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Catalano, S., Bâ, K., Diouf, N., Léger, E., Verocai, G., & Webster, J. Rodents of Senegal and their role as intermediate hosts of *Hydatigera* spp. (Cestoda: Taeniidae). *Parasitology*, 1-6.
doi:10.1017/S0031182018001427

The final publication is available at Cambridge Journals via
<http://dx.doi.org/10.1017/S0031182018001427>.

The full details of the published version of the article are as follows:

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

AUTHORS: Catalano, S., Bâ, K., Diouf, N., Léger, E., Verocai, G., & Webster, J.

JOURNAL TITLE: *Parasitology*

PUBLICATION DATE: 28 August 2018

PUBLISHER: Cambridge University Press: STM Journals

DOI: 10.1017/S0031182018001427

1 **TITLE**

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

3

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18

19 **RUNNING HEAD**

20 *Hydatigera* spp. in rodents of Senegal

21

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25 **SUMMARY**

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

41

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

44 **KEY FINDINGS**

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

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

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

48

49 **INTRODUCTION**

50 *Hydatigera* Lamarck, 1816 (Cestoda: Taeniidae) is a recently resurrected genus (Nakao *et al.*
51 2013) comprising four valid species: *Hydatigera taeniaeformis* (Batsch, 1786), *Hydatigera*
52 *parva* (Baer, 1924), *Hydatigera krepkogorski* Schulz and Landa, 1934, and the recently
53 discovered *Hydatigera kamiyai* Lavikainen *et al.*, 2016. Adult *Hydatigera* tapeworms occur in
54 the small intestine of felid and viverrid definitive hosts and are characterized by large rostellar
55 hooks. Larval taeniid stages are broadly known as metacestodes and specifically named
56 strobilocerci for *Hydatigera* species. These develop in tissues and body cavities of rodents as
57 intermediate hosts and feature prominent segmented strobilae (Nakao *et al.* 2013; Lavikainen
58 *et al.* 2016).

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

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

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

89

90 **MATERIALS AND METHODS**

91 *Trapping of small mammals*

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

94 2017, small mammals were trapped in the spring and autumn following methodologies
95 previously described (Catalano *et al.* 2018). Briefly, locally made wire-mesh live traps were
96 used, and trapping sites were classified into two types of habitats: (I) crop fields near human
97 dwellings; and (II) riparian habitat (i.e., habitat associated with bodies of water, dependent on
98 the existence of perennial, intermittent or other forms of water drainage) primarily composed
99 by thick reeds (*Typha* sp.). Each evening, the traps were baited with peanut butter and set in
100 lines over a period of 2-3 nights per site. Each morning, we inspected the traps and recorded
101 captures, misfires (i.e., any trap found sprung, missing, or not triggered) and by-catch (i.e., any
102 non-target species captured).

103

104 *Laboratory analyses*

105 The trapped small mammals were returned live to the laboratory and humanely euthanized by
106 intraperitoneal injection with sodium thiopental (300 mg/kg body weight). Death of the animal
107 was confirmed by cervical dislocation and absence of pedal withdrawal reflex. At post-mortem,
108 species, gender, sexual maturity and anatomical measurements of each individual were
109 recorded. Age classification of rodents as juveniles or adults was based on the combined body
110 weight, body length and reproductive status (Granjon and Duplantier, 2009; Herbreteau *et al.*
111 2011). During dissection, any cysts present in the thoracic and/or abdominal cavity was isolated
112 and preserved in 95% ethanol at -20 °C until DNA extraction.

113 After rehydration in nuclease-free water, DNA from individual specimens was
114 extracted using the Epicentre® MasterPure™ Complete DNA and RNA Purification Kit
115 (Epicentre Biotechnologies, Madison, WI, USA) following the manufacturer's instructions.
116 DNA extracts were eluted in 30 μ L TE buffer and amplified for a segment of the cytochrome
117 *c* oxidase subunit 1 (COI) gene of the mitochondrial DNA (mtDNA) using primers 2575 and
118 3021 (Bowles *et al.* 1992). Enzymatic amplification and thermocycling protocol for

119 polymerase chain reaction (PCR) were performed in a 25 μ L reaction mixture including
120 PuReTaq[™] Ready-To-Go[™] PCR Beads (GE Healthcare UK Limited, Little Chalfont, UK), 0.5
121 μ mol/L of each primer and 2 μ L of DNA template. Cycling parameters consisted of an initial
122 nucleic acid denaturation at 94 °C for 5 min, followed by 35 cycles of 94 °C for 30 s, 52 °C for
123 1 min, and 72 °C for 1 min, with a final 7 min extension at 72 °C. PCR products were sequenced
124 using the original PCR primers in a 3730xl DNA Analyzer system by GATC Biotech
125 (Konstanz, Germany). Assembly and editing of contigs were performed with CodonCode
126 Aligner (CodonCode Corporation, Centerville, MA, USA). The obtained COI sequences were
127 compared by alignment with data available in the National Center for Biotechnology
128 Information (NCBI) GenBank database.

129

130 *Statistical analyses*

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

144

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/working-with-wild-animals-160706.pdf). Trapping activities commenced after explicit approval
152 from local authorities and land owners. Approval for live trapping and euthanasia of small
153 mammals was obtained from the Clinical Research Ethical Review Board of the Royal
154 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

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

183

184 *Statistical analyses*

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

194 (84.2%) were captured during the spring. The prevalence of *H. parva* did not significantly vary
195 when tested against host gender, habitat, or locality ($P > 0.05$).

196

197 **DISCUSSION**

198 We identified rodent populations from the Senegal River Basin as intermediate hosts of
199 *Hydatigera* taeniids. To our knowledge, this is the first study using genetic tools to characterize
200 *H. parva* and *H. taeniaeformis* in autochthonous rodents of the African continent. Molecular
201 diagnostic approaches, alongside comparative morphology and a range of field data, provide
202 solid bases to identify and revise geographical distribution, host spectrum, and evolutionary
203 hypotheses of taeniids and other helminths of medical and veterinary importance (McManus,
204 2006; Nadler and Pérez-Ponce de León, 2011; Zhang *et al.* 2014). In fact, recent molecular and
205 phylogenetic evidence have demonstrated that *H. taeniaeformis* represents a cryptic species
206 complex (Jia *et al.* 2012; Nakao *et al.* 2013; Lavikainen *et al.* 2016). DNA sequence
207 comparisons with the specimen we isolated in a Senegalese Nile rat show identity to what is
208 described as *H. taeniaeformis sensu stricto*, a lineage that might have originated in Southeast
209 Asia and rapidly invaded Australia, the Americas, Europe, and Africa, where it has been
210 identified in Ethiopia and South Africa from *Rattus* spp. (Lavikainen *et al.* 2016; Mello *et al.*
211 2018). In contrast, the origin of *H. parva* is hypothesized in the African continent (see Alvarez
212 *et al.* 1990), since both its main definitive hosts (i.e., viverrids of the genus *Genetta*), and
213 intermediate hosts (i.e., rodents of the genera *Aethomys*, *Arvicanthis*, and *Mastomys*) are native
214 to Africa (Jones and Pybus, 2001; Granjon and Duplantier, 2009). The occurrence of *H. parva*
215 in Europe (see Jones and Pybus, 2001) could be the consequence of multiple, successful
216 introductions of the common genet from Maghreb to Europe, likely between the end of the
217 Upper Palaeolithic (c. 10,000 years ago) and the end of the Phoenician influence in the
218 Mediterranean (300 BC) (Gaubert *et al.* 2015). Host phylogeography suggests that *H. parva*

219 has followed its native host to Mediterranean Europe, where the parasite has found wood mice
220 (*Apodemus sylvaticus*) as suitable intermediate hosts (Alvarez *et al.* 1990; Lavikainen *et al.*
221 2008).

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

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

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

257

258 **ACKNOWLEDGEMENTS**

259 We thank Boubacar Bâ, Alassane Ndiaye, Alima Thiam, Cheikh Thiam, and Mariama Sène for
260 their outstanding support during fieldwork, and Kathryn Berger for her valuable comments on
261 both the manuscript and statistical analyses. We are grateful to the Senegalese communities
262 involved in the project for their friendly collaboration and hospitality. Finally, we acknowledge
263 the immense contribution of all the wild small mammals trapped and sacrificed during this
264 study.

265

266 **FINANCIAL SUPPORT**

267 This study was supported by the Royal Veterinary College and the Zoonoses and Emerging
268 Livestock Systems (ZELS) research initiative including the Department for International

269 Development, Biotechnology and Biological Sciences Research Council, Economic and Social
270 Sciences Research Council, Medical Research Council, Natural Environment Research
271 Council, and Defence Science and Technology Laboratory (grant numbers BB/L018985/1 and
272 BB/N503563/1).

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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.*).