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Life history and DNA barcode of *Oxyurella longicaudis* (Birgei, 1910) (Cladocera, Anomopoda, Chydoridae)

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Abstract

Background: Cladocera is an important group of freshwater zooplankton, and the species plays an important role in energy transfer and in aquatic food webs. *Oxyurella longicaudis* is a Chydoridae species that has been recorded in North and South America. The aim of this study is to investigate the life cycle aspects of parthenogenetic females of *O. longicaudis* cultured in laboratory under controlled conditions: temperature $(23^{\circ}C \pm 05^{\circ}C)$, photoperiod (12 h light/12 h dark), food supply, and reconstituted water.

Results: Embryonic development duration $(2.3 \pm 0.5 \text{ days})$, post-embryonic development $(5.2 \pm 0.69 \text{ days})$, mean fecundity (two eggs female⁻¹ brood⁻¹), total egg production $(22.55 \pm 3.98 \text{ eggs})$, average longevity (58 days), and body growth of the species were recorded. We also report the first DNA barcode for *O. longicaudis* isolated in Brazil, which will allow for easy identification in future zooplankton community studies. The analysis shows a genetic divergence of around 7% between our Brazilian isolate and *O. longicaudis* isolates from Mexico.

Conclusions: The time of embryonic and post-embryonic development of *O. longicaudis* was higher than that of the other species of the same family, which contributed to lower total egg production throughout its life cycle. The genetic divergence appears to be sufficient to classify the two isolates as different species.

Keywords: Conservation-priority areas; Zooplankton; Bionomics; Cryptic speciation; COI

Background

Cladocerans participate in energy transfer and aquatic food webs. In lakes and ponds, they represent a link in the food chain by consuming phytoplankton and are preyed upon by other invertebrates and fish (Sarma et al. 2005; Rocha et al. 2011). Cladocerans may be filter feeders, such as family members of Sididae, Moinidae, and Daphnidae or scrapers like the Macrothricidae and Chydoridae (Elmoor-Loureiro 2004; Castilho-Noll et al. 2010). The latter family feeds by scraping surfaces of the macrophytes or sediment.

Studies focusing on functional classification of Cladocera species are scarce, and its type of feeding is used for functional classification, so this gap in the literature needs to be addressed (Barnett et al. 2007). Studies have also shown

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that cladocerans' fine mesh filtering apparatus allows them to feed on small protozoa and the microbial flora of aquatic environments or feed on bacteria associated with algae (Geller and Müller 1981; Ooms-Wilms et al. 1995).

According to Frey (1980), representatives of the Chydoridae family are found in the littoral region of water bodies where they live associated with macrophytes, periphyton, and sediment. The distribution of the members of the Chydoridae family is directly related to the presence of macrophytes, most often occurring in specific association (Sacherová and Hebert 2003).

Oxyurella longicaudis is a Chydoridae species recorded in North and South America. In Brazil, they have been recorded in the northeast (Ceará, Pernambuco, Bahia, and Maranhão states), central west (Mato Grosso, Mato Grosso do Sul, and Goiás states), and the southeast (Rio de Janeiro, São Paulo, and Minas Gerais states)

© 2015 Castilho et al; licensee Springer. This is an Open Access article distributed under the terms of the Creative Commons Attribution License (http://creativecommons.org/licenses/by/4.0), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly credited. (Elmoor-Loureiro 2007; Van Damme and Dumont 2010; Rocha et al. 2011; Castilho and Santos-Wisniewski 2013).

This species is rare since it was found in only 3 of 40 water bodies sampled in priority regions for conservation in southern Minas Gerais State (Castilho and Santos-Wisniewski 2013). This species has been identified in oligotrophic environments and is probably sensitive to environmental changes. *O. longicaudis* individuals are found in low densities on plankton and have restricted occurrence in coastal regions, where they play a significant role in ecosystem productivity and nutrient cycling (Kotov 2006), serving as a food source for other animals. Considering studies of the coastal region, we may assume that this species may have a wider distribution, demonstrating their role in the aquatic environment.

Studies of the Cladocera life cycle are important because they provide a deeper understanding of the biology of these animals, in addition to providing information on secondary production, population dynamics, and interactions in the food chain in aquatic environments. Ecotoxicology studies aim to control the environmental quality and the ability of zooplankton organisms to swim against a gradient of turbulence (Seuront et al. 2004; Santos-Wisniewski et al. 2002; Freitas and Rocha 2006; Castilho et al. 2012). In Brazil, studies on the life cycle of Chydoridae have been done on species such as Chydorus dentifer and Acroperus harpae, Chydorus pubescens, Coronatella rectangula, and Alona iheringula by Melão (1997), Santos-Wisniewski et al. (2006), Viti et al. (2013), and Silva et al. (2014), respectively. High variation was observed in their life cycle, with a duration average varying between 9 and 46 days, with the greatest longevity recorded for A. iheringula cultured at 25°C. Although the number of studies has been increasing recently, the knowledge of the taxonomic diversity of Cladocera remains insufficient due to morphological differentiation, phenotypic variation, and historical factors.

Nowadays, molecular identification such as the DNA barcoding has been useful for ecological studies as it allows for precise identification and determination of cryptic species. The DNA barcode includes an analysis of partial sequences of the mitochondrial gene cytochrome oxidase I (COI). Its diversity has been used to identify and detect new species in many animal groups (Hebert et al. 2003), including the Crustacea (Costa et al. 2007; Young et al. 2012). For the Chydoridae, DNA barcoding has already been used to determine some species (Sacherová and Hebert 2003; Gutiérrez et al. 2008; Gutiérrez and Valdez–Moreno 2008; Jeffery et al. 2011; Silva et al. 2014).

The aim of this study is to investigate the aspects of the life cycle of parthenogenic females of *O. longicaudis* cultured in a laboratory under controlled conditions and characterize its DNA barcode in order to allow for easy identification in future ecological studies.

Methods

Study area and sampling date

Sampling was carried out on July 7, 2010 in the Epamig Pond (21° 56′ 33″ S 45° 18′ 56″ W) situated in a priority area for conservation in Serra da Mantiqueira, Minas Gerais State, Brazil. This pond is oligotrophic, with water which has slightly acidic pH (5.7), high concentration of dissolved oxygen (9.1 mg.L⁻¹), and low electrical conductivity (31 μ s.cm⁻¹). The pond is shallow and small in size (approximately 60 × 30 m), with an extensive macrophyte stand. The Epamig Pond is located next to the Parque Estadual de Nova Baden. The pond is comprised of a large forest fragment and located near a rice cultivation.

Sampling and acclimatization

Organisms for starting cultures were collected close to macrophyte stands in the littoral region of the Epamig Pond by horizontal hauls using a zooplankton 68-µm mesh size net. In the laboratory, parthenogenetic females of O. longicaudis (Figure 1) were isolated and placed in 2-L beakers containing reconstituted water. This culture medium had pH 7.6, conductivity 140 µs.cm⁻¹ and hardness of 46 mg.L⁻¹ CaCO₃. Experimental cultures were maintained in germination chambers (model 347-CDG) at a constant temperature of $23.0^{\circ}C \pm 0.5^{\circ}C$ and 12 h-light/ 12 h-dark photoperiod. O. longicaudis was fed a suspension of the small chlorophycean Raphidocelis subcapitata, cultured in Chu 12 medium and cropped in the exponential phase, at a concentration of 10^5 cells.mL⁻¹, and 0.02 mL of a mixed suspension of yeast, and fish ration added in equal proportions (1:1) (USEPA 1994; ABNT 2009).

Life cycle

Individuals were acclimated for about ten generations (30 days). Ten females were isolated and maintained until the production of neonates. A total of 30 neonates less than 24 h old were placed in 50-mL polypropylene bottles and kept in a germination chamber with the temperature, light, and feeding conditions specified above. These organisms were observed to obtain the parameters of the life cycle. Culture media and food suspensions were completely renewed daily with a fresh suspension at the same temperature, once or twice a day. The animals were observed under a stereomicroscope to determine the number of eggs produced per brood and the longevity. The body growth of each individual was measured daily under an optical microscope, using a micrometric grid and \times 50 magnification.

DNA barcode

For the DNA barcode analysis, the specimens were fixed with 95% EtOH and placed in pure water for 12 h for



cleaning. Genomic DNA was extracted using phenol extraction and ethanol precipitation (Bucklin 2000). To amplify the mitochondrial COI gene, the universal primers, LCO 1490 and HCO2198 (Folmer et al. 1994) were used. PCR reactions had a total volume of 25 µl and were performed according to Ivanova et al. (2009) using Platinum Taq (Invitrogen, Carlsbad, CA, USA) as the enzyme. The PCR conditions were 94°C for 2 min as initial denaturation and 40 cycles of 94°C for 40s, 55°C for 40s, and 72°C for 1 min. DNA sequencing was done by direct sequencing of PCR amplification products, carried out in a 3130xl Genetic Analyzer automated DNA sequencer, following the manufacturer's instructions (Applied Biosystems, Foster City, CA, USA). The sequences were obtained bi-directionally two times for accurate reading.

The *O. longicaudis* COI was aligned in MEGA 6 (Tamura et al. 2013) with other COI sequences that show high sequence similarity using the BLAST tool at Genbank (http://www.ncbi.nlm.nih.gov/pubmed/). The Kimura 2-parameter (K2P) distance model (Kimura 1980) was used to calculate sequence divergences. Neighbor-joining (NJ) trees using the K2P method were generated by MEGA 6 (Tamura et al. 2013) facilities. Nonparametric bootstrapping was performed using 1,000 replicates.

Results

Life cycle

The mean duration of embryonic development was 2.3 days, and the time of post-embryonic development was 5.2 days for *O. longicaudis*. Throughout the life cycle of the species, a mean of 12 broods per female and 22 eggs female⁻¹ were produced and the fecundity rate was 2 eggs female⁻¹ brood⁻¹. The mean longevity was 47 days, and maximum longevity was 58 days (Table 1).

Figure 2 shows mean individual growth curve of the species as a function of time (days). The neonate of *O. longicaudis* had an average size of 504 μ m and reached maturity with approximately 655 μ m. On average, two juvenile instars and nine instars were recorded throughout the life cycle of the species.

DNA barcode

The sequence region of the COI gene (barcode region) was 658 bp in length and was deposited as accession number JX501501 in the Genbank. The base composition for *O. longicaudis* COI sequence was as follows: T = 41.33%, C = 13.82%, A = 23.1%, and G = 21.73%. The calculated A-T content was 64.4 %.

A genetic divergence from other *O. longicaudis* from the GenBank was found ranging from 7.0% to 7.2% (Table 2). With other Chydoridae species including *Oxyurella* sp., *Kauralona penuelasi*, *Alona* sp., and *Alona setulosa*, the genetic divergence ranged from 16.8% to 20.1%.

The NJ tree with 14 COI analyzed sequences shows *O. longicaudis* from Brazil as closely related to seven other *O. longicaudis* from Mexico (100% bootstrap support) (Figure 3). For *Oxyurella* sp., a bootstrap support of 86% was found with all *O. longicaudis* and, *Alona sp., and A. setulosa* were separated as another clade (Figure 3).

Table 1 Life cycle parameters of	Oxyurella	longicaudis
(Cladocera: Chydoridae)		

Life cycle parameters	Values			
Adult mean size (µm)	883.7 ± 27.75			
Maximum adult size (µm)	940			
Neonate mean size (µm)	503.85 ± 52.77			
Primipara mean size (µm)	654.61 ± 45.09			
Minimum size of primipara (µm)	580			
Number of instars between neonate and primipara	1.88 ± 0.65			
Maximum number of instars in the whole life cycle	8.92 ± 1.23			
Mean number of eggs in the whole life cycle	22.55 ± 3.98			
Mean fecundity (eggs female $^{-1}$ brood $^{-1}$)	2			
Maximum longevity (days)	58			
Mean longevity (days)	46.96 ± 9.00			
Mean embryonic development time (days)	2.30 ± 0.5			
Primipara age (davs)	5.20 ± 0.69			

Cultured at $23.0^{\circ}C \pm 0.5^{\circ}C$ in a 12-h light/dark photoperiod, fed on a mixed suspension of *Raphidocelis subcapitata* (at 10^{5} cells.mL⁻¹) and yeast, and fish ration added in equal proportions.



Discussion

Life cycle of O. longicaudis

O. longicaudis occurred more abundantly in preserved environments, shallow oligotrophic water bodies, with low electrical conductivity, well-oxygenated concentration, and pH from neutral to alkaline (Rocha et al. 2011; Van Damme and Dumont 2010; Castilho and Santos-Wisniewski 2013).

Temperature is more important for determining the time of embryonic and post-embryonic development and genetic factors, such species size and size of the egg also influence these parameters. High temperatures promote quick development, while larger eggs take longer time to develop (Melão 1999). The embryonic development time observed for *O. longicaudis* at 23°C (2.3 days) is greater than that of the other Chydoridae species (Table 3): *A. iheringula* (510 µm) has an embryonic development time

greater than *O. longicaudis* (940 μ m) at the same temperature (23°C). In addition, *C. rectangula* (468 μ m) was less than *O. longicaudis* at 25°C, which, at this temperature, reduced the time of embryonic development. *A. harpae* at a higher temperature (25°C) (Melão 1997) has a shorter embryonic development time and at a lower temperature (20°C) takes longer in embryonic development (Bottrell 1975).

The post-embryonic development of *O. longicaudis* (5.2 days) was longer than that observed for other representatives of the Chydoridae family. *A. harpae, Alonella excisa, Leydigia acanthocercoides,* and *A. iheringula* reached maturity on the third day of life (Melão 1997; Sharma and Sharma 1998; Murugan and Job 1982; Silva et al. 2014), and *C. rectangula* reaches primipara age on the second day of life (Viti et al. 2013) (Table 3). By the fifth day of life, *O. longicaudis* began to show exponential body

Table 2 K2P Genetic distance between COI sequences of *Oxyurella longicaudis* and other *Oxyurella, Kauralona* and *Alona* species

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1. O. longicaudis (JX501501)														
2. O. longicaudis (KC617722)	0.072													
3. O. longicaudis (KC617723)	0.070	0.002												
4. O. longicaudis (KC617724)	0.072	0.000	0.002											
5. O. longicaudis (KC617725)	0.072	0.000	0.002	0.000										
6. Oxyurella sp.(KC617135)	0.168	0.153	0.151	0.153	0.153									
7. O. longicaudis (KC617136)	0.072	0.000	0.002	0.000	0.000	0.153								
8. O. longicaudis (KC617138)	0.072	0.000	0.002	0.000	0.000	0.153	0.000							
9. O. longicaudis (KC617139)	0.070	0.002	0.000	0.002	0.002	0.151	0.002	0.002						
10. <i>K. penuelasi</i> (KC617020)	0.188	0.192	0.190	0.192	0.192	0.217	0.192	0.192	0.190					
11. <i>K. penuelasi</i> (KC617021)	0.188	0.192	0.190	0.192	0.192	0.217	0.192	0.192	0.190	0.000				
12. K. penuelasi (KC617022)	0.188	0.192	0.190	0.192	0.192	0.217	0.192	0.192	0.190	0.000	0.000			
13. Alona sp.(KC617433)	0.181	0.197	0.195	0.197	0.197	0.184	0.197	0.197	0.195	0.208	0.208	0.208		
14. Alona setulosa (EU701997)	0.201	0.209	0.206	0.209	0.209	0.227	0.209	0.209	0.206	0.204	0.204	0.204	0.198	

Genbank access numbers are located after each species name.



growth (Figure 2). Therefore, the species began to allocate energy for reproduction only from this period onward, which is indicated by the increase of *O. longicaudis*' body, being larger than most representatives of the Chydoridae family. According to Lynch (1980), larger body species invest almost all of their energy and reproduction after reaching maturity. Additionally, the time duration for post-embryonic development is higher for the Cladocera species with larger bodies under the same feeding conditions (Hardy and Duncan 1994).

The fecundity rate (two eggs brood⁻¹) found for *O. longicaudis* is common in representatives of the Chydoridae family (Bottrell 1975; Murugan and Job 1982; Robertson, 1988; Sharma and Sharma 1998; Santos-Wisniewski et al. 2006; Silva et al. 2014). This rate is the lowest fecundity rate between the families of Cladocera. The flat body of Chydoridae members prevents a higher yield of eggs per brood, as occurs with the representatives of other Cladocera families. For example, the Daphnidae *Scapholeberis armata freyi* produce up to 16 eggs brood⁻¹ (Castilho et al. 2012) and the Sididae *Pseudosida ramosa* produces on average 3.4 eggs brood⁻¹ when cultured at 25° C (Freitas and Rocha 2006). Moreover, the low fecundity rate of Chydoridae is related to the low levels of population growth of species (Martínez-Jerónimo and Gómez-Díaz 2011).

Among the cladocerans, small species such as *Chy*dorus and *Alona* produce 20 eggs female⁻¹ on average

Table 3 Comparison	of life cycle	parameters of Ch	ydoridae species	s (data from the	present stud	y and the literature)
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Species	EDD	PA	F	CF	L	T (°C)	Author	
Oxyurella longicaudis	2.30	5.20	2	22	46.96	23	Present study	
Chydorus pubescens	1.96	2.37	2	22.3	25.44	23.6	Santos-Wisniewski et al. 2006	
Chydorus dentifer	2.20	5.73	2		11.39	25	Melão 1997	
Chydorus sphaericus	3.10		2		74	20	Bottrell 1975	
Acroperus harpae	1.56	3.70	1.59		9.79	25	Melão 1997	
Acroperus harpae	3.18				74	20	Bottrell 1975	
Pleuroxus uncinatus	3.16		2				Bottrell 1975	
Alonella excisa		3.17	2	46	73.4	19-23	Sharma and Sharma 1998	
Leydigia acanthocercoides		3.00	2	20	23.2	28-30	Murugan and Job 1982	
Leydigia ciliata			2	50	46	28-30	Venkataraman 1990	
Euryalona orientalis			2	20	23.8	28-30	Venkataraman 1990	
Coronatella rectangula	1.68	2.48	1.98	27.8	28.04	23.6	Viti et al. 2013	
Alona iheringula	1.79	3.24	2	47.6	46	25	Silva et al. 2014	

EDD embryonic development duration (days), *PA* primiparous age (days), *F* fecundity (eggs female⁻¹ brood⁻¹), *CF* cumulative fecundity (total number of eggs female⁻¹), *L* longevity (days), and *T* temperature (°C).

during their whole life cycle (Muro-Cruz et al. 2002). The total production of eggs of O. longicaudis over the course of its life cycle (22 eggs female⁻¹) was low compared to other Chydoridae, since it has a longer embryonic development time, and a later primipara. Similar production of eggs has been observed by Santos-Wisniewski et al. (2006) to C. pubescens (22.3 eggs female⁻¹), by Murugan and Job (1982) to L. acanthocercoides (20 eggs female⁻¹), and in *Euryalona orientalis* (20 eggs female⁻¹) by Venkataraman (1990), and longevity of these species ranged from 23 to 25 days. Longer-lived species such as A. excisa (73.4 days) (Sharma and Sharma 1998) and Leydigia ciliata (46 days) (Venkataraman 1990) produced 46 and 50 eggs female⁻¹ in their whole life cycle, respectively. A. excisa had a shorter embryonic development time, and L. ciliate, grown at a higher temperature by increasing the metabolism of organisms, probably lead to a shorter embryonic development. O. longicaudis stopped producing eggs near the end of its life cycle, contributing to lower total fertility.

The mean size of neonate of *O. longicaudis* was about 50% less than the maximum size of adults. Smaller species tend to produce offspring with a hatching length closer to their adult size than the larger species (Lynch 1980).

DNA barcode of O. longicaudis

This study established the first barcode region of COI for the Cladocera species *O. longicaudis* isolated in Brazil. The percentage found for A-T (64.4%) is consistent with the data range previously described for the 60% A-T percentage for COI of Chydoridae (Sacherová and Hebert 2003; Belyaeva and Taylor 2009).

One value to consider is the 7.2% and 7.0% value of genetic divergence among O. longicaudis from Brazil and the other seven isolates from Mexico. For the Branchiopoda group, a genetic divergence of 3% in the COI sequence is considered a parameter for distinguishing species at the molecular level. From 3% to 5%, the species is considered provisional, and its taxonomic status should be confirmed. Above 5%, the specimens are considered different species (Jeffery et al. 2011). From this view, a genetic divergence of around 7% found between our O. longicaudis and the specimens from Mexico should be sufficient to classify them as different species. In order to confirm this and create a new species name, it will be necessary to perform additional morphological detailed studies combined with other molecular markers. However, among all O. longicaudis from Mexico, the genetic divergence ranged from 0 to 0.2% (Table 2), emphasizing that they represent the same species names.

COI analysis represents an interesting approach to new studies of taxonomy and species recognition of Brazilian isolates as new species, including cryptic species. Also, COI can be used to analyze a zooplankton community to estimate species richness of an entire zooplankton community as already proposed by Machida et al. (2009) and for further phylogeographic studies and gene flow for subpopulations as recently described for copepods (Young et al. 2014). Also, our results using COI markers strengthen the continental endemism idea for Cladocera (Forró et al. 2008; Belyaeva and Taylor 2009) and the monopolization hypothesis for aquatic organisms such as cladocerans (De Meester et al. 2002).

Conclusions

The embryonic and post-embryonic development times of *O. longicaudis* were higher than those of the other species of the same family, which contributed to lower total egg production throughout its life cycle.

For the DNA barcoding, the roughly 7% genetic divergence found between our *O. longicaudis* and the specimens from Mexico highlights the possibility of a cryptic speciation for this species and the urgent necessity to clarify the taxonomic position.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

MCAC, TCO, and MJSW conceived and designed the experiments. MCAC and TCO performed the experiments. MCAC, CBA, TCO, and MJSW analyzed the data and wrote the paper. All authors read and approved the final manuscript.

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