

SHORT COMMUNICATION

FIRST UNEQUIVOCAL MERMITHID–LINYPHIID (ARANEAE) PARASITE–HOST ASSOCIATION

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ABSTRACT. The first description of a Mermithidae–Linyphiidae parasite–host association is presented. The nematode is preserved exiting the abdomen of the host, which is a juvenile *Tenuiphantes* species (Araneae, Linyphiidae), collected from the Isle of Mull, UK. An updated taxonomic list of known mermithid spider hosts is provided. The ecology of known spider hosts with regard to the direct and indirect life cycles of mermithid worms suggests that both occur in spiders.

Keywords: *Aranimermis*, Isle of Mull, Linyphiidae, Mermithidae, Nematoda

Nematode parasites of spiders are restricted to the family Mermithidae but are not uncommon (Poinar 1985, 1987) and were first reported almost two and a half centuries ago (Roesel 1761). However, given the difficulty of identifying and rearing post-parasitic juvenile mermithids, they have received inadequate systematic treatment (Poinar 1985). In addition, the complete life history is known for only one species of these spider parasites (Poinar & Early 1990). Poinar & Welch (1981) supported the use of the genus *Agamomermis* Stiles, 1903 for previously described mermithids that could not be placed in existing taxa and that were considered *species inquirendae*. This is the case for all spider mermithids described prior to 1986 (Poinar 1987). Currently three extant species of spider mermithid parasites are recognized: *Aranimermis aptispicula* Poinar & Benton 1986, *A. actereki* Gufarov & An 1987 (spider host species unknown) and *A. giganteus* Poinar & Early 1990. In addition, the fossil species *Heydenius araneus* Poinar 2000 (a genus restricted to Tertiary fossil nematodes [Poinar 2003]) has been described from a crab spider (Thomisidae) in Baltic amber.

Poinar (1985, 1987) provided lists of spider species with records of mermithid nematode parasitism. However, many of these taxa have now received taxonomic revisions and or transfers. In addition, a number of subsequent reports of parasitism have been published (Gufarov & An 1987; Poinar & Early 1990; Camino & de-Villalobos 1998; Matsuda 1999; Poinar 2000; Allard & Robertson 2003; Iida & Hasegawa 2003; Vandergast & Roderick 2003; Ahtiainen et al. 2004). We provide

an updated and taxonomically correct list in Table 1. Here we describe the first Mermithidae–Linyphiidae parasite–host association and discuss the ecology of known spider hosts with regard to the life cycles of mermithid worms.

This paper concerns three spider specimens, one with a worm in situ and two that are presumed to have been parasitized, but from which the worms have emerged and are lost. The specimens were collected during May 2004, in pitfall traps containing 50 ml of 70% alcohol, from a hazel forest in the Tireragan Estate on the Isle of Mull, UK. The spiders belong to the linyphiid genus *Tenuiphantes* but the female with the worm in situ cannot be identified to species because it is a juvenile. In the specimen with the mermithid, the anterior and posterior regions of the worm have exited the abdominal cavity just anterior to the epigastric furrow and close to the pedicel (Fig. 1), but at least one coil can be observed interiorly, as a distortion beneath the abdominal integument, which is devoid of white guanine pigmentation. The worm is pale white/cream with a diameter of 0.13 mm and an approximate length (assuming only one coil exists in the spider) of 15.6 mm. The body length of the spider is 2.14 mm. The two other specimens are both female *Tenuiphantes tenebricola* (Wider 1834) but no worms are visible, although the abdomens of both are severely damaged at the same point at which the worm is emerging in the other specimen. We consider it probable that both of these specimens were parasitized as well. One of the specimens has an emaciated, disk-shaped abdomen (similar to that of the specimen with the worm in situ), which gives

Table 1.—Spider hosts of mermithid worms: * *A. aptispicula*, ** *A. giganteus*, remainder *species inquirendae*.

Family	Species	Reference	Comments
Agelenidae	<i>Agelenopsis oregonensis</i> Chamberlin & Ivie 1935	in Poinar (1987)	
Amaurobiidae	<i>Eurocoelotes inermis</i> (L. Koch 1855)	in Poinar (1987)	as <i>Coelotes i.</i>
Antrodiaetidae	<i>Atypoides riversi</i> O.P.-Cambridge 1833	in Poinar (1987)	
Anyphaenidae	<i>Wulfila albens</i> (Hentz, 1847)*	in Poinar (1987)	as <i>W. alba</i>
Araneidae	<i>Aculepeira ceropegia</i> (Walckenaer 1802)	in Poinar (1987)	as <i>Araneus ceropegius</i>
Araneidae	<i>Araneus diadematus</i> Clerck 1757	in Poinar (1987)	
Araneidae	<i>Verrucosa arenata</i> (Walckenaer 1842)*	in Poinar (1987)	
Ctenidae	<i>Leptoctenus byrrhus</i> Simon 1888	Poinar (2000)	as <i>Ctenus bryrrbus</i>
Cybaeidae	<i>Argyroneta aquatica</i> (Clerck 1757)	in Poinar (1987)	
Gnaphosidae	<i>Cesonia bilineata</i> (Hentz 1847)*	in Poinar (1987)	
Gnaphosidae	<i>Gnaphosa lucifuga</i> (Walckenaer 1802)	in Poinar (1987)	
Hexathelidae	<i>Porrhothele antipodiana</i> (Walckenaer 1837)**	Poinar & Early (1990)	as <i>P. a.</i> (Dipluridae)
Idiopidae	<i>Misgolas borealis</i> (Forster 1968)**	Poinar & Early (1990)	as <i>Cantuaria b.</i> (Ctenizidae)
Linyphiidae?	<i>Micryphantes bicuspidatus</i> C.L. Koch 1838	in Poinar (1987)	<i>nomen dubium</i> (Platnick 2004)
Lycosidae	<i>Alopecosa inquilina</i> (Clerck 1757)	in Poinar (1987)	as <i>Tarentula i.</i>
Lycosidae	<i>Alopecosa trabalis</i> (Clerck 1757)	in Poinar (1987)	as <i>Lycosa vorax</i>
Lycosidae	<i>Arctosa alpigena</i> (Doleschall 1852)	Poinar (2000)	possible mermithid
Lycosidae	<i>Geolycosa patellonigra</i> Wallace 1942	in Poinar (1987)	
Lycosidae	<i>Hygrolycosa rubrofasciata</i> (Ohlert 1865)	Ahtiainen et al. (2004)	
Lycosidae	<i>Pardosa agrestis</i> (Westring 1861)	in Poinar (1987)	
Lycosidae	<i>Pardosa amentata</i> (Clerck 1757)	in Poinar (1987)	as <i>Lycosa saccata</i>
Lycosidae	<i>Pardosa furcifera</i> (Thorell 1875)	in Poinar (1987)	
Lycosidae	<i>Pardosa glacialis</i> (Thorell 1872)	in Poinar (1987)	
Lycosidae	<i>Pardosa hortensis</i> (Thorell 1872)	in Poinar (1987)	
Lycosidae	<i>Pardosa lugubris</i> (Walckenaer 1802)	in Poinar (1987)	
Lycosidae	<i>Pardosa milvina</i> (Hentz 1844)	in Poinar (1987)	as <i>P. nigropalpis</i> and <i>P. scita</i>
Lycosidae	<i>Pardosa palustris</i> (Linnaeus 1758)	in Poinar (1987)	as <i>Lycosa tarsalis</i>
Lycosidae	<i>Pardosa pseudoannulata</i> (Boesenberg & Strand 1906)	Iida & Hasegawa (2003)	
Lycosidae	<i>Pardosa riparia</i> (C.L. Koch 1833)	in Poinar (1987)	
Lycosidae	<i>Pardosa sphagnicola</i> (Dahl 1908)	in Poinar (1987)	as <i>Lycosa riparia s.</i>
Lycosidae	<i>Pardosa suwai</i> Tanaka 1985	Matsuda (1999)	
Lycosidae	<i>Pardosa vancouveri</i> Emerton 1917	in Poinar (1987)	
Lycosidae	<i>Rabidosa rabida</i> (Walckenaer 1837)	in Poinar (1987)	as <i>Lycosa scutulata</i>
Lycosidae	<i>Schizocosa saltatrix</i> (Hentz 1844)	in Poinar (1987)	as <i>Lycosa versimilis</i>
Lycosidae	<i>Sosippus floridanus</i> Simon 1898	in Poinar (1987)	
Nemesiidae	<i>Stanwellia kaituna</i> (Forster 1968)**	Poinar & Early (1990)	as <i>Aparua k.</i> (Dipluridae)

Table 1.—Continued.

Family	Species	Reference	Comments
Oxyopidae	<i>Oxyopes sertatus</i> L. Koch 1877	Okochi (1969)	
Oxyopidae	<i>Peucetia viridans</i> (Hentz 1832)	in Poinar (1987)	
Philodromidae	<i>Tibellus oblongus</i> (Walckenaer 1802)	in Poinar (1987)	
Salticidae	<i>Habronattus signatus</i> (Banks 1900)	Vandergast & Roderick (2003)	
Salticidae	<i>Myrmarachne formicaria</i> (De Geer 1778)	in Poinar (1987)	as <i>Salticus formicarius</i>
Salticidae	<i>Phidippus borealis</i> Banks 1895	in Poinar (1987)	
Salticidae	<i>Phidippus clarus</i> Keyserling 1885	in Poinar (1987)	
Salticidae	<i>Phidippus johnsoni</i> (Peckham & Peckham 1883)	in Poinar (1987)	
Salticidae	<i>Phidippus putnami</i> (Peckham & Peckham 1883)	in Poinar (1987)	
Salticidae	<i>Sitticus floricola palustris</i> (Peckham & Peckham 1883)	in Poinar (1987)	as <i>Sitticus p.</i>
Stiphidiidae	<i>Cambridgea foliata</i> (L. Koch 1872)	in Poinar (1987)	
Tetragnathidae	<i>Tetragnatha anuenue</i> Gillespie 2002	Vandergast & Roderick (2003)	
Tetragnathidae	<i>Tetragnatha brevignatha</i> Gillespie 1991	Vandergast & Roderick (2003)	
Tetragnathidae	<i>Tetragnatha praedonia</i> L. Koch 1878	Okochi (1969)	
Tetragnathidae	<i>Tetragnatha quasimodo</i> Gillespie 1991	Vandergast & Roderick (2003)	
Theridiidae	<i>Enoplognatha ovata</i> (Clerck 1757)	in Poinar (1987)	as <i>Theridion ovatum</i> and <i>T. redimitum</i>
Thomisidae	<i>Diaea dorsata</i> (Fabricius 1777)	in Poinar (1987)	
Thomisidae	<i>Misumenops tricuspidatus</i> (Fabricius 1775)	Okochi (1969)	
Thomisidae	<i>Xysticus deichmanni</i> Soerensen 1898	in Poinar (1987)	
Thomisidae	<i>Xysticus durus</i> (Soerensen 1898)	in Poinar (1987)	
Thomisidae	<i>Xysticus funestus</i> Keyserling 1880	in Poinar (1987)	
Zoridae	<i>Zora maculosa</i> Roewer 1951	in Poinar (1987)	as <i>Z. maculata</i> O.P.-C.; <i>nomen dubium</i> (Platnick 2005)

the impression of having been host to a worm. It has a normal degree of guanine pigmentation. The second specimen is not emaciated and has almost no guanine pigmentation. It cannot be ruled out that the specimens were damaged upon sorting the pitfall trap contents, but as no other spiders (including many smaller species) were damaged, we consider this unlikely. Alternatively, they may have been hosts to non-mermithid parasites, such as acrocerids or phorids. Unfortunately, the pitfall contents are no longer available to check for emerged worms. It is probable that the specimen with the worm also belongs to *T. tenebricola*, given that six other individuals (three males and three females) were also collected at the same time from the same locality,

whereas only one female of each of the following species was collected: *T. alacris* (Blackwall 1853), *T. cristatus* (Menge 1866) and *T. mendei* (Kulczynski 1882).

Poinar (1985, 1987) cited von Siebold (1848) as having identified an unknown mermithid worm in the spider *Micryphantes bicuspidatus* (listed in Table 1 under Linyphiidae?). At the time of von Siebold's paper (his description consisted of only five lines and no figures), only six spider families had been established, Linyphiidae was not erected until 1859. The genus *Micryphantes* C.L. Koch 1833 and *M. bicuspidatus* are both *nomina dubia* (Platnick 2005). Therefore, the new specimen described here represents the first described record of a mermithid-

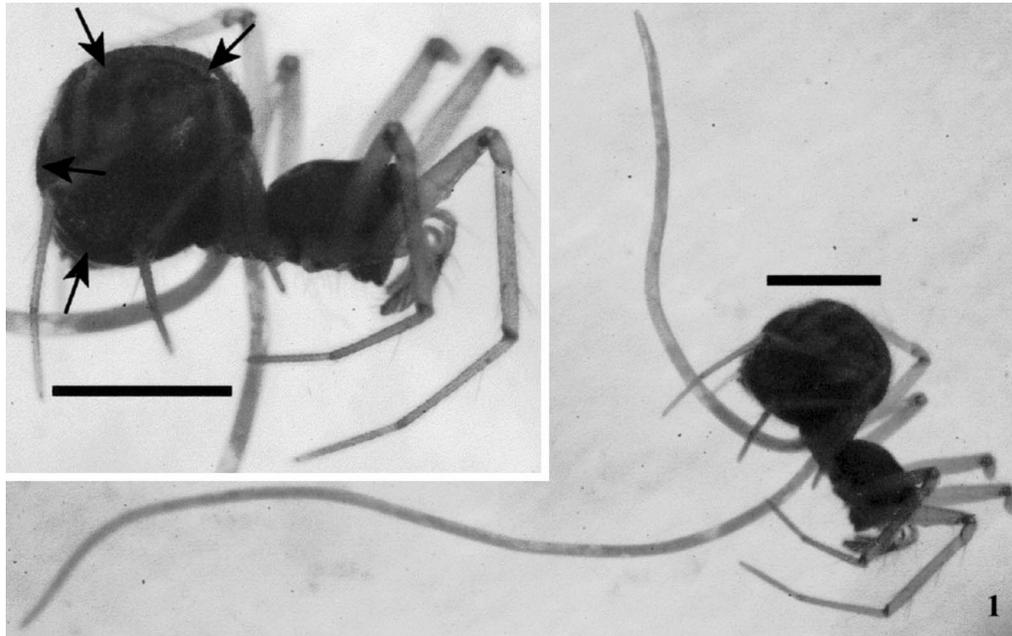


Figure 1.—The mermithid-carrying spider. Note the absence of abdominal guanine pigmentation, arrows point to the internal coil of the worm visible as a distortion in the integument. Scale lines = 1.0 mm.

linyphiid parasite–host association. Furthermore, the claims of Allard & Robertson (2003) of having identified mermithids in *Pardosa milvina* (Hentz) (Lycosidae) for the first time are unjustified, because they were previously reported by Montgomery (1903) under the junior synonyms *Pardosa nigropalpis* Emerton 1885 and *Pardosa scita* Montgomery 1902.

Being host to the worm carries a physiological cost for the spider in addition to its ultimate demise upon the emergence of the parasite. Infection signs generally start with a reduction or absence of digestive structures, and other organs may also be reduced in extreme cases (Poinar 1985). It is interesting to note the reduced amount of guanine deposition in two of the above specimens, and indeed the total absence of it in the specimen with the worm. Guanine is a crystalline purine excretory product, which accumulates in specialized, peripheral cells of the digestive diverticula lying directly beneath the hypodermis (Oxford & Gillespie 1998) and has a white, blocky appearance. Although patterns of guanine deposition can vary intraspecifically and throughout an individuals' development (Oxford 1998), there is usually a distinct pattern of guanine pigmentation present in *Tenuiphantes* Saaristo & Tanasevitch 1996 specimens (DP pers. obs). In the case of mermithid-carrying individuals however, the worm may be compromising the spider to such an extent, that the spider is receiving insufficient nourishment to produce enough of these met-

abolic waste products for pigmentation purposes. Further research would be required to confirm this hypothesis.

At the time of emergence from the spider host, mermithid worms are mature third stage postparasitic juveniles. Thus, the individual described above cannot be identified to species because diagnosis is based on adult characters. Mermithid life cycles are either direct or indirect. Direct life cycles are characterized by direct penetration of the spider host through the integument by the infective stage larva following emergence from the egg. Indirect life cycles involve a paratenic host (or a host in which significant development does not occur) in addition to the developmental (spider) host, which is infected by ingesting the infective stage of the parasite (Poinar 1985). The direct cycle is by far the most common among mermithids studied to date, however, it has been suggested that spider mermithids first undergo an indirect life cycle involving an aquatic paratenic host (Poinar 1987). Reasoning for this was based on observations of the life cycle of the spider mermithid *Aranimermis aptispicula* as follows: “adults were found in an aquatic habitat, whereas parasitized spiders were found in a variety of foraging habitats. Parasitized spiders were observed to enter the water and the nematodes were seen to emerge from the hosts' bodies. These observations support an indirect type of cycle, but further studies are required to substantiate this” (Poinar 1987). Poinar (1987) did not rule

out that some spider mermithid species may also have a direct life cycle. The life cycle of *A. actereki* presumably has an indirect life cycle because all worms studied (12 males, two females and four post-parasitic larvae) were collected from the bottom of a freshwater spring (Gufarov & An 1987). *A. giganteus* from New Zealand does have an indirect life cycle involving aquatic invertebrates (Poinar & Early 1990).

Given that most aquatic insect larvae have winged adults, the ecology of the spider hosts may provide insights that support or refute Poinar's idea regarding the indirect life cycle of *A. aptispicula*. For example, winged, flying insects are more likely to be consumed by web spinning or foliage/flower hunting spiders than they are by non-web spinning, ground hunters or burrowing, sit and wait predators, which can be expected to feed primarily on non-flying, mainly fully terrestrial prey and are thus, more likely to be hosts to mermithids with a direct life cycle. Interestingly, the ecology of all but one of the spiders reported by Poinar & Benton (1986) as hosts of *A. aptispicula* (Gnaphosidae, *Cesonia bilineata*; Thomisidae, *Misumenops* sp. and *Tmarus* sp.; Salticidae, *Phidippus* sp.; Araneidae, *Verrucosa arenata*; Amaurobiidae, *Wadotes* sp. and Anyphaenidae, *Wulfila albens*), supports the idea of an indirect life cycle for this parasitic worm. The potential problem species of those listed is *C. bilineata* (Gnaphosidae). These are fast moving, agile hunters usually found under loose leaf litter at ground level and males are often found in pitfall traps. However, they have been collected by sweeping low vegetation and have also been collected from malaise traps (Platnick & Shadab 1980), which are primarily designed for catching flying insects.

The large number of non-web spinning, cursorial Lycosidae (Table 1; 38% of all species, excluding *nomina dubia*) with undescribed mermithids, suggests that a direct life cycle may be involved in some instances. Admittedly, some lycosids are common by freshwater, such as *Hygrolycosa rubrofasciata* and *Pardosa pseudoannulata* (known to be mermithid hosts, see Table 1) and may be hosts to worms with indirect life cycles. However, lycosid genera such as *Pirata* and the pisaurid genus *Dolomedes*, which are encountered almost exclusively near freshwater are unknown as mermithid hosts. The mermithid life cycle type in relation to the spider host *Argyroneta aquatica* also poses interesting questions, as this spider spends its entire life under water. Clearly, much work needs to be done before we can fully understand these interesting host-parasite relationships, but a knowledge of the ecology of the host spiders can provide helpful clues in resolving these.

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LITERATURE CITED

- Ahtiainen, J.J., R.V. Alatalo, R. Kortet & M.J. Rantala. 2004. Sexual advertisement and immune function in arachnid species (Lycosidae). *Behavioural Ecology* 15:602–606.
- Allard, C. & M.W. Robertson. 2003. Nematode and dipteran endoparasites of the wolf spider *Pardosa milvina* (Araneae, Lycosidae). *Journal of Arachnology* 31:139–141.
- Camino, N.B. & L.C. de Villalobos. 1998. First occurrence of a mermithid (Nematoda: Mermithidae) parasitizing a spider (Arachnida: Araneida) in Argentina. *Revista de la Sociedad Entomologica Argentina* 57:6.
- Gafurov, A.K. & P.N. An. 1987. A new species of mermithid *Aranimermis actereki* sp. n. (Mermithidae, Nematoda) from the Kirghizia. *Izvestiya Akademii Nauk Kirgizskoi SSR Khimiko Tekhnologicheskije Biologicheskije Nauki* 1987:79–82. [In Russian].
- Iida, H. & H. Hasegawa. 2003. First record of a mermithid nematode emerging from the wolf spider *Pardosa pseudoannulata* (Araneae: Lycosidae). *Acta Arachnologica* 52:77–78.
- Matsuda, M. 1999. Two intersexual spiders of the family Lycosidae from Japan. *Bulletin of the Higashi Taisetsu Museum of Natural History* 21:5–54. [In Japanese].
- Montgomery, T.H. 1903. Studies on the habits of spiders, particularly those of the mating period. *Proceedings of the Academy of Natural Sciences of Philadelphia* 55:80–90.
- Okochi, T. 1969. Reports on parasites of spiders. *Kishidaia* 9:2–. [In Japanese].
- Oxford, G.S. 1998. Guanine as a colorant in spiders: development, genetics, phylogenetics and ecology. Pp. 121–131. *In* *Proceedings of the 17th European Colloquium of Arachnology*, Edinburgh, 1997. (P.A. Selden, ed.). British Arachnological Society, Bucks.
- Oxford, G.S. & R.G. Gillespie. 1998. Evolution and ecology of spider coloration. *Annual Review of Entomology* 43:619–643.
- Platnick, N.I. 2005. The world spider catalog, version 5.5. American Museum of Natural History, online at <http://research.amnh.org/entomology/spiders/catalog/INTRO1.html>.
- Platnick, N.I. & M.U. Shadab. 1980. A revision of the spider genus *Cesonia* (Araneae, Gnaphosidae). *Bulletin of the American Museum of Natural History*. 165:335–386.
- Poinar, G.O. Jr. 1985. Mermithid (Nematoda) par-

- asites of spiders and harvestmen. *Journal of Arachnology* 13:121–128.
- Poinar, G.O. Jr. 1987. Nematode parasites of spiders. Pp. 299–308. *In Ecophysiology of Spiders*. (W. Nentwig, ed.). Springer Verlag, Heidelberg.
- Poinar, G.O. Jr. 2000. *Heydenius araneus* n. sp. (Nematoda: Mermithidae), a parasite of a fossil spider, with an examination of helminths from extant spiders (Arachnida: Araneae). *Invertebrate Biology* 119:388–393.
- Poinar, G.O. Jr. 2003. Trends in the evolution of insect parasitism by nematodes as inferred from fossil evidence. *Journal of Nematology* 35:129–132.
- Poinar, G.O. Jr. & C.L.B. Benton Jr. 1986. *Aranimermis aptispicula* n.g., n.sp. (Mermithidae: Nematoda), a parasite of spiders. *Systematic Parasitology* 8:33–38.
- Poinar, G.O. Jr. & J.W. Early. 1990. *Aranimermis giganteus* n. sp. (Mermithidae: Nematoda), a parasite of New Zealand mygalomorph spiders (Araneae: Arachnida). *Revue de Nématologie* 13:403–410.
- Poinar, G.O. Jr. & H.E. Welch. 1981. Parasites of invertebrates in the terrestrial environment. Pp. 947–954. *In Review of Advances in Parasitology*. (W. Slusarski, ed.). Polish Scientific Publications, Warsaw.
- Roesel, A.J. 1761. *Insectenbelustigung*. Johann Joseph Fleishmann, Nürnberg.
- Vandergast, A.G. & G.K. Roderick. 2003. Mermithid parasitism of Hawaiian *Tetragnatha* spiders in a fragmented landscape. *Journal of Invertebrate Pathology* 84:128–136.
- von Siebold, C.T.E. 1848. Ueber die Fadenwurmer der Insekten. *Entomologische Zeitung* 9:290–300.

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