JOURNAL OF THE TENNESSEE ACADEMY OF SCIENCE 79(1):1–7 JANUARY 2004

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, stylets 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 circlets of spines as well as three stylets. 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 whether 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, 1898*a.* 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 (1898*a*) mentions that a blattid served as host to this species and Schmidt Rhaesa et al. (2003) reported *Periplaneta fulginosa* and *Parcoblatta* sp. as hosts. Studier et al. (1991) reported parasitism by this hairworm in the camel cricket, *Ceuthophilus stygius* and cave cricket, *Hadenoecus subterraneus.*

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

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

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

Gordionus platycephalus (Montgomery 1898*a*) has been reported from the Ungava Region of Eastern Canada, Montana, Pennsylvania, Wyoming, Guatemala (Montgomery, 1898*a,* 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).

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

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

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

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

Gordius difficilis Montgomery 1898*a* (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, 1898*a*; 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 vulgare* Harris (May, 1919), *Scudderia furcata* Brunner (May, 1919), *Phaneroptera furcata* (Brunner), (Thorne, 1940), *Steiroxys* 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 californensis de Miralles and de Villalobos 1995 has been reported only from California.

Neochordodes occidentalis (Montgomery 1898*a*) 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 tegonotus Poinar, Rykken and Labonte (2004) has only been reported from Oregon. Developmental hosts are the ground beetles *Pterostichus inopinus* Casey, *Pterostichus 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 *Nemobius 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* sp.), black flies (*Simulium* spp.) and corixids (*Sigara* 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 mermithid nematodes. Until further evidence to the contrary, these records are considered as representing paratenic hosts.

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

Pseudochordodes manteri Carvalho 1942 has been reported only from Nebraska.

Pseduochordodes taxanus Schmidt-Rhaesa et al., 2003 was described from a cave in Texas, which is the only known locality.

TABLE 1. Species of hairworms (with synonyms) reported from North America.

Species	Synonym
Chordodes morgani Montgomery 1898*a*	*C. puerilis* Montgomery 1898*a*
Gordionus densareolatus (Montgomery 1898*a*) nov. comb	*Parachordodes densareolatus* (Montgomery 1898*a*) (Camerano, 1915) (Schmidt-Rhaesa et al., 2003) *Gordius densareolatus* Montgomery 1898*a* *G. leidyi* Montgomery 1898*a*
Gordionus lineatus (Leidy 1851) (Schmidt-Rhaesa et al., 2003)	*Parachordodes lineatus* (Leidy 1851) (Camerano, 1915) *Gordius lineatus* Leidy 1851
Gordionus longareolatus (Montgomery 1898*b*) (Schmidt-Rhaesa et al., 2003)	*Parachordodes longareolatus* (Montgomery 1898*b*) (Camerano, 1915) *Gordius longareolatus* Montgomery 1898*b*
Gordionus platycephalus (Montgomery 1898*a*) (Schmidt-Rhaesa et al., 2003)	*Parachordodes platycephalus* (Montgomery 1898*a*) (Camerano, 1915) *Gordius platycephalus* Montgomery 1898*a*
Gordionus sinepilosus Schmidt-Rhaesa et al. 2003	
Gordionus violaceus (Baird 1853) (Heinze, 1935)	*Parachordodes violaceus* (Baird 1853) (Camerano, 1897) *Gordius violaceus* Baird 1853
Gordius alascensis Montgomery 1907	*Gordionus alascensis* (Montgomery 1907) (Schmidt-Rhaesa et al., 2003) *Parachordodes alascensis* (Montgomery 1907) (Chandler, 1985).
Gordius attoni Redlich 1980	
Gordius difficilis Montgomery 1898*a*, (Smith, 1994)	*Gordius aquaticus difficilis* Montgomery 1898*a*
Gordius robustus Leidy 1851	*Gordius aquaticus robustus* Montgomery 1898*a* *G. agassizi* Montgomery 1898*a* *G. lacustris* Leidy 1871 *G. subspiralis* Diesing 1861 *G. californicus* Camerano 1915 *G. villoti* Rosa 1881 (Montgomery, 1907) *G. fasciatus* Baird 1853 *G. hawaiiensis* Heinze 1934
Neochordodes californensis de Miralles & de Villalobos 1995	
Neochordodes occidentalis (Montgomery 1898*a*)	*Chordodes occidentalis* Montgomery 1898*a*
Parachordodes tegonotus Poinar et al. 2004	
Paragordius varius (Leidy 1851) (Camerano, 1897)	*Gordius varius* Leidy 1851 *G. longilobatus* Leidy 1870 *Chordodes varius* Römer 1897
Pseudochordodes gordioides (Mongomery 1898*a*) (de Miralles et al., 1997)	*Chordodes gordioides* Montgomery 1898*a* *Pseudochordodes bedriagae* (Camerano 1896) (Schmidt-Rhaesa et al., 2003)
Pseudochordodes manteri Carvalho 1942	
Pseudochordodes texanus Schmidt-Rhaesa et al. 2003.	

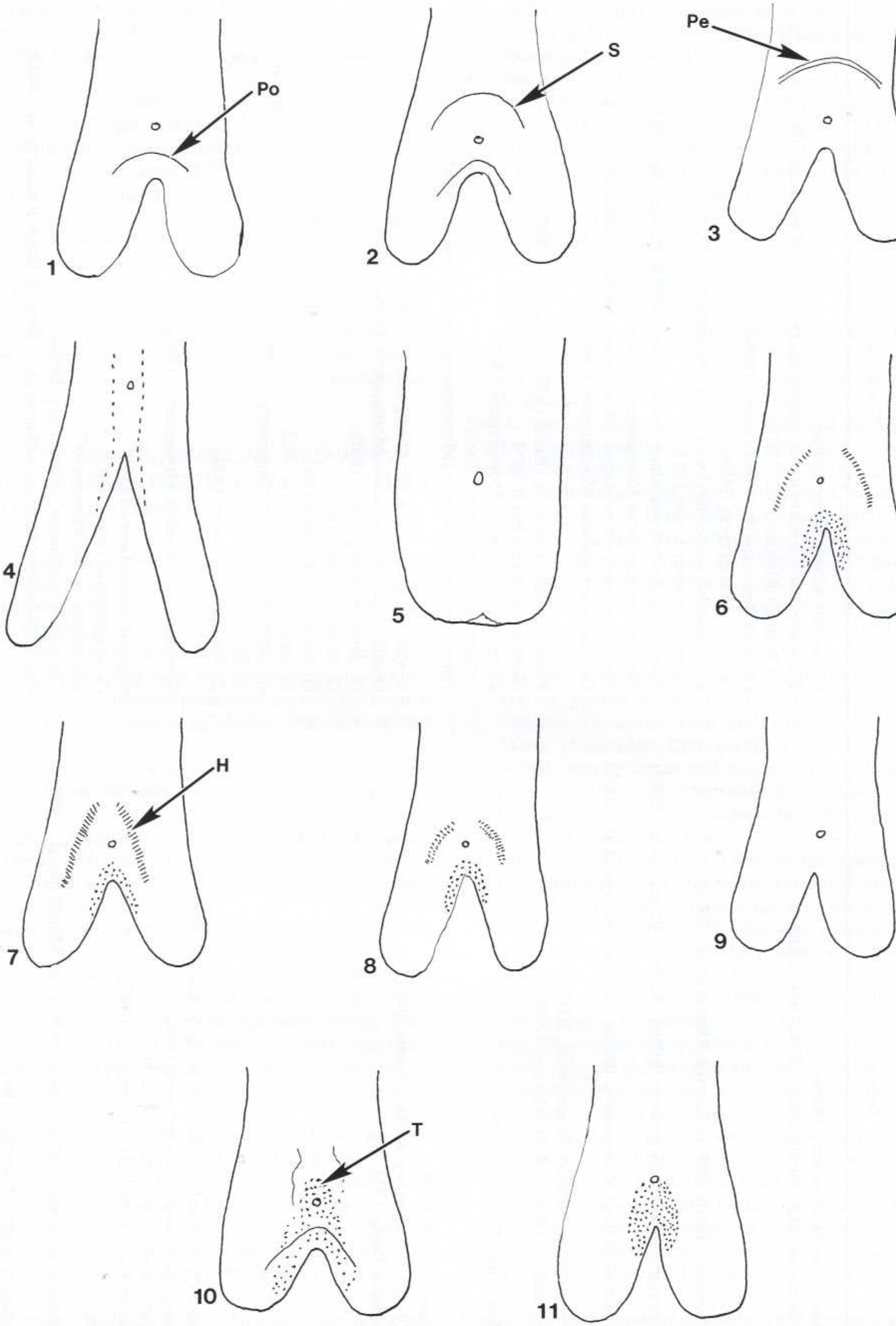

FIG. 1. Male tails of North American hairworms. 1. *Gordius robustus.* 2. *Gordius difficilis* and *Gordius paranensis.* 3. *Gordius alascensis.* 4. *Paragordius varius.* 5. *Neochordodes* and *Chordodes* spp. 6. *Gordionus violaceus.* 7. *Gordionus lineatus.* 8. *Parachordodes tegonotus.* 9. *Gordionus platycephalus.* 10. *Gordionus densareolatus.* 11. *Gordionus longareolatus.* Po = postcloacal fold or crescent; Pe = precloacal fold or crescent; S = semicircular hairline; H = hairline; T = tubercles.

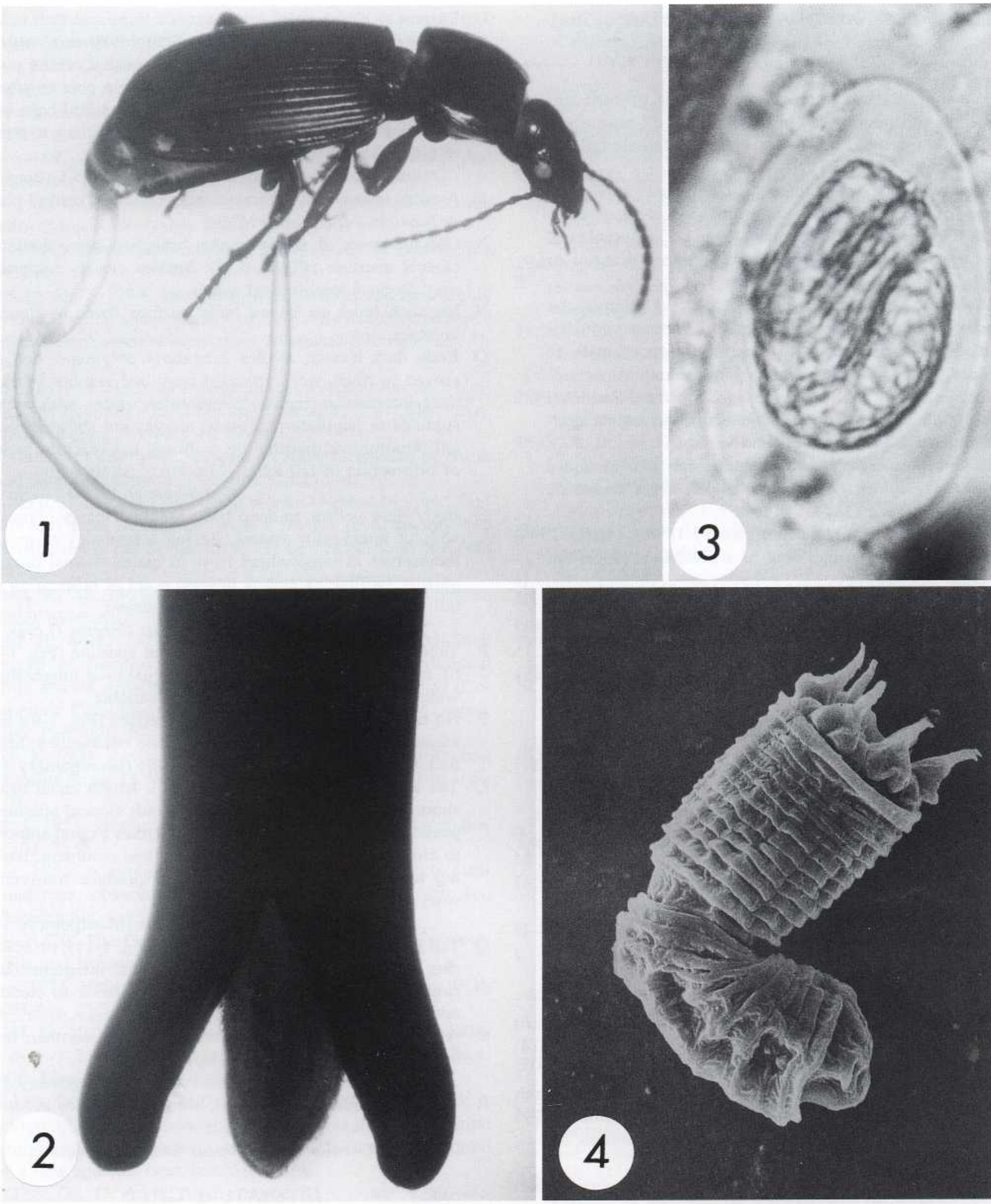

FIG. 2. 1. *Pterostichus amethystinus* Mann. (Coleoptera: Carabidae) serving as a developmental host to the hairworm, *Parachordodes tegonotus* in Oregon. 2. Female tail of *Paragordius varius* from California. 3. Encysted larva of *Parachordodes tegonotus* teased out of the gut tissues of the predatory 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 circlet 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, 2, 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 attoni* 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 1898*a,* (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

F Male 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 1898*a,b*) (Poinar and Doelman 1974)

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

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

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 gordioides* (Montgomery 1898*a*)

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 taxanus* 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, Rykken and LaBonte 2004

M Areoles of one (microareolar) type, lacking a central pore or tubercle—*Gordionus* 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

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

O 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. . . . . *Gordionus 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 . . . . *Gordionus lineatus* (Leidy 1851)

P Tubercles located behind male cloacal aperture (Fig. 1-7, 8); tale 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 .. *Gordionus platycephalus* (Montgomery 1898*a*)

Q Tail lobes of males short (Fig. 1-10), length equal to or shorter than width; black ring surrounds cloacal aperture; postcloacal integumentary 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. . . . . *Gordionus densareolatus* (Montgomery 1898*a*)

Q Tail lobes of males longer than wide (Fig. 1-11); no black ring around cloacal aperture; postcloacal integumentary ridge absent; tubercles not extending anterior to cloacal aperture . . . . R

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

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

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