SYNOPSIS AND IDENTIFICATION OF NORTH AMERICAN HAIRWORMS
(GORDIOIDEA: NEMATOMORPHA)

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ABSTRACT—The present work reviews the hosts, distributions, synonyms and taxonomic characters of North American hairworms (Gordioidea: Nematomorpha) and presents a key based on adult morphological characters that can be observed under the dissecting and light microscopes. A total of 18 described species are recognized in the present work. However the field is complicated by incomplete descriptions, lack of knowledge of morphological variation within species and sexual dimorphism.

Hairworms, or Gordioidea, are fresh water members of the Phylum Nematomorpha. These enigmatic organisms, which stand apart from other invertebrates, have been little studied due to their secretive habits, difficulty in rearing, lack of economic importance and problems regarding their identification. All known species develop in invertebrates, especially insects, but the larvae are capable of encysting (without development) in a wide range of animals, including vertebrates (Poinar, 2001; Schmidt-Rhaesa, 1997; Smith, 2001).

The present work reviews the hosts, distributions, synonyms and taxonomic characters used in the identification of North American hairworms and presents a key based on adult morphological characters that can be observed under the dissecting and light microscopes (Fig. 1).

TAXONOMIC CHARACTERS USED TO IDENTIFY HAIRWORMS

First stage hairworm larvae are transparent and provided with an array of hooks, styllets and assorted devices for penetrating into the body cavity of potential hosts (Fig. 2-4). While these characters could be used for generic and even specific placement, too few larvae have been examined to make this method of identification practical. Thus only adult characters are used in identifying hairworms. Moreover, since the adults are normally opaque, only external characters are practical.

Diagnostic characters of adult hairworms include: 1) the presence and nature of the areoles (raised areas on the cuticle), especially their type, shape, size, arrangement, and association with pore canals, bristles, warts and papillae, 2) body shape, size and color pattern, especially that associated with the anterior (calotte) and posterior ends and, 3) features of the male tail, including first, whether it is simple or forked and then if it bears pre- or postcloacal ridges, folds, hairlines, bristle fields or tubercles. Caution should be taken since the adults frequently exhibit sexual and age dimorphism in relation to body size, shape and coloration as well as areole arrangement. In addition, fixation artifacts such as body ridges, folds, etc. may result from specimens remaining in alcohol for extended periods (the majority of hairworm species have been described from museum specimens that have been in preservative for a number of years). Unfortunately, the intraspecific variation of most diagnostic characters is unknown, since many species have been described from a single specimen or only one or two specimens have been examined in detail.

When available, scanning electron microscopy is a useful tool for studying fine details on the surface of hairworms. However this technique is not necessary for identification purposes if good light microscopes are available. Methods for preserving and preparing specimens for optical microscopic examination can be found elsewhere (Poinar, 2001; Smith, 2001).

BIOLOGICAL ASSOCIATIONS

Basically, all hairworms develop inside invertebrates, with a free-living stage in an aquatic habitat where mating and oviposition occur. Most, if not all, hairworms have an indirect life cycle, involving an aquatic paratenic host (Fig. 2-3) and a terrestrial (or rarely aquatic) developmental host (Fig. 2-1). The paratenic host (one that carries a parasite internally but does not support its growth or reproduction) ingests hairworm eggs containing preparasitic larvae or free-living preparasitic larvae in the water habitat. These preparasitic larvae enter the body cavity of the paratenic host by burrowing through the intestinal wall. Penetration is assisted by an extensible proboscis bearing circles of spines as well as three styllets. After passing through the gut wall, the preparasitic stage then encysts, usually in the fat body, intestinal wall, connective tissue or muscle tissue of the paratenic host (Fig. 2-3). The range of paratenic hosts is more extensive than that of developmental hosts and can include fish, frogs and even humans. Presumably, chemical cues signal whether a host is suitable for development or encystment.

Growth and development of the hairworm larva occurs after the paratenic host is consumed and the hairworm larva enters the body cavity of a developmental (or definitive) host, usually an insect predator or omnivore. In some cases, instead of developing, the hairworm larva will re-encyst inside the predator. In this case, the predator becomes a secondary paratenic host (Fig. 2-3). When reporting hairworm hosts, it is important to state wheth-
er it is a paratenic or developmental host, which is not always clear from the literature (White, 1969).

A list of the 18 species of North American hairworms recognized in this work, and their synonyms, is given in Table 1. Available information on naturally occurring paratenic and developmental hosts of North American hairworms, along with notes on their distribution, is presented below, followed by a key to the adults. It should be noted that collection data on North American hairworms is quite sparse. Thus the geographic ranges presented below present a biased view of the actual range of species. It is likely that most North American hairworms occur throughout North America, but only in certain ecological habitats. Certain species, e.g. Gordius robustus and Paragordius varius, appear to be more widespread than others. Distribution depends on climatic and ecological conditions and available hosts. Environmental disruption by humans has a direct impact on hairworms and limits their occurrence to more remote habitats with natural water sources.

SYNOPSIS OF NORTH AMERICAN HAIRWORM SPECIES WITH GEOGRAPHIC LOCATION AND HOST RECORDS (IN ALPHABETICAL ORDER)

Chordodes morgani Montgomery, 1898a. This is essentially an eastern North American species with reports from as far south as Florida and as far west as Nebraska (Chandler, 1985). Montgomery (1898a) mentions that a blattid served as host to this species and Schmidt Rhaesa et al. (2003) reported Periplaneta fuliginosa and Parcoblatta sp. as hosts. Studier et al. (1991) reported parasitism by this hairworm in the camel cricket, Ceothophilus stygius and cave cricket, Hadenoecus subterraneus.

Gordius densareolatus (Montgomery 1898a) nov. comb. has been reported from Western North America (Montgomery, 1907).

Gordius lineatus (Leidy 1851) has been reported from eastern North America (Montgomery, 1898a, 1907; Leidy, 1851), including a cave in the Great Smoky Mountains National Park (Reeves, 2000).

Gordius longareolatus (Montgomery 1898b) has only been reported from California (Montgomery, 1898b).

Gordius platycephalus (Montgomery 1898a) has been reported from the Ungava Region of Eastern Canada, Montana, Pennsylvania, Wyoming, Guatemala (Montgomery, 1898a, 1907) California and Utah (Poinar and Weissman, 2004) suggesting that it occurs throughout North America. Hosts include the orthopteran, Stenopelmatus spp. (Poinar and Weissman, 2004).

Gordius siplepis Schmidt-Rhaesa et al., 2003 has been reported only from one locality in British Columbia.

Gordius violaceus (Baird 1853) occurs throughout North America (Smith, 1991; Schmidt-Rhaesa et al., 2003).

Gordius alascensis Montgomery 1907, which was assigned to the genus Gordius by Schmidt-Rhaesa et al. (2003), has been reported only from Alaska (Montgomery, 1907).

Gordius attonti Redlich 1980 has been reported from northern North America (Redlich, 1980; Schmidt-Rhaesa et al., 2003).

Gordius difficiliis Montgomery 1898a (Smith 1994) has been reported from eastern North America (Smith, 1994). The ground beetles, Chlaenius prasinus (Coleoptera: Carabidae) and Pterostichus melanarius have been reported as developmental hosts for this species (Hanelt and Janovy, 2000; Bolek and Coggins, 2001).

Gordius robustus Leidy 1851 occurs throughout North America, including Mexico (Chandler, 1985; Camerano, 1915) and Hawaii (Montgomery, 1898a; Heinze, 1934). The North American developmental hosts for this species include various Acrididae (Ward and Whipple, 1918). Odonata (Cappucci, 1977), the orthopterans, Stenopelmatus fuscus Brunner (Cappucci, 1977, Stenopelmatus spp. (Poinar and Weissman, 2004), Anabrus simplex Haldeman (Thorne, 1940), Orchelimum nigripes Scudder (May, 1919), Orchelimum vilgare Harris (May, 1919), Scudderia fasciata Brunner (May, 1919), Planeropera fuscata (Brunner), (Thorne, 1940), Steiroxyx sp. (Poinar and Weissman, 2004), Conocephalus nemoralis (Scudder), C. fasciatus (May, 1919), Gryllus sp. (Poinar and Weissman, 2004) and the carabid, Gastrellarius honestus Say (Leidy, 1856).

Neochordodes californiensis de Miralles and Villalobos 1995 has been reported only from California.

Neochordodes occidentalis (Montgomery 1898a) has been reported from western North America (Chandler, 1985), including Mexico (Poinar and Weissman, 2004). Developmental hosts include the orthopterans Stenopelmatus spp. and Pediodectes sp. (Poinar and Weissman, 2004). Ward and Whipple (1918) state that an acridid is also a developmental host, while mosquito larvae served as experimental paratenic hosts in studies by Poinar and Doelman (1974).

Parachordodes tegnotus Poinar, Rykken and Labonte (2004) has only been reported from Oregon. Developmental hosts are the ground beetles Pterostichus inopinus Casey, P. castaneus Dej. and Pterostichus amethystinus Mann. (Carabidae: Coleoptera) (Fig. 2-1). Paratenic hosts include mayfly larvae and larvae of the caddis fly, Rhyacophila sp. (Fig. 2-3). The latter is a predator and probably represents a secondary paratenic host, having ingested mayfly primary paratenic hosts.

Paragordius varius (Leidy 1851) occurs throughout North America (Chandler, 1985) including Hawaii (Camerano, 1901). Developmental hosts include the orthopterans, Gryllus sp., Gryllus assimilis (Fab.), Gryllus pennsylvanicus and Nemosibius fasciatus (DeGreer) (Montgomery, 1903; Poinar and Weissman, 2004; Schmidt-Rhaesa et al., 2003; Ward and Whipple, 1918). White (1969) mentions larval mayflies (Baetes spp., Leptophlebia sp., Ephemerella spp.), caddis flies (Brachycentrus spp.), black flies (Simulium spp.) and corixids (Sigaer sp.) as hosts for the larvae of P. varius. Unfortunately, it is not clear whether the hairworm larvae were developing or just encysted in these hosts. However, the likelihood of hairworms developing in such small hosts as blackflies is negligible. It is possible that some of the infections, especially those in the blackflies, were caused by merobenth nematodes. Until further evidence to the contrary, these records are considered as representing paratenic hosts.

Pseudochordodes gordienoides (Montgomery 1898a) has been reported from Western United States (Schmidt-Rhaesa et al., 2003).

Pseudochordodes manteri Carvalho 1942 has been reported only from Nebraska.

Pseudochordodes taxanus Schmidt-Rhaesa et al., 2003 was described from a cave in Texas, which is the only known locality.
<table>
<thead>
<tr>
<th>Species</th>
<th>Synonym</th>
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<tr>
<td><em>Chordodes morgani</em> Montgomery 1898a</td>
<td><em>C. puerilis</em> Montgomery 1898a <strong>(Camerano, 1915)</strong></td>
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<td><em>Gordius densareolatus</em> (Montgomery 1898a)</td>
<td><em>Parachordodes densareolatus</em> (Montgomery 1898a) <strong>(Schmidt-Rhaesa et al., 2003)</strong></td>
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<td>nov. comb</td>
<td><em>Gordius densareolatus</em> Montgomery 1898a</td>
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<td><em>Gordius lineatus</em> (Leidy 1851)</td>
<td><em>G. leidyi</em> Montgomery 1898a</td>
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<td>(Schmidt-Rhaesa et al., 2003)</td>
<td><em>Parachordodes lineatus</em> (Leidy 1851) <strong>(Camerano, 1915)</strong></td>
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<td><em>Gordius longareolatus</em> (Montgomery 1898b)</td>
<td><em>Gordius lineatus</em> Leidy 1851 <strong>(Camerano</strong>,** 1915)**</td>
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<td>(Schmidt-Rhaesa et al., 2003)</td>
<td><em>Parachordodes longareolatus</em> (Montgomery 1898b)</td>
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<td><em>Gordius platycephalus</em> (Montgomery 1898a)</td>
<td><em>Gordius longareolatus</em> Montgomery 1898b</td>
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<td>(Schmidt-Rhaesa et al., 2003)</td>
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<td><em>Gordius sinepilosus</em> Schmidt-Rhaesa et al.</td>
<td><em>Parachordodes platycephalus</em> Montgomery 1898a</td>
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<td>2003</td>
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<td><em>Gordius violaceus</em> (Baird 1853)</td>
<td><em>Gordius violaceus</em> Baird 1853 <strong>(Camerano, 1897)</strong></td>
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<td>(Heinze, 1935)</td>
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<td><strong>Gordius alascensis</strong> Montgomery 1907</td>
<td><em>Gordius alascensis</em> Montgomery 1907 <strong>(Schmidt-Rhaesa et al., 2003)</strong></td>
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<td><em>Gordius difficilis</em> Montgomery 1898a,</td>
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<td>(Smith, 1994)</td>
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<td><em>Gordius robustus</em> Leidy 1851</td>
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<td><strong>Neochordodes californensis</strong> de Miralles &amp;</td>
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<td>de Villalobos 1995</td>
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<td><em>Neochordodes occidentalis</em> (Montgomery</td>
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<td>1898a</td>
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<td><em>Parachordodes tegonotus</em> Poinar et al. 2004</td>
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<td><em>Paragordius varius</em> (Leidy 1851) (Camerano,</td>
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<td><strong>Pseudochordodes gordioides</strong> (Montgomery</td>
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<td>1898a) <strong>(de Miralles et al., 1997)</strong></td>
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<td><strong>Pseudochordodes manteri</strong> Carvalho 1942</td>
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<td><strong>Pseudochordodes texanus</strong> Schmidt-Rhaesa</td>
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<td>et al. 2003</td>
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FIG. 2. 1. *Pterostichus amethystinus* Mann. (Coleoptera: Carabidae) serving as a developmental host to the hairworm, Parachordodes tegonotus in Oregon. 2. Female tail of *Paragordius varius* from California. 3. Encysted larva of Parachordodes tegonotus teased out of the gut tissues of the predatory caddis fly, *Rhyacophila* sp. (Trichoptera) in Oregon. The caddis probably served as a secondary paratenic host. 4. Scanning electron microscope image of a preparasitic larva of *Chordodes morgani* from Tennessee. Note cirrlet of spines protruding from anterior end.
KEY TO THE NORTH AMERICAN HAIRWORM SPECIES

A. Cuticle smooth, lacking areoles or with flat, smooth areoles; male tail bilobed (as in Figs. 1.1, 1.2, 1.3), with a postcloacal or precloacal ridge or crescent; female tail entire—*Gordiidae* May 1919—*Gordius* L. .......... B

A. Cuticle with distinct areoles usually ornamented with bristles or tubercles; male tail entire (Fig. 1.5) or if bilobed, then without a postcloacal (Fig. 1.1) or precloacal ridge or crescent (as in Fig. 1.3); female tail entire or trilobed (Fig. 2.2) .......... E

B. Male cuticle with large white spots; broad semicircular postcloacal crescent present (Fig. 1.1); elongate white triangular streak from neck to anterior fourth of body in both sexes; head tapers (spindle-shape) .......... *Gordius attini* Redlich 1980

B. Male cuticle with or without white spots, lacking an elongate white triangular streak; head variable .......... C

C. Male with both a precloacal semicircular hairline and a postcloacal ridge (Fig. 1.2); areoles present or absent on females .......... *Gordius difficilis* Montgomery 1898a, (Smith 1994)

C. Male with either a postcloacal or a precloacal ridge, but not both .......... D

D. Male with a precloacal ridge (Fig. 1.3) areoles confluent, interconnected ..... *Gordius alascensis* Montgomery 1907

D. Male with a postcloacal ridge (Fig. 1.1); areoles absent .......... *Gordius robustus* Leidy 1851

E. Female tail trilobed (Fig. 2.2); male tail bilobed with length of lobes greater than twice their width (Fig. 1.4); head end obliquely truncated .......... *Paragordius varius* (Leidy 1851)

E. Female tail entire; male tail bilobed with length of lobes equal to or less than twice their width (as in Fig. 1.1, 2, 3), or male tail entire (Fig. 1.5) .......... F

F. Male tail bilobed .......... M

M. Female tail entire, lobes absent or abbreviated .......... G

G. Cuticle with normally one kind of areole—*Neochordodes* Carvalho 1942 .......... H

G. Cuticle with two or more types of areoles .......... J

H. Areoles containing short bristles and tubercles (some specimens possess a smaller type of areole) .......... *Neochordodes occidentalis* (Montgomery 1898a,b) (Poinar and Doelman 1974)

H. Areoles lacking bristles or tubercles .......... *Neochordodes californiensis* de Miralles and de Villalobos 1995

J. Areoles with prominent tubercles, crowns or papillae; female cloacal aperture terminal .......... *Chordodes morgani* (Montgomery 1898a)

J. Areoles without prominent tubercles, crowns or papillae; female cloacal aperture subterminal—*Pseudochordodes* Carvalho 1942 .......... K

K. Smaller areoles with knobs on surface; arranged randomly ..... *Pseudochordodes gordoiides* (Montgomery 1898a)

K. Smaller areoles without knobs on surface, arranged in uneven rows .......... L

L. Large elevated areoles in clusters of usually two .......... *Pseudochordodes manteri* Carvalho 1942

L. Large elevated areoles in clusters of three and four .......... *Pseudochordodes tarsanus* Schmidt-Rhaesa et al. 2003

M. Areoles of two types, large megareoles with a central pore or tubercle and small microareoles lacking a pore or tubercle; broad hair line of short simple and branched hairs beginning anterior to cloacal aperture but not reaching to point of bifurcation of tail lobes (Fig. 1.8) .......... *Parachordodes tegonotus* Poinar, Rhyken and LaBonte 2004

M. Areoles of one (microareolar) type, lacking a central pore or tubercle—*Gordius* Müller .......... N

N. Oblique rows of single and/or branched hairs flanking cloacal aperture (Fig. 1.6, 7); areoles closely opposed, may produce longitudinal ridges .......... O

O. No such hairs on lateral body surface flanking cloacal aperture .......... P

P. Body dark brown; areoles irregularly polygonal, not arranged in rows, well separated from one another by distinct interareolar region; interareolar spaces with small spinules or papillate processes; areoles not showing sexual dimorphism; hairline on male tail not reaching point of bifurcation of tail lobes (Fig. 1.6); calotte white .......... *Gordius violaceus* (Baird 1853)

O. Body light yellow to deep buff; areoles closely opposed without intervening spaces, having a tendency to group themselves in longitudinal rows in males (sexual dimorphism); hairline extending beyond point of bifurcation of tail lobes (Fig. 1.7); calotte dark or absent .......... *Gordius lineatus* (Leidy 1851)

P. Tubercles located behind male cloacal aperture (Fig. 1.7, 8); tail lobes of male shorter than, equal to or longer than wide; female tail not swollen; head variable .......... Q

P. No tubercles behind male cloacal aperture (Fig. 1.9); tail lobes of male longer than wide; female tail swollen; head flattened .......... *Gordius platyccephalus* (Montgomery 1898a)

Q. Tail lobes of males short (Fig. 1.10), length equal to or shorter than width; black ring surrounds cloacal aperture; postcloacal ingumentary ridge; tubercles extend anterior to cloacal aperture; areoles more or less confluent, tending to merge with one another and produce transverse rows, head usually cylindrical .......... *Gordius densareolatus* (Montgomery 1898a)

Q. Tail lobes of males longer than wide (Fig. 1.11); no black ring around cloacal aperture; postcloacal ingumentary ridge absent; tubercles not extending anterior to cloacal aperture .......... R

R. Areoles elongated, well separated from one another; few interareolar structures (tubercles) .......... *Gordius longareolatus* (Montgomery 1898b)

R. Areoles rounded to polygonal, numerous bristles in interareolar spaces .......... *Gordius sinepoxius* Schmidt-Rhaesa et al. 2003

LITERATURE CITED


CAMERANO, L. 1892. Descrizione di una nuova specie di *Gor-


