obviously has a relationship to other dorylaims, particularly some forms in the Leptonchidae. The esophagus, spear and extensions, reproductive structures, and development of the spear in the esophagus of molting specimens all are characters of the dorylaimid type. On the other hand, the two very outstanding features of this nematode, the prominent cephalic setae and the heavily annulated, plate-like cuticle, have not been previously known in the Dorylaimida. The cephalic setae in particular suggest a relationship to the free-living marine forms of the Enoplida. Further studies on this, and related forms, will be required to establish more clearly the phylogenetic relationships in the dorylaims.

Biology of *Mastophorus numidica* (Seurat, 1914) Read and Millemann, 1953 (Nematoda: Spiruridae) with a Description of the Juvenile Stages

*William G. Dyer*² and *O. Wilford Olsen*

Life histories of several species of *Mastophorus* have been investigated. Leuckart (1867) and Marchi (1871) showed that *M. muris* (Gmelin, 1790) Chitwood, 1938 develops in meal worms (*Tenebrio molitor*). Adults were obtained in *Mus decumanus* which had eaten infected meal worms. Cram (1926) recovered encysted juveniles from the body cavities of cockroaches (*Blatella germanica*) fed embryonated eggs of *M. muris* (= *Protospirura columbiana* Cram, 1926). Adults were obtained experimentally in rats. Hall (1929) showed that scarabaeid beetles (*Aphodius fimetarius*) are natural intermediate hosts of *M. muris* (= *Protospirura gracilis* Cram, 1924). Marcandier and Pirot (1937) observed juveniles of *M. muris* in the oriental rat flea (*Xenopsylla cheopis*) collected from *Mus decumanus*. Adults were found in the stomachs of rats. Miyata (1939) demonstrated that cockroaches (*Periplaneta americana*), fleas (*Leptopsylla musculi*, *Ceratophyllus anisus*, *C. fasciatus*, *X. cheopis*), and moths (*Tinea granella*) could serve as intermediate hosts of *M. muris*.

Brumpt (1931) found that *M. bonnei* (Ortlipp, 1924) Read and Millemann, 1953 from domestic rats develops in cockroaches (*Rhy tarobia maderae*, *Blatella germanica*, and *Periplaneta orientalis*). *M. muricola* (Gedoelst, 1916) Read and Millemann, 1953 was reported from three species of captive monkeys (*Cebus capucinus*, *Ateles darentis*, and *Aotus zonalis*) by Foster and Johnson (1939). Infective juveniles were identified from the body cavities of cockroaches (*Leucophaca maderae*).

Crook and Grundmann (1964) exposed 15 species of native insects occurring naturally in association with deer mice and four common laboratory insects to eggs of *M. numidica*. Only tenebrionid beetles (*Eleodes tuberculata patruelis*) were naturally and experimentally infected.

Because of the need for more detailed information on the life cycle in *Mastophorus*, further study of *M. numidica* was undertaken. On the basis of the findings, an account of the life cycle and descriptions of the morphology of the developmental stages are presented in this paper.

**Materials and Methods**

Infective eggs containing first-stage juveniles were obtained as required by immersing ovigerous female worms from the stomachs of *P. maniculatus* in physiological saline. A single
feeding of eggs was given to individual grasshoppers (Melanoplus femur-rubrum), crickets (Acheta domestica), and beetles (Eledodes obsoleta) which had been starved for at least one day. Specimens of each species were used as controls to determine if natural infections were present. All test and control specimens of M. femur-rubrum and E. obsoleta were collected in the Cache la Poudre Canyon, Larimer County, northern Colorado. Specimens of A. domestica were obtained from Baton Rouge, Louisiana. Anesthetized insects were pinned to the bottom of plastic petri dishes, dissected in 87.6 per cent Ringer's solution, and examined for the presence of juveniles.

Deer mice used for experimental infections were determined to be free of M. numidica by frequent examination of the feces over a period of several months. Some were fed infected insects and others isolated cysts containing third-stage juveniles removed from the hemocoels of insects. The feces of these deer mice were checked daily for eggs to determine the prepatent period.

Infected mice were examined by opening the esophagus, stomach, and small intestine separately and agitating each part in a jar of saline to free the worms, the majority of which was found readily upon gross examination. The mucosa was scraped from the walls of each part of the alimentary canal and placed in separate containers of warm saline to allow embedded juveniles to migrate from the tissues into the fluid. The contents of the containers were stirred, sedimented, decanted several times, and examined for juveniles after addition of fresh saline.

Microscopic preparations were made of both living and fixed worms. Since certain structures appeared more clearly in living specimens, some juveniles were relaxed in saline by gently applying heat sufficient to reduce activity. Others were killed in hot saline, fixed in 70 per cent ethanol and 3 per cent glycerine, cleared, dehydrated, and mounted in glycerine. A phase contrast microscope was used in morphological studies.

Drawings of the several stages were prepared from fixed and living specimens. All measurements are in millimeters except where otherwise indicated.

### Table 1. Results of feeding 40 eggs of M. numidica per insect to grasshoppers (Melanoplus femur-rubrum), crickets (Acheta domestica), and beetles (Eledodes obsoleta); 24 days after exposure.

<table>
<thead>
<tr>
<th>Insects</th>
<th>No. examined</th>
<th>No. infected</th>
<th>No. of cysts recovered</th>
<th>Mean</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>M. femur-rubrum</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Exposed</td>
<td>50</td>
<td>31</td>
<td>9.5</td>
<td>2-19</td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>42</td>
<td>1</td>
<td></td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>A. domestica</td>
<td></td>
<td></td>
<td></td>
<td>8.3</td>
<td>6-18</td>
</tr>
<tr>
<td>Exposed</td>
<td>46</td>
<td>18</td>
<td>8.9</td>
<td>1-15</td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>95</td>
<td>0</td>
<td></td>
<td>0.5</td>
<td>1-2</td>
</tr>
<tr>
<td>E. obsoleta</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Exposed</td>
<td>20</td>
<td>18</td>
<td>8.9</td>
<td>1-15</td>
<td></td>
</tr>
<tr>
<td>Control</td>
<td>12</td>
<td>4</td>
<td>0.5</td>
<td>1-2</td>
<td></td>
</tr>
</tbody>
</table>

**Results**

Experimental infections were obtained in all three species of insects (M. femur-rubrum, A. domestica, and E. obsoleta) fed eggs of M. numidica (Table 1). Control specimens of M. femur-rubrum and E. obsoleta showed natural infections of 2.4 and 33.3 per cent, respectively.

Following is an account of the life cycle of M. numidica as it occurs in the cricket (A. domestica) and the deer mouse. The verbal descriptions and the illustrations are based on specimens from these hosts.

**Development and morphology in the cricket**

About 3.5 to 4.5 hr postinfection, the crop contained eggs which were 0.054 to 0.059 by 0.043 to 0.046, embryonated, thick shelled, and otherwise indistinguishable from those occurring in the definitive host's feces. At about 7.5 hr most eggs were in the stomach, a few still in the crop and gizzard; some evidently had hatched, as first-stage juveniles were found in the intestine. At about 10 to 15 hr neither eggs nor juveniles were observed in the digestive tract.

**First-stage juvenile:** At 10.5 hr post-exposure, the abdominal portion of the hemocoel contained a few first-stage juveniles (Fig. 1). Five days after exposure both free and encysted first-stage juveniles were present, and measured 0.392 to 0.407 by 0.045 to 0.055; anterior end rounded; posterior portion tapering slightly with tip of tail ending in characteristic short conical process; cuticle thin, trans-
parent, with very fine transverse striations; oral opening leading into a transparent esophagus approximately one-fifth of body, slightly swollen at posterior end; intestine granular, connecting posteriorly with a very short rectum surrounded by two rectal glands (Fig. 2).

Juveniles undergo the first molt 7 to 9 days after experimental infection as indicated by a detached cuticle in the tail region (Fig. 3). On the 8th day, some showed a partially detached cuticle, others had completed the first molt and were in the second stage.

Second-stage juvenile: Only second-stage juveniles were observed by the ninth day. The bulbous swelling at the posterior part of the esophagus was not as prominent as in the preceding stage. Fourteen-day-old juveniles measured 2.068 to 2.189 by 0.77 to 0.81; body tapering toward each extremity; tip of tail rounded, having lost the conical process with shedding of first cuticle (Fig. 4); cuticle thin, transparent and with very fine transverse striations; oral opening leading into a buccal capsule 0.001 to 0.012 deep; esophagus about one-third of body length, divided into muscular and glandular portions, terminal swelling absent; intestine simple and narrow; rectum surrounded by three large rectal glands; nerve ring and excretory pore 0.108 to 0.111 and 0.130 to 0.135 from anterior extremity, respectively.

Juveniles recovered on the 19th day post-infection were molting. The partially detached cuticle was observed at the posterior end (Figs. 5, 6). By the 21st day, a few juveniles still showed a partially detached cuticle while the majority had completed the second molt and were in the third stage of development.

Third-stage juvenile: By the 22nd day, third-stage juveniles only were observed. Those recovered on the 24th day measured 2.684 to 2.737 by 0.094 to 0.099; body tapering toward each extremity; tail conical terminating in a characteristic rosette of spinous processes (Fig. 10); cuticle thick and transversely striated; lips trilobed similar to adult, median lobe larger than dorsal or ventral (Fig. 7), each lobe armed with two teeth; four submedian papillae present, located at bases of dorsal and ventral lobes; buccal capsule 0.040 to 0.042 deep; esophagus similar to that of second-stage juvenile but broader near posterior end; nerve ring and excretory pore 0.125 to 0.128 and 0.145 to 0.148 from anterior end, respectively. Sex could be differentiated at this stage; male genital primordium elliptical in shape about 0.032 to 0.034 by 0.015, located ventrally between body wall and intestine, 0.630 to

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Table 4. Determination of the prepatent period of *Mastophorus numidica* in the deer mouse.

<table>
<thead>
<tr>
<th>No. of deer mice</th>
<th>No. of encysted juveniles administered/mouse</th>
<th>Age of cysts from crickets (days)</th>
<th>Ova first appeared in feces (days)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>25</td>
<td>10</td>
<td>35</td>
</tr>
<tr>
<td>1</td>
<td>25</td>
<td>22</td>
<td>35</td>
</tr>
<tr>
<td>1</td>
<td>31</td>
<td>37</td>
<td>35</td>
</tr>
<tr>
<td>4</td>
<td>24</td>
<td>32</td>
<td>41</td>
</tr>
<tr>
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<td>22</td>
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<tr>
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<td>22</td>
<td>40</td>
<td>43</td>
</tr>
<tr>
<td>2</td>
<td>22</td>
<td>45</td>
<td>48</td>
</tr>
</tbody>
</table>

* Ova absent in one daily examination.

0.635 from posterior end, composed of 2 large epithelial cells enclosing a group of germinal cells (Fig. 9); female genital primordium also somewhat elliptical, about 0.031 by 0.011, attached to body wall ventrally by means of a cell, 0.874 to 0.876 from tip of tail (Fig. 8).

**Development and morphology of worms in the deer mouse**

Infection was established in deer mice fed 38- to 45-day-old encysted juveniles removed from the hemocoels of crickets (Table 2) as well as in those fed crickets 38 to 45 days after exposure of the latter to eggs of *M. numidica* (Table 3). Similar results were obtained with grasshoppers and beetles. Since older juveniles were not administered, it was not determined if infectivity of juveniles decreases with age.

Transition to the fourth stage occurred in the stomach of the deer mouse 8 to 11 days after ingestion of cysts containing infective third-stage juveniles. In a late phase of the impending molt, two thick cuticles are clearly observable, an outer one with a rosette of spinous processes at the terminus of the tail and an inner one with small elevations at the caudal tip (Figs. 11, 12). By the end of the 11th day, all juveniles examined had completed the third molt and were in the fourth stage.

**Fourth-stage juvenile:** Examination of a deer mouse 14 days after ingestion of cysts containing third-stage juveniles revealed fourth-stage females only; body 7.425 to 8.360 by 0.187 to 0.196; cuticle thick and transversely striated; lips well developed; buccal capsule 0.072 to 0.080 deep; nerve ring and excretory pore 0.180 to 0.192 and 0.252 to 0.286 from anterior end, respectively; primitive vulva posterior to mid-body; vagina short and curved posteriorly; muscular ovjector followed by short trunk which branches into an anterior and a posterior uterus; oviduct narrow; tail conoid with small cuticular elevations at tip giving it a rough appearance.

Two females recovered from the stomach of a deer mouse examined 15 days postinfection were beginning the fourth molt. They showed a partially detached thick outer cuticle with cuticular elevations at the caudal tip and the thick inner cuticle was smooth at the tip of the tail (Fig. 13). By the 17th day, all specimens examined had completed the fourth molt and were fifth stage. The adult stage has been described by Seurat (1914) and warrants no further description here.

**Determination of prepatent period**

At 35 to 42 days after ingestion of infective juveniles, sexually mature adults were present as evidenced by the appearance of eggs in the feces of experimentally infected deer mice (Table 4).

**Discussion**

With the exception of studies reported by Hall (1929) and Crook and Grundmann (1964), all prior life history investigations of *Mastophorus* were conducted with insects which are commonly used in the laboratory and probably are not the intermediate hosts under natural conditions. Though several orders of insects (Coleoptera, Orthoptera, Siphonaptera, and Lepidoptera) have been found to contain members which serve as intermediate hosts of *Mastophorus*, grasshoppers have not been reported previously to function as such. Results with other orthopteran insects suggest that grasshoppers may play an important role under natural conditions as intermediate hosts for species of *Mastophorus* other than *M. numidica*.

Crook and Grundmann (1964) reported that grasshoppers (*M. femur-rubrum*) did not be-
come infected when exposed to feces of deer mice containing eggs of *M. numidica*. However, in the present experiment, grasshoppers became infected when fed the eggs concentrated on a small piece of lettuce which had been thoroughly washed with tap water. Since grasshoppers are not coprophagic, it seems probable that they become infected in nature by eating contaminated vegetation rather than fecal matter.

The time intervals required in the intermediate hosts for development to infectivity by juveniles of *M. muris* and *M. numidica* are similar. Cram (1926) found that 41 days were necessary for development of infective *M. muris* in the hemocoel of *Blatta germanica*. Crook and Grundmann (1964) reported that infective cysts occurred in the hemocoel of *E. tuberculata patruelis* 40 days after ingestion of eggs of *M. numidica*. Similar results were obtained in the present study; 38 days after ingestion of eggs of *M. numidica* by the grasshopper (*M. femur-rubrum*), infective cysts were observed in the hemocoel. The prepatent period reported for *M. muris* is about 115 days as compared with about 36 days for *M. numidica*, as found by Crook and Grundmann (1964). In the present study, this period ranged from 35 to 42 days.

**Summary**

An account of the life cycle of *Mastophorus numidica* as it occurs in the cricket (*Acheta domestica*) and the deer mouse (*Peromyscus maniculatus*) is described and illustrated. Experimental infections were obtained in all three species of insects (*Melanoplus femur-rubrum*, *Eleodes obsOLEta*, and *A. domestica*) fed eggs of *M. numidica*. Control specimens of *M. femur-rubrum* and *E. obsOLEta* showed natural infections. The first and second molts occur in the hemocoel of crickets 7 to 9 and 19 to 22 days postinfection, respectively.

Infection was established in deer mice fed 38- to 45-day-old encysted juveniles removed from the hemocoel of crickets as well as in those fed crickets 38 to 45 days after exposure of the latter eggs of *M. numidica*. Similar results were obtained with grasshoppers and beetles. The fourth and fifth molts occur in the stomach of deer mice 8 to 11 and 15 to 17 days postinfection, respectively. The prepatent period ranged from 35 to 42 days.

**Literature Cited**


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