *Damaeus onustus*. Phylogenetic analysis of the bacterium was conducted based on the 16S rDNA sequence.

Results: To the best of our knowledge, we present a novel finding of *Wolbachia* infection in the sexually reproducing oribatid mite, *D. onustus*. The presence of uninfected individuals (ca. 93%) suggests that the bacteria do not function as primary symbionts. A comparison of the bacterial 710-bp 16S rDNA sequence detected in the oribatid mite with the sequences deposited in GenBank revealed its 92–93% similarity to the 16S rDNA sequences of *Wolbachia* identified in some springtails (Collembola) and *Bryobia* sp. mite. Bacteria from *D. onustus* showed phylogenetic relationships with *Wolbachia* from springtails, *Megalothorax minimus* and *Neelus murinus*, which were included by other authors into a separate *Wolbachia* clade.

Conclusion: Our finding suggests that the strains of *Wolbachia* from *D. onustus* may form a new *Wolbachia* supergroup.

Keywords: *Wolbachia*, 16S rDNA, Oribatida, Phylogenetic analysis

Findings

Wolbachia is one of the most frequent intracellular symbiont of invertebrates: arthropods and nematodes. It is estimated that 52% of arthropod species are infected with *Wolbachia* (Weinert et al. 2015; Huang et al. 2019). The bacterium is responsible mainly for manipulating its host reproduction (Ali et al. 2016; Mariño et al. 2017) and causing sex-ratio distortion in the infected population (Salunkhe et al. 2014; Duploux and Hornett 2018). However, the range of its impact is much broader and includes host fitness (Zug and Hammerstein 2015; Liu et al. 2018), viral infection inhibition (Geoghegan et al. 2017; Tan et al. 2017), and defense against pathogens through the involvement in the production of host anti-predator and alarm pheromones (Becerra et al. 2015).

Wolbachia is transmitted vertically through the egg cytoplasm, from mother to offspring within the host population (Zhao et al. 2013; Guo et al. 2018). Horizontal transmission of the endosymbiont between hosts can also occur (Kremer and Huigens 2011; Brown and Lloyd 2015; Ahmed et al. 2016; Pietri et al. 2016) and is usually inferred from the presence of similar or identical bacterial strains in two unrelated host species. Food may be a medium for *Wolbachia* transmission among similarly feeding invertebrates, and sharing the same diet may promote horizontal transmission of these bacteria (Haine et al. 2005; Sintupachee et al. 2006; Li et al. 2016; Chrostek et al. 2017). The ingestion of infected carcasses or eggs could be a possible source of *Wolbachia* introduction, and eating dead invertebrates with bacterial cells inside their tissues may facilitate horizontal transmission of *Wolbachia* (Brown and Lloyd 2015).

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Outside the host tissue, *Wolbachia* cannot be cultured in laboratory conditions using conventional bacteriological techniques. Identification and distribution of the endosymbiont in different hosts rely on molecular PCR-based screening methods. Sequence analysis of 16S rDNA and housekeeping genes of *Wolbachia* provides information useful in typing, evolutionary research, and phylogeny of these bacteria (Baldo et al. 2006; Werren et al. 2008). Different sets of genes are applied in the symbiont characterization. Phylogenetic analysis is based on 16S rDNA and housekeeping genes, for example, *atpD* (ATP synthase beta chain), *dnaA* (chromosomal replication initiator protein), and *topI* (DNA topoisomerase I) (Crainey et al., 2010). The *wsp* gene coding for the *Wolbachia* surface protein is also a reliable tool in the bacteria phylogeny (Baldo et al. 2006). Currently, strains of genus *Wolbachia* are divided into supergroups A-Q (Glowska et al. 2015).

Although a few studies on endosymbionts in oribatid mites (Acari: Oribatida) have been conducted (Pierrot-Minnot and Norton 1997; Weeks et al. 2003; Liana and Witaliński 2010; Konecka and Olszanowski 2015, Konecka and Olszanowski 2019a, Konecka and Olszanowski 2019b, Konecka and Olszanowski 2019c, Konecka and Olszanowski 2019d, Konecka et al. 2019), still little is known about the distribution and phylogeny of microorganisms in this arthropod group. We identified *Wolbachia* in *Damaeus onustus*. Phylogenetic analysis of the bacterium was conducted based on the 16S rDNA sequence.

Fifteen individuals of the oribatid mite, *D. onustus* (Acari: Oribatida) were isolated from a sample of soil and litter collected in a deciduous forest in the Wkrzańska Forest, West Pomeranian Voivodeship in Poland (53° 58' N, 14° 43' E).

DNA was extracted using the Genomic Mini kit (A&A Biotechnology). Amplifications of the 781-bp product of *Wolbachia* 16S rDNA were performed in a standard PCR mixture with 553F_W (5'-CTTCATRYACTCGAGT TGCWGAGT-3') and 1334R_W (5'-GAKTTAAAYC-GYGCAGGBGTT-3') primers, as presented by Simões et al. (2011). A negative control without DNA template was included in the reaction. The PCR program was as follows: 94 °C for 2 min; 35 cycles of 94 °C for 30 s, 62 °C for 30 s, and 72 °C for 45 s; and 72 °C for 10 min (Simões et al. 2011). Amplicons were electrophoresed, sequenced with BigDye Terminator v3.1 on an ABI Prism 3130XL Analyzer (Applied Biosystems), and analyzed with BLASTn. The 710-bp 16S rDNA sequence was deposited in GenBank under accession no. MH921824.

The 16S rDNA sequence of *Wolbachia* from *D. onustus* was aligned with the loci identified in other invertebrate hosts. The alignment of 32 *Wolbachia* sequences was constructed with the use of CLUSTAL W (Thompson et al. 1994). An outgroup of *Ehrlichia* spp. sequences was added. The jModelTest 2 software (Darriba et al. 2012) was used to select the optimal model of sequence evolution. The General Time Reversible model with gamma distribution among site rate variation (GTR +G) was selected. Phylogenetic analysis was conducted using MEGA

Table 1 *Wolbachia* strains used in phylogenetic analysis

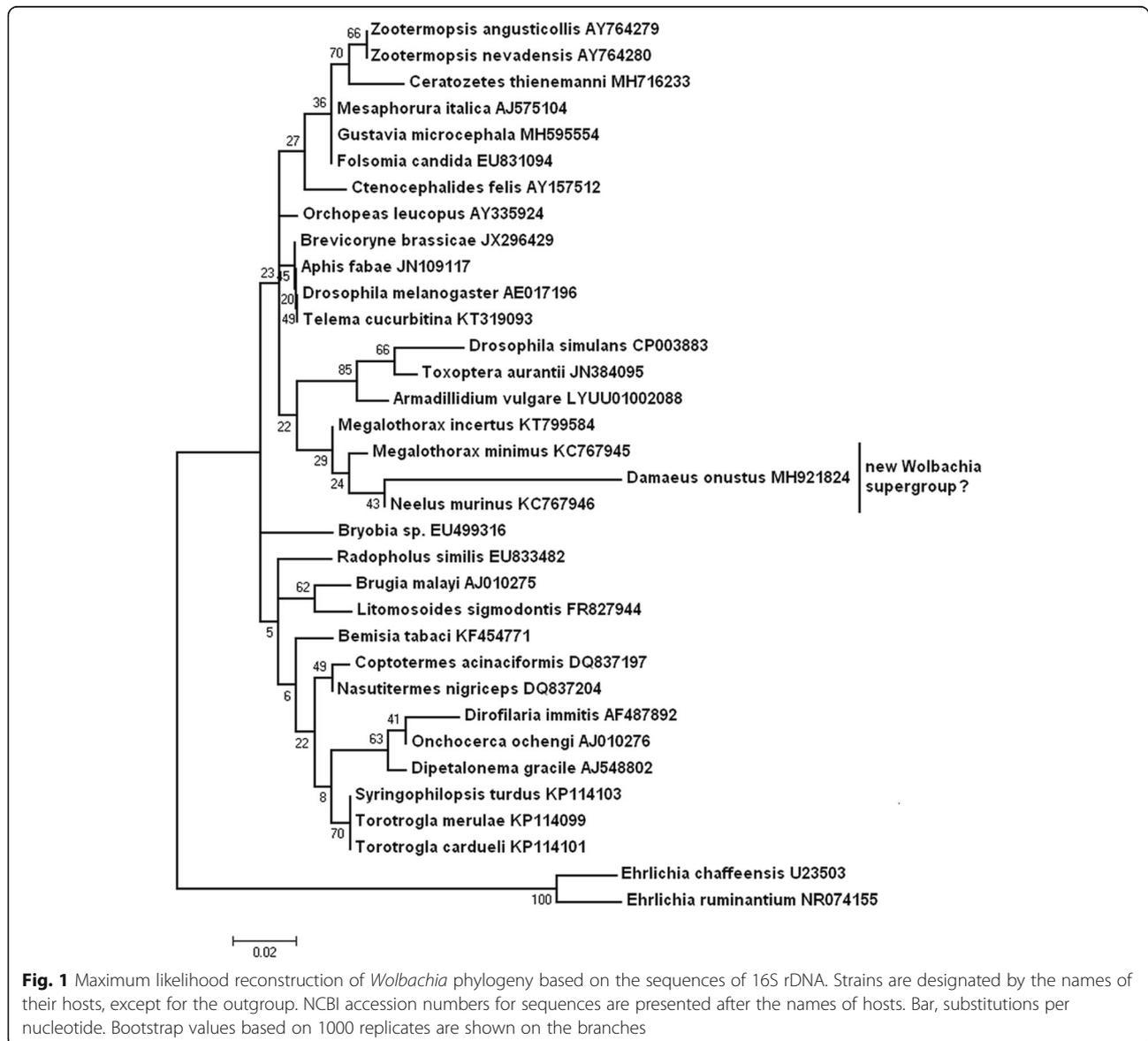
Designation of <i>Wolbachia</i> supergroup	Host of <i>Wolbachia</i>
A	<i>Drosophila melanogaster</i> , <i>Telema cucurbitina</i>
B	<i>Drosophila simulans</i> , <i>Armadillidium vulgare</i>
C	<i>Dirofilaria immitis</i> , <i>Onchocerca ochengi</i>
D	<i>Litomosoides sigmodontis</i>
E	<i>Ceratozetes thienemanni</i> , <i>Mesaphorura italica</i> , <i>Gustavia microcephala</i> , <i>Folsomia candida</i> , <i>Megalothorax incertus</i>
F	<i>Coptotermes acinaciformis</i> , <i>Nasutitermes nigriceps</i>
H	<i>Zootermopsis angusticollis</i> , <i>Zootermopsis nevadensis</i>
I	<i>Ctenocephalides felis</i> , <i>Orchopeas leucopus</i>
J	<i>Dipetalonema gracile</i>
K	<i>Bryobia</i> sp.
L	<i>Radopholus similis</i>
M	<i>Brevicoryne brassicae</i> , <i>Aphis fabae</i>
N	<i>Toxoptera aurantii</i>
O	<i>Bemisia tabaci</i>
P	<i>Syringophilopsis turdus</i> , <i>Torotrogla merulae</i>
Q	<i>Torotrogla cardueli</i>
?	<i>Damaeus onustus</i> , <i>Megalothorax minimus</i> , <i>Neelus murinus</i>

version 6.0 (Tamura et al. 2013). The maximum likelihood bootstrap support was determined by using 1000 bootstrap replicates. Recombination in genes between strains was detected by the ϕ test using the SplitsTree4 software (Huson and Bryant 2006).

To the best of our knowledge based on an extensive literature search, this is the first report of *Wolbachia* infection in the sexually reproducing oribatid mite *D. onustus*. We examined 15 specimens of *D. onustus* and only one of them was infected with *Wolbachia*. The low occurrence of infected individuals in this small sample (ca. 7%) suggests that the bacteria do not function as primary symbionts.

The 710-bp 16S rDNA sequence of *Wolbachia* was deposited in GenBank under accession no. MH921824. The ϕ test did not find statistically significant evidence of

recombination ($p = 0.4885$). A comparison of the bacterial 16S rDNA sequence detected in *D. onustus* with the sequences deposited in GenBank revealed similarity of 92–93% to the 16S rDNA sequences of *Wolbachia* identified in springtails (Collembola): *Megalothorax minimus* (accession no. KC767945), *M. incertus* (accession no. KT799584), and *Neelus murinus* (accession no. KC767946). The *Wolbachia* sequence was also highly similar (92%) to mite, *Bryobia* sp. (accession no. EU499316). These sequences were included in phylogenetic analysis of bacteria together with *Wolbachia* sequences representing supergroups A–Q (Table 1). Phylogeny based on the 16S rDNA and *ftsZ* gene sequences of *M. minimus* and *N. murinus* bacteria was presented by Tanganelli et al. (2014). These authors found that *Wolbachia* from the two species of springtails did not cluster with known *Wolbachia* supergroups and formed a separate



clade. Our research confirmed their findings. *Wolbachia* from the oribatid mite, *D. onustus*, showed phylogenetic relationships with *Wolbachia* from *M. minimus* and *N. murinus*, and these three bacterial strains clustered together (Fig. 1). Oribatida and Collembola may coexist in the same soil habitat (Kováč et al. 2001; Huhta et al. 2010), and horizontal transfer of bacteria between these two groups of invertebrates cannot be excluded, which may explain the close relationship between the bacterial strains from *D. onustus* and springtails.

Our study is consistent with the observation of Tangelini et al. (2014) that *Wolbachia* strains from *M. minimus* and *N. murinus* are phylogenetically distinct from supergroup E bacteria from other springtails, *Mesaphorura italica* and *Folsomia candida*. Supergroup E is also represented by oribatid mites: *Gustavia microcephala* (Konecka et al. 2019) and *Ceratozetes thienemanni* (Konecka and Olszanowski 2019a). Our results suggested that *Wolbachia* from Oribatida formed two distantly related supergroups and confirmed the fact that the bacteria that infected Collembola also clustered into two separate supergroups. Further analysis, including bacteria phylogeny based on the sequences of house-keeping genes is required to explain the membership of *Wolbachia* from *D. onustus* to a potentially new *Wolbachia* supergroup.

In conclusion, our study presents for the first time the occurrence of *Wolbachia* infection in Oribatida *D. onustus*. The analysis of the 16S rDNA sequence of *Wolbachia* from the mite indicated similarity and phylogenetic relationship with bacteria found in springtails, *M. minimus* and *N. murinus*. Our discovery suggested that the strains may form a new *Wolbachia* supergroup. The role of these bacteria in *D. onustus* remains unknown and also needs further investigations. Nevertheless, the effect of parthenogenesis induction by *Wolbachia* could be excluded considering the fact that *D. onustus* is a sexually reproducing species.

Competing interests

The authors declare no conflicts of interest.

Ethics approval and consent to participate

All work performed in studies involving invertebrate animals (mites) was done in compliance of the ethical standards following for the environmental samples. This article does not contain any studies with human participants, laboratory animals, or vertebrate animals. The informed consent was not applicable.

Authors' contributions

EK and ZO designed the study and planned the experiments. AJ collected the sample. EK, ZO, and AJ carried out the experiments. EK analyzed the data and wrote the manuscript with input from ZO. The authors read and approved the final manuscript.

Funding

N/A

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Received: 16 October 2019 Accepted: 13 May 2020

Published online: 15 June 2020

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