TITLE

Rodents of Senegal and their role as intermediate hosts of *Hydatigera* spp. (Cestoda: Taeniidae)

AUTHORS

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RUNNING HEAD

Hydatigera spp. in rodents of Senegal

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SUMMARY

Hydatigera (Cestoda: Taeniidae) is a recently resurrected genus including species seldom investigated in sub-Saharan Africa. We surveyed wild small mammal populations in the areas of Richard Toll and Lake Guiers, Senegal, with the objective to evaluate their potential role as intermediate hosts of larval taeniid stages (i.e., metacestodes). Based on genetic sequences of a segment of the mitochondrial DNA gene cytochrome *c* oxidase subunit 1 (COI), we identified *Hydatigera parva* metacestodes in 19 out of 172 (11.0%) Hubert's multimammate mice (*Mastomys huberti*) and 1 out of 6 (16.7%) gerbils (*Taterillus* sp.), and *Hydatigera taeniaeformis sensu stricto* metacestodes in 1 out of 215 (0.5%) Nile rats (*Arvicanthis niloticus*). This study reports epidemiological and molecular information on *H. parva* and *H. taeniaeformis* in West African rodents, further supporting the phylogeographic hypothesis on the African origin of *H. parva*. Our findings may indicate significant trophic interactions contributing to the local transmission of *Hydatigera* spp. and other parasites with similar life cycle mechanisms. We therefore propose that further field investigations of rodent population dynamics and rodent-borne infectious organisms are necessary to improve our understanding of host-parasite associations driving the transmission risks of rodent parasites in West Africa.

Key words: *Arvicanthis niloticus*, *Hydatigera parva*, *Hydatigera taeniaeformis*, *Mastomys huberti*, parasites, Taeniidae, *Taterillus*, West Africa, wildlife.

KEY FINDINGS

First molecular data of *H. parva* and *H. taeniaeformis* in West African rodents.

Significant relationship between *H. parva* prevalence and older intermediate hosts.

Epidemiology of *Hydatigera* strobilocerci as proxy for host-parasite dynamics.

INTRODUCTION

Hydatigera Lamarck, 1816 (Cestoda: Taeniidae) is a recently resurrected genus (Nakao *et al.* 2013) comprising four valid species: *Hydatigera taeniaeformis* (Batsch, 1786), *Hydatigera parva* (Baer, 1924), *Hydatigera krepkogorski* Schulz and Landa, 1934, and the recently discovered *Hydatigera kamiyai* Lavikainen *et al.*, 2016. Adult *Hydatigera* tapeworms occur in the small intestine of felid and viverrid definitive hosts and are characterized by large rostellar hooks. Larval taeniid stages are broadly known as metacestodes and specifically named strobilocerci for *Hydatigera* species. These develop in tissues and body cavities of rodents as intermediate hosts and feature prominent segmented strobilae (Nakao *et al.* 2013; Lavikainen *et al.* 2016).

Human-mediated introductions, in addition to ancestral migratory and colonization events, of hosts and their taeniid parasites have made the geographical distribution of *Hydatigera* spp. cosmopolitan, with reports and molecular data generated from intermediate and definitive hosts worldwide (Jones and Pybus, 2001; Lavikainen *et al.* 2016). However, information on *Hydatigera* spp. from Africa remains limited. Aside from the description of adult *H. parva* in a common genet (*Genetta genetta*) from South Africa (Baer, 1924) and in an African wildcat (*Felis silvestris lybica*) from the Democratic Republic of the Congo (Baer and Fain, 1965), polycephalic strobilocerci identified as *H. parva* have been described in Nile rats (*Arvicanthis niloticus*) from Sudan (Elowni and Abu Samra, 1988), in pygmy mice (*Mus minutoides*) from Nigeria (George *et al.* 1990), in greater Egyptian gerbils (*Gerbillus*

pyramidum) from Tunisia (Bernard, 1963), in southern multimammate mice (*Mastomys coucha*) from South Africa (Julius *et al.* 2017), and in Guinea multimammate mice (*Mastomys erythroleucus*) from Sierra Leone and the Democratic Republic of the Congo (Southwell and Kirshner, 1937; Mahon, 1954). Larval stages of *H. taeniaeformis* have been observed in rats and other wild rodents from Egypt (Wanas *et al.* 1993), Nigeria (Udonsi, 1989; Ivoke, 2009), South Africa (Julius *et al.* 2017), and Sudan (Fagir and El-Rayah, 2009), whereas Nelson and Rausch (1963) observed *Cysticercus fasciolaris* Rudolphi, 1808 (i.e., *C. fasciolaris* is a historical synonym of *H. taeniaeformis* (Nakao *et al.* (2013)) in the liver of black rats (*Rattus rattus*) in Kenya. Nevertheless, to our knowledge, the identity of *Hydatigera* isolates from the African continent has been molecularly confirmed only for specimens found in *Rattus* spp. from Ethiopia and South Africa (Lavikainen *et al.* 2016).

Studies on helminth communities of rodents in Senegal have enhanced our understanding of the impact of spatio-temporal factors on both biodiversity/abundance of rodent parasites (e.g., Brouat *et al.* 2007; Sall-Dramé *et al.* 2010) and host population dynamics (e.g., Brouat and Duplantier, 2007; Diagne *et al.* 2016). Nevertheless, knowledge gaps on rodents and their parasites still exist in Senegal as in the rest of sub-Saharan Africa (Bordes *et al.* 2015). We surveyed wild small mammal populations of the Senegal River Basin as potential intermediate hosts of larval taeniids. Our aim was to evaluate host-parasite associations between small mammal species and larval taeniids, and whether any transmission patterns relative to habitat and host characteristics could be observed.

MATERIALS AND METHODS

Trapping of small mammals

The study was conducted in sites in and around the town of Richard Toll (16°27′N, 15°41′W) and on the shores of Lake Guiers (16°15′N, 15°51′W), Senegal. Between May 2016 and April

2017, small mammals were trapped in the spring and autumn following methodologies previously described (Catalano *et al.* 2018). Briefly, locally made wire-mesh live traps were used, and trapping sites were classified into two types of habitats: (I) crop fields near human dwellings; and (II) riparian habitat (i.e., habitat associated with bodies of water, dependent on the existence of perennial, intermittent or other forms of water drainage) primarily composed by thick reeds (*Typha* sp.). Each evening, the traps were baited with peanut butter and set in lines over a period of 2-3 nights per site. Each morning, we inspected the traps and recorded captures, misfires (i.e., any trap found sprung, missing, or not triggered) and by-catch (i.e., any non-target species captured).

Laboratory analyses

The trapped small mammals were returned live to the laboratory and humanely euthanized by intraperitoneal injection with sodium thiopental (300 mg/kg body weight). Death of the animal was confirmed by cervical dislocation and absence of pedal withdrawal reflex. At post-mortem, species, gender, sexual maturity and anatomical measurements of each individual were recorded. Age classification of rodents as juveniles or adults was based on the combined body weight, body length and reproductive status (Granjon and Duplantier, 2009; Herbreteau *et al.* 2011). During dissection, any cysts present in the thoracic and/or abdominal cavity was isolated and preserved in 95% ethanol at -20 °C until DNA extraction.

After rehydration in nuclease-free water, DNA from individual specimens was extracted using the Epicentre® MasterPure™ Complete DNA and RNA Purification Kit (Epicentre Biotechnologies, Madison, WI, USA) following the manufacturer's instructions. DNA extracts were eluted in 30 μL TE buffer and amplified for a segment of the cytochrome *c* oxidase subunit 1 (COI) gene of the mitochondrial DNA (mtDNA) using primers 2575 and 3021 (Bowles *et al.* 1992). Enzymatic amplification and thermocycling protocol for

polymerase chain reaction (PCR) were performed in a 25 μL reaction mixture including PuReTaq™ Ready-To-Go™ PCR Beads (GE Healthcare UK Limited, Little Chalfont, UK), 0.5 μmol/L of each primer and 2 μL of DNA template. Cycling parameters consisted of an initial nucleic acid denaturation at 94 °C for 5 min, followed by 35 cycles of 94 °C for 30 s, 52 °C for 1 min, and 72 °C for 1 min, with a final 7 min extension at 72 °C. PCR products were sequenced using the original PCR primers in a 3730xl DNA Analyzer system by GATC Biotech (Konstanz, Germany). Assembly and editing of contigs were performed with CodonCode Aligner (CodonCode Corporation, Centerville, MA, USA). The obtained COI sequences were compared by alignment with data available in the National Center for Biotechnology Information (NCBI) GenBank database.

Statistical analyses

Relative abundance of small mammals was assumed to be reflected in their effective capture rate, recorded for each trapping session and site as the number of captured animals as a whole per number of trap-nights (Brouat *et al.* 2007; Liccioli *et al.* 2014). Furthermore, we calculated the proportion of adult animals out of the total number of captures, since older animals are predicted to be more likely infected by *Hydatigera* metacestodes (Burlet *et al.* 2011). Variations in the proportion of adult rodents among seasons were tested using Pearson's chi-squared (χ^2) test. Logistic regression was performed to understand the association between gender (females versus males), age (adults versus juveniles), season (autumn versus spring), habitat (crop field versus riparian vegetation), and locality (Lake Guiers versus Richard Toll), included as dichotomous independent variables, on the occurrence of *Hydatigera* spp., included as the dichotomous response variable (with 0 for negative and 1 for infected individual). Statistical tests were implemented in R version 3.1.2 "Pumpkin Helmet" (https://www.r-project.org) and were considered significant when $P \leq 0.05$.

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145 *Ethics statement*

146 The species of small mammals involved in the study are classified as "Least Concern" by the
147 International Union for Conservation of Nature Red List. Animals were treated in compliance
148 with the guidelines of the American Veterinary Medical Association Council
149 (https://www.avma.org/KB/Policies/Documents/euthanasia.pdf) and the Animals (Scientific
150 Procedures) Act as implemented by the Home Office in Great Britain
151 (https://www.gov.uk/government/uploads/system/uploads/attachment_data/file/535574/worki
152 ng-with-wild-animals-160706.pdf). Trapping activities commenced after explicit approval
153 from local authorities and land owners. Approval for live trapping and euthanasia of small
154 mammals was obtained from the Clinical Research Ethical Review Board of the Royal
155 Veterinary College, University of London (reference number: 2016 1505).

156

157 **RESULTS**

158 *Trapping of small mammals*

159 We captured 420 small mammals including 215 Nile rats (*A. niloticus*), 172 Hubert's
160 multimammate mice (*Mastomys huberti*), 27 shrews (*Crocidura* sp.), and 6 gerbils (*Taterillus*
161 sp.). Identification of *Taterillus* gerbils and *Crocidura* shrews was made to the genus level
162 given the presence of sympatric species that are morphologically undistinguishable (Granjon
163 and Duplantier, 2009; Galan *et al.* 2012). We set 2,531 trap-nights for an overall capture rate
164 of 20.1% when accounting for misfires (n = 2,043).

165

166 *Laboratory data*

167 One to three translucent cysts with the diameter of approximately 10 mm were observed in the
168 abdominal cavity of infected individuals (Fig. 1), with the exception of a *M. huberti* in which

two cysts were present in the thoracic cavity. Based on the molecular analysis of the mtDNA COI gene (396 base pairs), we identified *H. parva* in 19 out of 172 *M. huberti* (11.0%) and 1 out of 6 *Taterillus* sp. (16.7%), while *H. taeniaeformis sensu stricto* was detected in 1 out of 215 *A. niloticus* (0.5%) (Fig. 2). Alignment of the COI sequences showed the presence of 2 different haplotypes of *H. parva* (identity ≥ 99.50%) isolated in *M. huberti*. Table 1 summarizes the results of trapping activities and parasitological analyses. Pairwise comparisons of the generated *H. parva* COI sequences with NCBI GenBank data available from Spain (EU544580) showed 98.74% identity; comparisons between our *H. taeniaeformis sensu stricto* COI sequence and data from Ethiopia (KT693060, KT693063) and South Africa (KT693064) showed 99.24-99.50% identity (Table 2). The COI sequence data from individual specimens were deposited in the GenBank database under the accession numbers MH036503-MH036508 for *H. parva*, and MH036509 for *H. taeniaeformis sensu stricto*. Representative specimens of *Hydatigera* spp. were archived in the collection of the Natural History Museum (London, UK) under the accession numbers 2018.3.7.1-32.

Statistical analyses

Capture rates for each trapping season and habitat varied markedly (Table 1). Statistical comparisons showed that the proportion of trapped adult rodents (viz., *A. niloticus*, *M. huberti*, and *Taterillus* sp.) significantly differed across season ($\chi^2 = 4.85$; d.f. = 1; $P = 0.028$), with a peak in autumn (74.1% adults out of 170 trapped rodents) and a decrement in spring (63.7% adults out of 223 trapped rodents). Logistic regression was performed only on *H. parva* occurrence in *M. huberti* due to the small number of infected *Taterillus* sp. and *A. niloticus*. Age demonstrated a significant association with probability of infection ($P = 0.017$), where 17 out of 19 infected *M. huberti* (89.5%) were adults. Likewise, season was significantly associated with infection probability ($P = 0.011$), where 16 out of 19 infected *M. huberti*

(84.2%) were captured during the spring. The prevalence of *H. parva* did not significantly vary when tested against host gender, habitat, or locality ($P > 0.05$).

DISCUSSION

We identified rodent populations from the Senegal River Basin as intermediate hosts of *Hydatigera* taeniids. To our knowledge, this is the first study using genetic tools to characterize *H. parva* and *H. taeniaeformis* in autochthonous rodents of the African continent. Molecular diagnostic approaches, alongside comparative morphology and a range of field data, provide solid bases to identify and revise geographical distribution, host spectrum, and evolutionary hypotheses of taeniids and other helminths of medical and veterinary importance (McManus, 2006; Nadler and Pérez-Ponce de León, 2011; Zhang *et al.* 2014). In fact, recent molecular and phylogenetic evidence have demonstrated that *H. taeniaeformis* represents a cryptic species complex (Jia *et al.* 2012; Nakao *et al.* 2013; Lavikainen *et al.* 2016). DNA sequence comparisons with the specimen we isolated in a Senegalese Nile rat show identity to what is described as *H. taeniaeformis sensu stricto*, a lineage that might have originated in Southeast Asia and rapidly invaded Australia, the Americas, Europe, and Africa, where it has been identified in Ethiopia and South Africa from *Rattus* spp. (Lavikainen *et al.* 2016; Mello *et al.* 2018). In contrast, the origin of *H. parva* is hypothesized in the African continent (see Alvarez *et al.* 1990), since both its main definitive hosts (i.e., viverrids of the genus *Genetta*), and intermediate hosts (i.e., rodents of the genera *Aethomys*, *Arvicanthis*, and *Mastomys*) are native to Africa (Jones and Pybus, 2001; Granjon and Duplantier, 2009). The occurrence of *H. parva* in Europe (see Jones and Pybus, 2001) could be the consequence of multiple, successful introductions of the common genet from Maghreb to Europe, likely between the end of the Upper Palaeolithic (c. 10,000 years ago) and the end of the Phoenician influence in the Mediterranean (300 BC) (Gaubert *et al.* 2015). Host phylogeography suggests that *H. parva*

has followed its native host to Mediterranean Europe, where the parasite has found wood mice (*Apodemus sylvaticus*) as suitable intermediate hosts (Alvarez *et al.* 1990; Lavikainen *et al.* 2008).

In our study, the presence of *Hydatigera* strobilocerci was related to the age of the rodents, with *H. parva* prevalence significantly higher in adult *M. huberti*. Similar studies on *H. taeniaeformis* in deer mice (*Peromyscus maniculatus*) from California, USA (Theis and Schwab, 1992), in water voles (*Arvicola terrestris*) from Switzerland (Burlet *et al.* 2011), and in common voles (*Microtus arvalis*) from France (Fichet-Calvet *et al.* 2003) further supported the positive relationship between metacestode prevalence and older rodent hosts. In addition, we found a significantly higher relative abundance of adult rodents trapped during the autumn, which appears to be in contrast with the higher *H. parva* prevalence in *M. huberti* observed during the spring season. However, such differences may be explained by complex host population dynamics, including reproductive patterns driving age structures and density-dependent effects between definitive and intermediate hosts, which all play important roles in the exposure to *Hydatigera* spp. infectious stages (Fichet-Calvet *et al.* 2003; Deter *et al.* 2006; Burlet *et al.* 2011). Furthermore, the development of *H. parva* strobilocerci in *M. huberti* and *Taterillus* sp., while *A. niloticus* harboured *H. taeniaeformis sensu stricto*, may indicate specific predator-prey dynamics between definitive hosts (i.e., viverrids and felids) and rodents in our study area. Such trophic interactions are applicable to the transmission of *Hydatigera* spp., but they could also be used as a proxy for any rodent-borne parasite with similar life cycle mechanisms. The zoonotic protozoan *Toxoplasma gondii* (Nicolle and Manceaux, 1908) is a particularly relevant example considering its public health importance and the limited publicly accessible data on *T. gondii* infections in West Africa (Keats Shwab *et al.* 2014).

Rodents are an abundant and diverse vertebrate order, predicted as the most important reservoir of infectious diseases of public health concern, particularly in tropical regions and

ever-growing urban areas (Han *et al.* 2015, 2016; Young *et al.* 2017). The synanthropic habits and resilience to anthropogenic disturbance of some rodent species, together with their wide geographical distribution and invasive potential, makes long-term surveys on the ecology of rodents and rodent-borne diseases a priority in many areas worldwide (Meerburg *et al.* 2009; Bordes *et al.* 2015). In West Africa, initiatives are being taken to address the knowledge gap that still exists in our understanding of ecological dynamics driving transmission risks of rodent-borne infectious organisms (e.g., Lecompte et al. 2006; Garba *et al.* 2014; Catalano *et al.* 2018). Herein, we report epidemiological and molecular information on *H. parva* and *H. taeniaeformis sensu stricto*, further supporting the phylogeographic hypothesis on the African origin of *H. parva*. Our results highlight that future field investigations of host population ecology and parasite communities of small mammals in West Africa have the potential to shed light on host-parasite associations at different temporal and spatial scales, and to identify significant relationships contributing to pathogen transmission in the region.

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412 Fig. 1. Cysts containing polycephalic strobilocerci of *Hydatigera parva* (indicated by white
413 arrows) isolated during the post-mortem of a Hubert's multimammate mouse (*Mastomys*
414 *huberti*) before (A, B) and after (C) dissection in 90 mm diameter Petri dish.
415
416 Fig. 2. Map of trapping localities in northern Senegal and occurrence of *Hydatigera parva* in
417 19 *Mastomys huberti* mice (black circles) and 1 *Taterillus* gerbil (black triangle), and of
418 *Hydatigera taeniaeformis sensu stricto* in 1 *Arvicanthis niloticus* rat (black square).
419
420 Table 1. Number of captured Nile rats (*Arvicanthis niloticus*), Hubert's multimammate mice
421 (*Mastomys huberti*), shrews (genus *Crocidura*), and gerbils (genus *Taterillus*), and percentage
422 of hosts harbouring *Hydatigera parva* (*Hp*) and *Hydatigera taeniaeformis sensu stricto* (*Ht*)
423 per habitat type, season, and small mammal age class (not applicable = NA).
424
425 Table 2. Range of pairwise similarity scores (%) for the partial sequence (396 base pairs) of
426 the mitochondrial cytochrome *c* oxidase subunit 1 gene within and between *Hydatigera* species
427 (*H. taeniaeformis sensu stricto* is reported as *H. taeniae s.s.*).