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ANIMAL SCIENCE

A new wild strain of *Caenorhabditis elegans* associated with *Allograpta exotica* (Syrphidae) in Argentina: an update of its ecological niche and worldwide distribution

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Abstract: *Caenorhabditis elegans* is a free-living nematode, belonging to the bacterivorous trophic group. Although it was cited in several countries, in different types of ecosystems and in associations with other organisms, the wild habitats of this nematode have not yet been precisely defined. In Argentina, *C. elegans* was recently isolated from the hoverfly *Allograpta exotica*, a voracious predator with potential biological control against aphids in horticultural crops. In this frame, the objectives of this study were (i) to characterize it molecularly and morphologically (ii) to report a wild strain of *C. elegans* for the first time from Argentina, (iii) to present a new ecological niche by associating it with *A. exotica* and (iv) to evaluate the pathogenicity against these insects. The results of the morphological and molecular analyses made it possible to determine that the isolated nematode was *C. elegans*, thus establishing the ARGLP1900 wild strain as the first record of this nematode for Argentina. A new association was described, since there are no records of interaction between *C. elegans* and *A. exotica*, providing information on a new ecological niche. The new wild strain found in this work, could be appropriate for comparative genomic studies with other *C. elegans* strains.

Key words: *Allograpta exotica, Caenorhabditis elegans, wild strain,* Argentina.

INTRODUCTION

Caenorhabditis elegans is a free-living nematode, belonging to the bacterivorous trophic group. It was found in Europe, America, Africa, Oceania and rarely in Asia and prefers humid temperate areas with a wealth of decaying vegetation (Kiontke et al. 2011, Félix & Duveau 2012, Petersen et al. 2014, Cook et al. 2016). It is considered an important model species used in a range of biological research, due to its short life cycle, invariant pattern of cell division during its development (Ewe et al. 2020) and easy maintenance on agar plates inoculated with *Escherichia coli* (Frézal & Félix 2015). Since the 90s, *C. elegans* has been established as a model organism for studying the genetic architecture of complex traits using quantitative genetic analyses based on genetic variation (Gaertner & Phillips 2010, Gao et al. 2018). Over the years, digital platforms have been created to gather valuable information on the ecology, physiology, and phylogeny of new *C. elegans* strains and its worldwide distribution. Among them we can mention Wormatlas (https://www.wormatlas.org/), *Caenorhabditis* Genetics Center (https://cgc.umn.edu), Wormbuilder (http://www.wormbuilder.org), The National BioResource Project (NBRP) (https://shigen.nig.ac.jp/c.elegans) and the online review Wormbook (http://www.wormbook.org). Cook et al. (2016) introduced the *C. elegans* Natural

Diversity Resource (CeNDR) to enable statistical genetics and genomics studies of *C. elegans* and to connect the results to human disease. Snoek et al. (2020) launched Worm Quantitative Trait Loci 2 (WormQTL2), a database for comparative investigations in *C. elegans* genetics. These platforms provide the scientific community with a comprehensive database to examine natural variation in wild strains of *C. elegans*.

C. elegans was originally isolated in rich soil or compost but has been also found in decomposing plant material, such as thick herbaceous stems (Hodgkin & Doniach 1997, Félix & Duveau 2012). This nematode is thus associated with horticultural human activity but also found in rotting fruits and wilder settings like woods. *C. elegans* is commonly found in phoresis with invertebrates, such as *Porcellio scaber* and *P. spinicornis* (Isopoda) in Scotland (Cutter 2006), slugs, snails and also chilopods in France (Barrière and Félix 2005, 2007, Félix & Duveau 2012, Petersen et al. 2015, Frézal & Félix 2015). A facultative necromenic habit for *C. elegans* was also reported under laboratory conditions, where the nematode secure the body of the associated animal as a future food source (Kiontke & Sudhaus 2006). However, the natural habitat of *C. elegans* is not well known, therefore, new records of wild strains and their habitats and ecological niches provides valuable information on this model organism (Kiontke et al. 2011).

In Argentina, *C. elegans* was recently isolated from the hoverfly *Allograpta exotica* Wiedemann (Diptera: Syrphidae), a voracious predator with potential biological control against aphids in horticultural crops, according to Bugg et al. 2008. In this frame, the objectives of this study were (i) to characterize *C. elegans* molecularly and morphologically (ii) to report a wild strain of *C. elegans* for the first time from Argentina, (iii) to present a new ecological niche by associating it with *A. exotica* and (iv) to evaluate the pathogenicity against these insects.

MATERIALS AND METHODS

Insect sampling and nematode isolate

Larvae of hoverflies were collected in strawberry crops from an agro-ecological site, where no agrochemical inputs were applied, in the horticultural production area known as Horticultural Green Belt of La Plata, Buenos Aires, Argentina (35° 01'21.3"S 58° 03'25.5"W) during the spring and summer of 2018-2019. In the laboratory, it was observed that several hoverfly larvae were found dead containing a large number of nematodes inside. Those larvae were dissected in Petri dishes with distilled water under a stereoscopic microscope (Nikon SMZ1270) and nematodes were recovered according to the Poinar technique (Poinar 1975).

Morphologic characterization

Nematodes were measured using a camera lucida and an ocular micrometer in a Leica LC-500 microscope. For each individual, we determined the total length (TL), cephalic diameter (CD), width at the level of the nerve ring (WLR), anterior distance to nerve ring (ANR), esophagus length (EL), anterior distance to median bulb (AMB), greatest width (GW), width at the level of the vulva (WV), vulva width (VW), posterior-end width (PEW), tail length (TAL), body length divided by the head-vulva distance (V), spicule length (SL) and spicule width (SW). All measurements were given in micrometers (µm) unless otherwise stated. Photographs were taken with a Leica TCS SP5 camera. Voucher (MLP-He 7693) specimens have been deposited in the Museo de Ciencias Naturales de La Plata, Buenos Aires, Argentina.

DNA characterization and phylogenetic analysis

To confirm the nematode identification, a molecular approach was performed utilizing adult specimens fixed in absolute ethanol (n=30). Genomic DNA was extracted using 100 µl of a 5% suspension of Chelex in deionized water and 2 µl of 10 mg/ml proteinase K, followed by overnight incubation at 56°C, boiling at 90°C for 8 minutes and centrifugation at 14,000 rpm for 10 minutes. An aliquot of 1 µl of the supernatant was utilized as a template for PCR. The samples were utilized in a Polymerase Chain Reaction (PCR) to amplify a set of nuclear loci containing the following sequences: 18S ribosomal RNA gen (partial sequence), internal transcribed spacer ITS1, 5.8S ribosomal RNA gen, ITS2 and 28S ribosomal RNA gen (partial sequence). The primers [ITS-F (5´TTGAACCGGGTAAAAGTCG-3´) and ITS-R (5´-TTAGTTTCTTTTCCTCCGCT-3´)] were utilized according to Maneesakorn et al. (2011) with the Master Mix (PBL). The thermocycler conditions were: 94ºC for 15 min (one cycle); 92°C for 30 s, 56°C for 40 s; 72°C for 110 s (35 cycles); a single final extension period of 72°C for 10 min (one cycle). PCR products were analyzed by electrophoresis on 1% agarose gels and visualized by staining with ethidium bromide. The consensus sequences obtained were compared with sequences in the BLAST tool available in the National Center for Biotechnology Information (NCBI) database (http: //www.ncbi.nlm.nih. gov).

Phylogeny tree of the isolated nematode based on 5.8S-ITS2-28S rDNA was performed through maximum likelihood (Tamura et al. 2004). First, ClustalO software (Sievers et al. 2011) was used for multiple alignment. The evolutive model (TPM2u+F+I+G4) and tree topology was inferred by using the IQTree software (Trifinopoulos et al. 2016), and ultrafast bootstrap values were estimated (10000 pseudo-replicates). The tree was drawn to scale, with branch lengths in the same proportions as the evolutionary distances used to infer the phylogenetic tree. FigTree V1.4.4 (Rambaut & Drummond 2018) and Inkscape (v 1.0, www.inkscape.org) were used to visualize and edit the tree, respectively.

Potential pathogenicity against *A. exotica*

To determine the association grade of *C. elegans* with *A. exotica* a pathogenicity assay was realized. Isolated nematodes were replicated and maintained in the CEPAVE (Centro de Estudios Parasitológicos y de Vectores, CCT La Plata, CONICET/UNLP) following the protocols of Stiernagle & Hope (1999). Nematodes were transferred to Petri dishes with nutrient agar culture medium, *E. coli* OP50 strain was sown as food for nematodes. These plates were incubated for 24 hours at 30°C in order to allow the complete growth of the bacterial grass. Nematodes were deposited on the plates and placed in an incubation chamber at 22°C and 75% humidity.

For the infection assay, 16 Petri dishes (3 cm diameter) with 500 mm of solid agar-agar were used. In each plate three L3 larvae of *A. exotica* were deposited, then a 100 µl inoculum of a 1000 juveniles/ 1 ml of sterilized water solution of the nematodes was inoculated. The plates were covered with plastic wrap and placed in an incubation chamber at 24°C and 75% humidity. The mortality of *A. exotica* was recorded every 24 hours for four days. A control group was tested adding 100 µl of sterilized water to a Petri dish with 500 mm of solid agar-agar and three *A. exotica* larvae. Bioassays were conducted three times.

RESULTS

The results obtained in this work allowed us to establish that the nematodes isolated from the

interior of *A. exotica* larvae belong to *C. elegans* (Figure 1). This new strain was named as *C. elegans* ARGLP1900, thus constituting the first record of this model nematode for Argentina. The morphometric data of the *C. elegans* specimens prospected can be seen in Table I. Among the *C. elegans* specimens initially surveyed, juveniles (n=60), hermaphrodites (n=40) (Figure 2a, b) and males (Figure 2c) (n=3) were found. The alignment BLAST of the segment 18S ribosomal RNA gen (partial sequence), internal transcribed spacer ITS1, 5.8S ribosomal RNA gen, ITS2 and 28S ribosomal RNA gen (partial sequence) nucleotide sequence was 1047 bp. The bioinformatics analysis revealed high nucleotide sequence identity to the nematode *C. elegans* with identity values ranging between 97.7 % to 99.6%. The sequence generated from this study was submitted to the NCBI GenBank database (http:// www.ncbi.nlm.nih.gov) and can be accessed using the GenBank accession number: MK511992. The phylogenetic analysis placed MK511992 *C. elegans* ARGLP1900 as a member of a clade related to four populations of *C. elegans* (Figure 3). Based on the results obtained, the cosmopolitan distribution of *C. elegans* was updated, since there are no records of this nematode for Argentina to date (Figure 4). Regarding the pathogenicity assay of the ARGLP1900 strain, no mortality of *A. exotica* larvae was recorded at 24, 48, 72 and 96 hours since the beginning of the experiment.

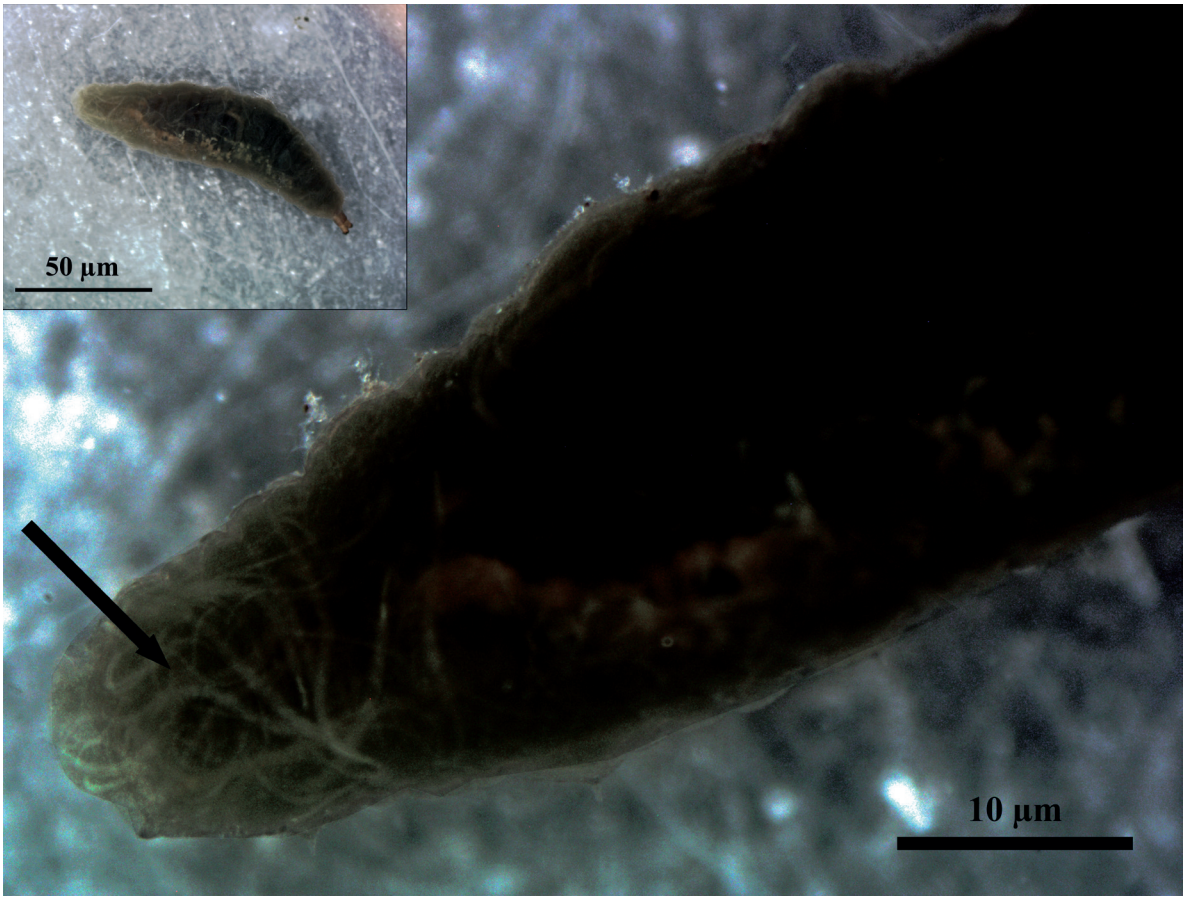

Figure 1. ***Allograpta exotica*** **larva (L3) collected from a horticultural crop in La Plata, Buenos Aires, Argentina. A large number of nematodes can be observed within the larvae of the insect (black arrow). This image shows the first report of the association between** ***Caenorhabditis elegans*** **and** ***A. exotica*** **(photo taken with a Nikon SMZ1270).**

Table I. Morphometry measures (µm) of *Caenorhabditis elegans* juvenile stages (J2, J3 and J4), immature and mature hermaphrodite and male. Morphometric characteristics: Total length (TL), cephalic diameter (CD), width at the level of the nerve ring (WLR), anterior distance to nerve ring (ANR), esophagus length (EL), anterior distance to median bulb (AMB), greatest width (GW), width at the level of the vulva (WV), vulva width (VW), posterior-end width (PEW), tail length (TAL), body length divided by the head-vulva distance (V), spicule length (SL) and spicule width (SW), were measured using a camera lucida and an ocular micrometer in a Leica LC-500 microscope.

	TL	CD	WLR	GW	PEW	WV	ANR	EL	AMB	TAL	VL	V	SL	SW
J2 (n=20)	373.5 ± 46.76 (315-423)	7.88 ±1.89 (4.5-8.8)	13.2 ± 2.82 (11.5-18)	15 ± 4.06 (11.5-20.5)	9.5 ± 1.12 (9-11.5)	-	59.4 ± 3.76 (54-63)	102.6 ± 4.93 (94.5-108)	41.4 ± 3.76 (36-45)	45 ± 8.42 (31.5-54)				
J3 (n=20)	494.30 ± 33.96 (450-567)	7.88 ± 1.93 (4.5-9)	18.85 ± 1.18 (18-20.5)	19.98 ± 4.11 (11.2-27)	13.12 ± 4.01 (9-20.5)	-	76.05 ± 9.82 (67.5-99)	114.58 ± 9.48 (99-130.5)	47.86 ± 3.03 (45-54)	62.59 ± 9.95 (45-81)				
J4 (n=20)	607.91 ± 25.01 (576-648)	8.91 ± 0.10 (8.8-9)	25.67 ± 5.17 (19-36)	27.59 ± 3.57 (20.5-36)	16.32 ± 2.47 (11.5-18)	-	87.89 ± 4.74 (81-94.5)	133.55 ± 12.65 (99-144)	60.14 ± 3.64 (54-63)	69.60 ± 13.21 (45-88)				
Immature hermaphrodite (n=20)	826.2 ± 24.97 (801-864)	10.5 ± 1.36 (9-11.5)	26.6 ± 3.92 (20.5-31.5)	41.4 ± 3.76 (36-45)	20.7 ± 4.02 (18-27)	-	104.4 ± 8.04 (99-117)	129.6 ± 22.81 (108-166.5)	64.8 ± 5.13 (58.5-72)	84.6 ± 12.07 (72-99)				
Mature hermaphrodite (n=20)	825.95 ± 93.52 (720-1044)	10.11 ± 1.28 (9-11.5)	30.15 ± 4.27 (27-36)	41.32 ± 3.38 (36-45)	22.18 ± 6.62 (18-40.5)	48.73 ± 5.95 (36-54)	99 ± 11.81 (81-117)	148.91 ± 14.85 (126-180)	65.05 ± 8.39 (54-81)	90 ± 20.22 (63-135)	17.27 ± 5.7 (11.5-27)	53.20 ± 1.48 (51.1-55.6)		
Male (n=1)	855	8.8	27	36	22.5	-	99	112.5	76.5	45			30.5	4.5

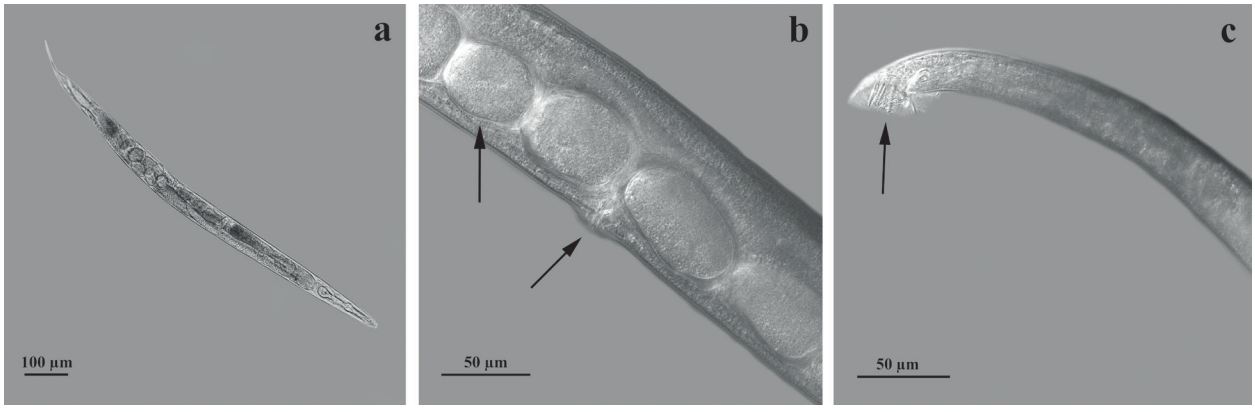

Figure 2. *Caenorhabditis elegans* isolated from the interior of larvae (S3) of *Allograpta exotica* in a horticultural crop in La Plata, Buenos Aires, Argentina. a. Hermaphrodite; b. Vulvar region of the hermaphrodite, the black arrows points to vulva opening and eggs; c. Posterior region of the male, the black arrow points the papillae arrengment (photo taken with a Leica TCS SP5).

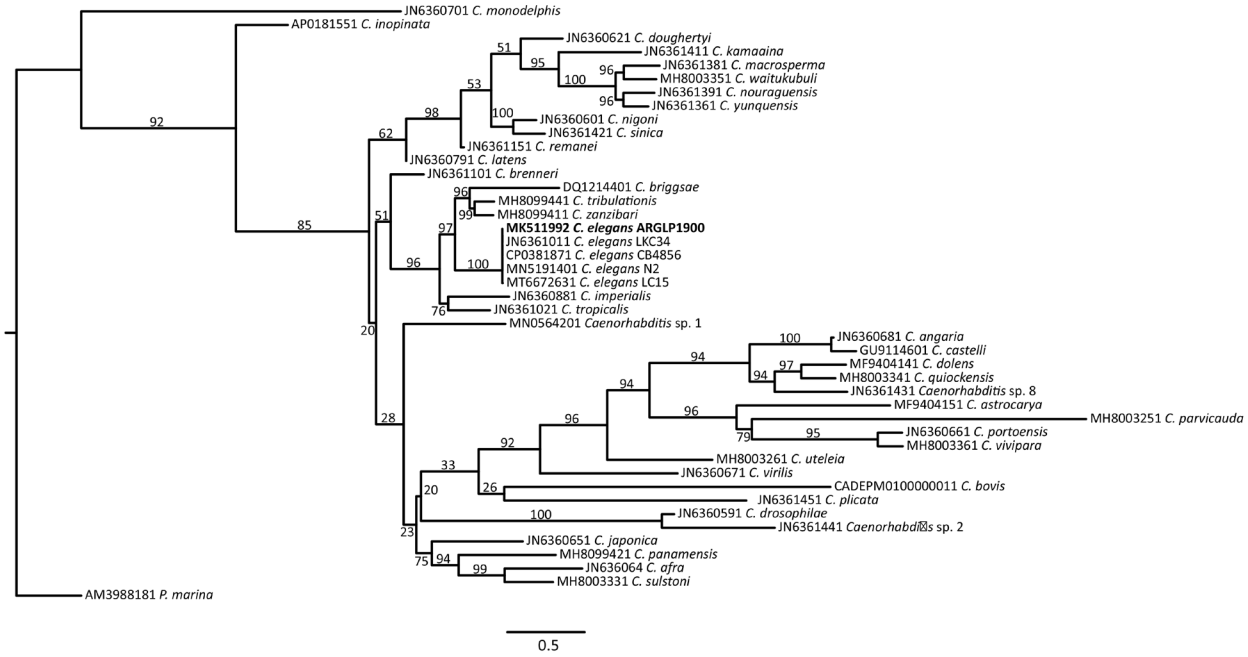

Figure 3. Phylogeny of *Caenorhabditis elegans* based on 5.8S-ITS2-28S rDNA data including the new strain MK511992 *Caenorhabditis elegans* ARGLP1900. The tree topology was inferred by maximum likelihood (ML), and ultrafast bootstrap values were reported. The tree is drawn to scale, with branch lengths in the same proportions as the evolutionary distances used to infer the phylogenetic tree.

DISCUSSION

Morphometrical data reported in this work are similar to those of Cassada & Russell 1975 and Bird & Bird 1991 for *C. elegans*. This nematode can be recognized morphologically by the position and the shape of the vulva and the egg shape in the hermaphrodites, and by the male tail composed of an elongated bursa and a cuticularized fan (*caudal alae*) with nine pairs of sensory rays (*caudal papillae*).

The primers ITS-F and ITS-R by Maneesakorn et al. (2011) were able to amplify the 18S ribosomal RNA gen (partial sequence), internal transcribed spacer ITS1, 5.8S ribosomal RNA gen, ITS2 and 28S ribosomal RNA gen (partial sequence). This new sequence also grouped with four GenBank sequences belonging to *C. elegans* corroborating the species. The maximum similarity percentage (99.6%) was observed with *C. elegans* LC15 (MT 6672631) from citrus orchard soil from South Africa. In the tree topology inferred by maximum likelihood (ML), bootstrap values showed that our new strain, *C. elegans* ARGLP1900, is related to the species *C. briggsae*, *C. tribulationis*, *C. zanzibari* (BV = 97) and *C. imperialis* and *C. tropicalis* (BV = 96). Furthermore, the analysis shows a match (BV = 100) of the new strain with four GenBank sequences from the *C. elegans* strains: JN6361011 *C. elegans* LKC34, CPO381871 *C. elegans* CB4856, MNS191401 *C. elegans* N2 and MT6672631 *C. elegans* LC15.

Eyualem-abebe et al. (2011) demonstrated that some species of the genus *Caenorhabditis* (e.g. *C. elegans*, *C. briggsae*, *C. remanei* and *C. brenneri*) in association with some bacteria such as *Serratia* sp. can be pathogenic under laboratory conditions. We believe that ARGLP1900 strain 162 possibly is not associated with an entomopathogenic bacteria. This could be the explanation for the negative result of the pathogenicity assay carried out in this study, since in research with entomopathogenic nematodes,

Figure 4. Worldwide distribution of *Caenorhabditis elegans* based on the data published by Frézal & Félix 2015 and the new register of MK511992 *Caenorhabditis elegans* ARGLP1900 wild strain for Argentina (35° 01'21.3"S 58° 03'25.5"W) provided by this research work (black star).

infectivity is observed mainly within 48 hours after the start of the experiment (Nithiskarani et al. 2019, Eliceche et al. 2020). Although pathogenicity could not be demonstrated, in this work the close association of *C. elegans* with larvae of *A. exotica*, a voracious predator with potential biological control against aphids in horticultural crops is cited for the first time in field conditions.

The geographical updating of a model organism used in evolutionary and human health studies is of great importance. In South America, we can find a total of nine wild strains of this nematode: three in Peru and Chile, two in Brazil and one in Uruguay (Schulenburg & Félix 2017). In our work we provided the first record of *C. elegans* for Argentina being the tenth register for South America.

In *C. elegans* there are hermaphrodites and males. The males have extremely low natural occurrence rate, which is around 0.1% and they occur by spontaneous non-disjunction in the hermaphrodite germ line during meiosis (Wood 1988). Hermaphrodites will produce exact replicas without genetic variability, so copulation with males increases the probability of mutations in the progeny and has been studied that this event increase the future appearance of males by up to 50% (Riddle et al. 1997, Altun & Hope 2009, Barriére & Félix 2015). For this reason, in this study we highlight the finding of male individuals of *C. elegans* in a vegetable field. Unifying the information on strains facilitates future studies on natural variation in the *Caenorhabditis* species community, contributing to various topics ranging from evolutionary

process studies to those related to human health.

In the present work we update the worldwide distribution of *C. elegans*, described a new ecological niche for *C. elegans* population isolated from Argentina, associated in field conditions to *Allograpta exotica*. We also provide new data in the ecology, genetic and phylogeny of this model nematode.

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Author contributions

MR and FDL did the samplings, JMR and AS identified and characterized morphologically the nematodes, JMR, AS, MFA, DB did the molecular characterization, DB performed the phylogenetic analysis, AS, JMR, FDL carried out the insects and nematodes colony maintenance and pathogenicity assay, JMR, AS, MFA wrote the manuscript.