Parasitology

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

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Abstract

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 one out of six (16.7%) gerbils (*Taterillus* sp.) and *Hydatigera taeniaeformis sensu stricto* metacestodes in one 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.

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.*, 2018) 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.*, 2018) 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

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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

This 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 two to three 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^{-1} body weight). Death of the animal was confirmed by cervical dislocation and the 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^{-1} 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 a 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 *vs* males), age (adults *vs* juveniles), season (autumn *vs* spring), habitat (crop field *vs* riparian vegetation) and locality (Lake Guiers *vs* 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 $P \leqslant 0.05$.

Results

Trapping of small mammals

We captured 420 small mammals including 215 Nile rats (*A. niloticus*), 172 Hubert's multimammate mice (*Mastomys huberti*), 27 shrews (*Crocidura* sp.) and six gerbils (*Taterillus* sp.). Identification of *Taterillus* gerbils and *Crocidura* shrews was made to the genus level given the presence of sympatric species that are morphologically undistinguishable (Granjon and Duplantier, 2009; Galan *et al.*, 2012). We set 2531 trap-nights for an overall capture rate of 20.1% when accounting for misfires ($n = 2043$).

Laboratory data

One to three translucent cysts with the diameter of approximately 10 mm were observed in the 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 one out of six *Taterillus* sp. (16.7%), while *H. taeniaeformis sensu stricto* was detected in one out of 215 *A. niloticus* (0.5%) (Fig. 2). Alignment of the COI sequences showed the presence of two 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 and 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

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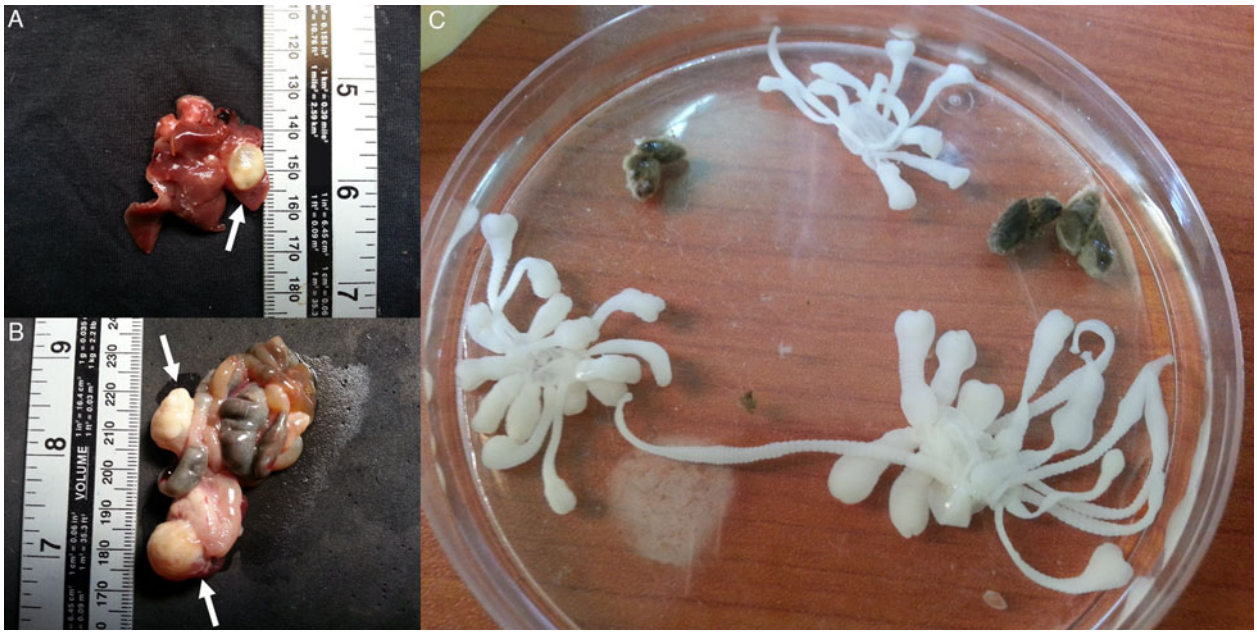

Fig. 1. Cysts containing polycephalic strobilocerci of *Hydatigera parva* (indicated by white arrows) isolated during the post-mortem of a Hubert's multimammate mouse (*Mastomys huberti*) before (A, B) and after (C) dissection in a 90 mm diameter Petri dish.

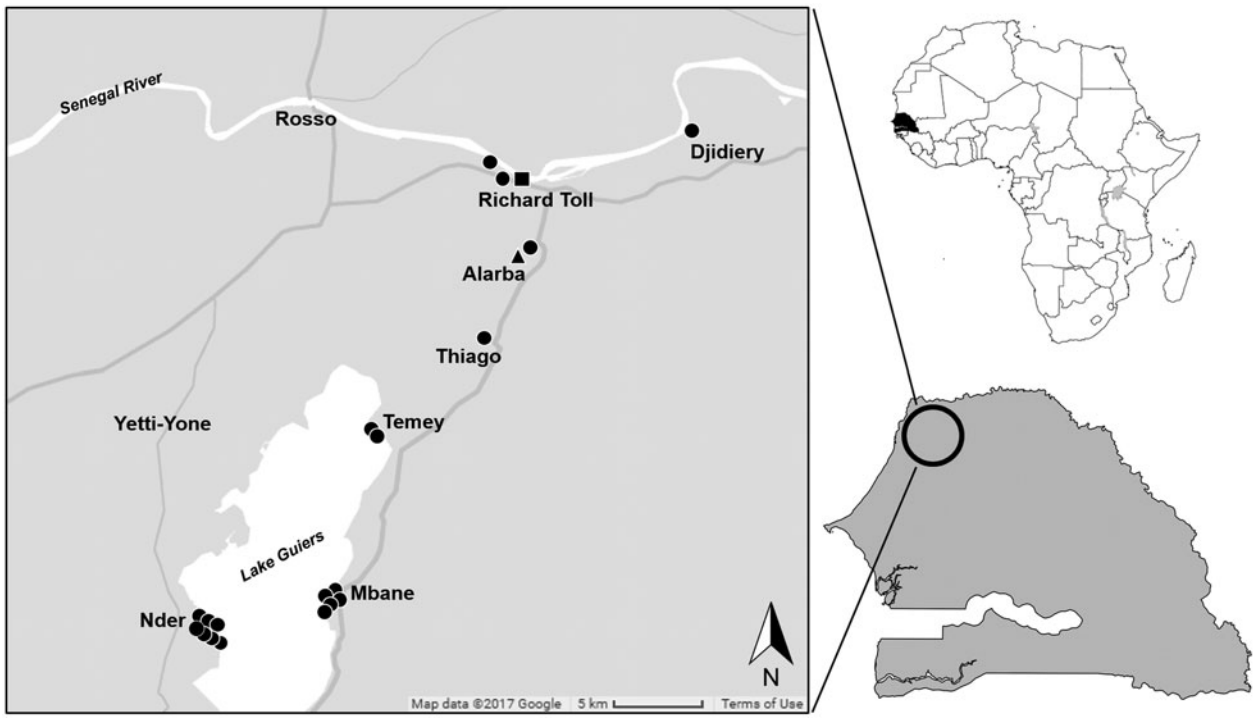

Fig. 2. Map of trapping localities in northern Senegal and occurrence of *Hydatigera parva* in 19 *Mastomys huberti* mice (black circles) and one *Taterillus* gerbil (black triangle) and of *H. taeniaeformis sensu stricto* in one *Arvicanthis niloticus* rat (black square).

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%)

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Table 1. Number of captured Nile rats (*Arvicanthis niloticus*), Hubert's multimammate mice (*Mastomys huberti*), shrews (genus *Crocidura*) and gerbils (genus *Taterillus*), and percentage of hosts harbouring *Hydatigera parva* (*Hp*) and *H. taeniaeformis sensu stricto* (*Ht*) per habitat type, season and small mammal age class (NA, not applicable)

	Crop field						Riparian vegetation					
	Spring (capture rate 18.7%)			Autumn (capture rate 28.7%)			Spring (capture rate 14.2%)			Autumn (capture rate 22.0%)		
	Juveniles	Adults	Total	Juveniles	Adults	Total	Juveniles	Adults	Total	Juveniles	Adults	Total
Arvicanthis niloticus	29	67	96	27	54 *Ht* 1.9%	81 *Ht* 1.2%	7	10	17	7	14	21
Mastomys huberti	4	8 *Hp* 25.0%	12 *Hp* 16.7%	1	8 *Hp* 25.0%	9 *Hp* 22.2%	39 *Hp* 5.1%	56 *Hp* 21.4%	95 *Hp* 14.7%	9	47 *Hp* 2.1%	56 *Hp* 1.8%
Crocidura	NA	NA	8	NA	NA	8	NA	NA	9	NA	NA	2
Taterillus	2	1	3	0	3 *Hp* 33.3%	3 *Hp* 33.3%	0	0	0	0	0	0

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 has 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

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Table 2. Range of pairwise similarity scores (%) for the partial sequence (396 base pairs) of the mitochondrial COI gene within and between *Hydatigera* species (*H. taeniaeformis sensu stricto* is reported as *H. taeniae s.s.*)

Hydatigera species	*Hydatigera parva*	*Hydatigera taeniae s.s.*	*Hydatigera kamiyai*	*Hydatigera krepkogorski*
Hydatigera parva	98.74–100	–	–	–
Hydatigera taeniae s.s.	85.35–87.12	95.71–99.75	–	–
Hydatigera kamiyai	85.10–87.12	89.90–91.92	98.48–98.99	–
Hydatigera krepkogorski	84.85–85.61	90.15–90.91	90.15–91.67	99.75–100

The sequences included are MH036504, MH036507, MH036508 (our study) and EU544580 for *H. parva*; MH036509 (our study), AB745096, KT693044, KT693060, KT693063, KT693064 and KT693072 for *Hydatigera taeniae s.s.*; AB731761, AB745098, EU544596 and KT693093 for *H. kamiyai*; AB731762 and MF281972 for *H. krepkogorski*.

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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Conflicts of interest. None

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

References

Alvarez F, Iglesias R, Bos J, Tojo J and Sanmartin ML (1990) New findings on the helminth fauna of the common European genet (*Genetta genetta* L.): first record of *Toxocara genettae* Warren, 1972 (Ascarididae) in Europe. *Annales de Parasitologie Humaine et Comparée* **65**, 244–248.

Baer JG (1924) Contribution à la faune helminthologique Sud-Africaine. *Annales de Parasitologie Humaine et Comparée* **2**, 239–247.

Baer JG and Fain A (1965) Cestodes. In de Witte Mission G. F. (ed.), (1933–1935). *Exploration du Parc National Albert*. Brussels, Belgium: Institute des Parcs Nationaux du Congo Belge, pp. 3–8.

Bernard J (1963) Cysticerques polycéphales chez le mulot. *Archives de l'Institut Pasteur de Tunis* **40**, 269–277.

Bordes F, Blasdell K and Morand S (2015) Transmission ecology of rodent-borne diseases: new frontiers. *Integrative Zoology* **10**, 424–435.

Bowles J, Blair D and McManus DP (1992) Genetic variants within the genus *Echinococcus* identified by mitochondrial DNA sequencing. *Molecular and Biochemical Parasitology* **54**, 165–173.

Brouat C and Duplantier JM (2007) Host habitat patchiness and the distance decay of similarity among gastro-intestinal nematode communities in two species of *Mastomys* (southeastern Senegal). *Oecologia* **152**, 715–720.

Brouat C, Kane M, Diouf M, Bâ K, Sall-Dramé R and Duplantier JM (2007) Host ecology and variation in helminth community structure in *Mastomys* rodents from Senegal. *Parasitology* **134**, 437–450.

Burlet P, Deplazes P and Hegglin D (2011) Age, season and spatio-temporal factors affecting the prevalence of *Echinococcus multilocularis* and *Taenia taeniaeformis* in *Arvicola terrestris*. *Parasites & Vectors* **4**, 6.

Catalano S, Sène M, Diouf ND, Fall CB, Borlase A, Léger E, Bâ K and Webster JP (2018) Rodents as natural hosts of zoonotic *Schistosoma* species and hybrids: an epidemiological and evolutionary perspective from West Africa. *The Journal of Infectious Diseases* **218**, 429–433.

Deter J, Berthier K, Chaval Y, Cosson JF, Morand S and Charbonnel N (2006) Influence of geographical scale on the detection of density dependence in the host-parasite system, *Arvicola terrestris* and *Taenia taeniaeformis*. *Parasitology* **132**, 595–605.

Diagne C, Ribas A, Charbonnel N, Dalecky A, Tatard C, Gauthier P, Haukisalmi V, Fossati-Gaschignard O, Bâ K, Kane M, Niang Y, Diallo M, Sow A, Piry S, Sembène M and Brouat C (2016) Parasites and invasions: changes in gastrointestinal helminth assemblages in invasive and native rodents in Senegal. *International Journal for Parasitology* **46**, 857–869.

Elowni EE and Abu Samra MT (1988) Observations on a polycephalic cestode larva from a Nile rat (*Arvicanthis niloticus*). *Folia Parasitologica* **35**, 75–76.

Fagir DM and El-Rayah EA (2009) Parasites of the Nile rat in rural and urban regions of Sudan. *Integrative Zoology* **4**, 179–187.

Fichet-Calvet E, Giraudoux P, Quéré JP, Ashford RW and Delattre P (2003) Is the prevalence of *Taenia taeniaeformis* in *Microtus arvalis* dependent on population density? *Journal of Parasitology* **89**, 1147–1152.

Galan M, Pagès M and Cosson JF (2012) Next-generation sequencing for rodent barcoding: species identification from fresh, degraded and environmental samples. *PLoS ONE* **7**, e48374.

Garba M, Dalecky A, Kadaoure I, Kane M, Hima K, Veran S, Gagare S, Gauthier P, Tatard C, Rossi JP and Dobigny G (2014) Spatial segregation between invasive and native commensal rodents in an urban environment: a case study in Niamey, Niger. *PLoS ONE* **9**, e110666.

Gaubert P, Del Cerro I, Centeno-Cuadros A, Palomares F, Fournier P, Fonseca C, Paillat JP and Godoy JA (2015) Tracing historical

introductions in the Mediterranean Basin: the success story of the common genet (*Genetta genetta*) in Europe. *Biological Invasions* **17**, 1897–1913.

George T, Obiamiwe BA and Anadu PA (1990) Cestodes of small rodents of the rainforest zone of mid-western Nigeria. *Helminthologia* **27**, 47–53.

Granjon L and Duplantier JM (2009) *Les Rongeurs de l'Afrique Sahélo-Soudanienne*, IRD Edn. Marseille, France: Publications Scientifiques du Muséum.

Han BA, Schmidt JP, Bowden SE and Drake JM (2015) Rodent reservoirs of future zoonotic diseases. *Proceedings of the National Academy of Sciences* **112**, 7039–7044.

Han BA, Kramer AM and Drake JM (2016) Global patterns of zoonotic disease in mammals. *Trends in Parasitology* **32**, 565–577.

Herbreteau V, Jittapalapong S, Rerkamnuaychoke W, Chaval Y, Cosson JF and Morand S (2011) *Protocols for Field and Laboratory Rodent Studies*. Bangkok, Thailand: Kasetsart University Press.

Ivoke N (2009) Studies on the seasonal variations and prevalence of helminth fauna of the black rat, *Rattus rattus* (L) (Rodentia: Muridae) from different microhabitats in Nsukka, Nigeria. *Animal Research International* **6**, 1063–1071.

Jia W, Yan H, Lou Z, Ni X, Dyachenko V, Li H and Littlewood DTJ (2012) Mitochondrial genes and genomes support a cryptic species of tapeworm within *Taenia taeniaeformis*. *Acta Tropica* **123**, 154–163.

Jones A and Pybus MJ (2001) Taeniasis and echinococcosis. In Samuel WM, Pybus MJ and Kocan AA (eds), *Parasitic Diseases of Wild Mammals*, 2nd Edn. Ames, USA: Iowa State University Press, pp. 150–192.

Julius RS, Schwan EV and Chimimba CT (2018) Helminth composition and prevalence of indigenous and invasive synanthropic murid rodents in urban areas of Gauteng Province, South Africa. *Journal of Helminthology* **92**, 445–454.

Keats Shwab E, Zhu XQ, Majumdar D, Pena HFJ, Gennari SM, Dubey JP and Su C (2014) Geographical patterns of *Toxoplasma gondii* genetic diversity revealed by multilocus PCR-RFLP genotyping. *Parasitology* **141**, 453–461.

Lavikainen A, Haukisalmi V, Lehtinen MJ, Henttonen H, Oksanen A and Meri S (2008) A phylogeny of members of the family Taeniidae based on the mitochondrial *cox*1 and *nad*1 gene data. *Parasitology* **135**, 1457–1467.

Lavikainen A, Iwaki T, Haukisalmi V, Konyaev SV, Casiraghi M, Dokuchaev NE, Galimberti A, Halajian A, Henttonen H, Ichikawa-Seki M, Itagaki T, Krivopalov AV, Meri S, Morand S, Näreaho A, Olsson GE, Ribas A, Terefe Y and Nakao M (2016) Reappraisal of *Hydatigera taeniaeformis* (Batsch, 1786) (Cestoda: Taeniidae) sensu lato with description of *Hydatigera kamiyai* n. sp. *International Journal for Parasitology* **46**, 361–374.

Lecompte E, Fichet-Calvet E, Daffis S, Koulémou K, Sylla O, Kourouma F, Doré A, Soropogui B, Aniskin V, Allali B, Kan SK, Lalis A, Koivogui L, Günther S, Denys C and ter Meulen J (2006) *Mastomys natalensis* and lassa fever, West Africa. *Emerging Infectious Diseases* **12**, 1971–1974.

Liccioli S, Kutz SJ, Ruckstuhl KE and Massolo A (2014) Spatial heterogeneity and temporal variations in *Echinococcus multilocularis* infections in wild hosts in a North American urban setting. *International Journal for Parasitology* **44**, 457–465.

Mahon J (1954) *Tapeworms from the Belgian Congo*. Tervuren, Belgium: Annales du Musée Royal du Congo Belge.

McManus DP (2006) Molecular discrimination of taeniid cestodes. *Parasitology International* **55**, S31–S37.

Meerburg BG, Singleton GR and Kijlstra A (2009) Rodent-borne diseases and their risks for public health. *Critical Reviews in Microbiology* **35**, 221–270.

Mello ÉM, Furtado LFV, Rabelo ÉML and Pinto HA (2018) DNA barcoding of metacestodes found in the *Guerlinguetus ingrami* (Rodentia: Sciuridae) reveals the occurrence of *Hydatigera taeniaeformis* sensu stricto (Cyclophyllidea: Taeniidae) in the Americas. *Parasitology International* **67**, 115–118.

Nadler SA and Pérez-Ponce de León G (2011) Integrating molecular and morphological approaches for characterizing parasite cryptic species: implications for parasitology. *Parasitology* **138**, 1688–1709.

Nakao M, Lavikainen A, Iwaki T, Haukisalmi V, Konyaev S, Oku Y, Okamoto M and Ito A (2013) Molecular phylogeny of the genus *Taenia* (cestoda: Taeniidae): proposals for the resurrection of *Hydatigera* Lamarck, 1816 and the creation of a new genus *Versteria*. *International Journal for Parasitology* **43**, 427–437.

Nelson GS and Rausch RL (1963) *Echinococcus* infections in man and animals in Kenya. *Annals of Tropical Medicine & Parasitology* **57**, 136–149.

Sall-Dramé R, Brouat C, Bâ CT and Duplantier JM (2010) Variation in cestode assemblages of *Mastomys* and *Arvicanthis* species (rodents: Muridae) from Lake Retba in Western Senegal. *Journal of Parasitology* **96**, 675–680.

Southwell T and Kirshner A (1937) Description of a polycephalic cestode larva from *Mastomys erythroleucus*, and its probable identity. *Annals of Tropical Medicine & Parasitology* **31**, 37–42.

Theis JH and Schwab RG (1992) Seasonal prevalence of *Taenia taeniaeformis*: relationship to age, sex, reproduction and abundance of an intermediate host (*Peromyscus maniculatus*). *Journal of Wildlife Diseases* **28**, 42–50.

Udonsi JK (1989) Helminth parasites of wild populations of the black rat, *Rattus rattus* (L.), from urban, rural residential and other ecological areas of Nigeria. *Acta Parasitologica Polonica* **34**, 107–116.

Wanas MQ, Shehata KK and Rashed AA (1993) Larval occurrence of *Hydatigera taeniaeformis* Batsch (1786) (Cestoda: Taeniidae) in the liver of wild rodents in Egypt. *Journal of the Egyptian Society of Parasitology* **23**, 381–388.

Young HS, McCauley DJ, Dirzo R, Nunn CL, Campana MG, Agwanda B, Otarola-Castillo ER, Castillo ER, Pringle RM, Veblen KE, Salkeld DJ, Stewardson K, Fleischer R, Lambin EF, Palmer TM and Helgen KM (2017) Interacting effects of land use and climate on rodent-borne pathogens in central Kenya. *Philosophical Transactions of the Royal Society B: Biological Sciences* **372**, 20160116.

Zhang G, Chen J, Yang Y, Liu N, Jiang W, Gu S, Wang X and Wang Z (2014) Utility of DNA barcoding in distinguishing species of the family Taeniidae. *Journal of Parasitology* **100**, 542–546.

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