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# *Thaumamermis zealandica* n. sp. (Mermithidae: Nematoda) parasitising the intertidal marine amphipod *Talorchestia quoyana* (Talitridae: Amphipoda) in New Zealand, with a summary of mermithids infecting amphipods

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**Abstract**

A new nematode, *Thaumamermis zealandica* n. sp. (Mermithidae; Nematoda), is described parasitising the intertidal marine amphipod *Talorchestia quoyana* Milne-Edwards (Talitridae) from the coast of South Island, New Zealand. The new species is characterised by the degree of dimorphism of the spicules, the arrangement of the genital papillae, the shape and length of the vagina and the anteriorly-placed amphids. This is the first known marine host of a member of the family Mermithidae. Published records of mermithid nematodes from amphipods are presented.

## Introduction

The family Mermithidae Braun, 1883 constitutes a unique group of nematodes, which parasitise a wide range of invertebrates, especially insects (Poinar, 1983). Crustaceans are unusual hosts for mermithids and are limited to terrestrial members of the Isopoda (see Poinar, 1981) and fresh-water representatives of the Amphipoda, with hosts in the families Gammaridae (see Rubstov & Bekman, 1979; von Linstow, 1893), Corophiidae (see Bacesco, 1948) and Hyalellidae (see Camino, 1989) (Table 1). We describe here a new species of mermithid parasitising an intertidal marine amphipod, *Talorchestia quoyana* Milne-Edwards (Talitridae), from the coastal sands of South Island, New Zealand.

## Materials and methods

Amphipods were collected during November, 2001 on Long Beach, just north of Dunedin, South Island, New Zealand, from under tidal debris along the strand-line. The amphipods were hand-picked from the sand; only larger individuals were taken because these are more likely to harbour mermithids (Poulin & Rate, 2001). Hosts were maintained in the laboratory in moist sand at room temperature and under a natural photoperiod. Post-parasitic juvenile mermithids that emerged from their hosts within 10 days of capture were used for the following description. They were maintained in wet sand until they moulted and initiated mating, then were killed in hot water (75 °C), fixed in 5% formalin and processed to glycerine for taxonomic studies. Microscopic observations and photographs were made on living and dead nematodes with a Nikon Optiphot microscope. In the following quantitative description, all measurements are in micrometres unless otherwise specified. The first figure represents the mean value and is followed by the range in parentheses.

**Mermithida Rubstov, 1978**
**Mermithidae Braun, 1883**

***Thaumamermis* Poinar, 1981**

*Diagnosis* (amended from Poinar, 1981). Medium to large-sized nematodes with adult cuticle lacking cross-fibres, but post-parasitic cuticle with fine to extremely

fine fibres; six cephalic papillae in one plane; no mouth papillae; six hypodermal cords at mid-body in adults; vagina medium to long, flexed from one to three times (modified S-shape); amphids cup or goblet-shaped, medium in size, located on same plane as, or anterior to, cephalic papillae; spicules paired, showing extreme dimorphism, one being short and thick and other extremely long and slender; post-parasitic juvenile with small to medium-sized caudal appendage. Type-species *T. cosgrovei* Poinar, 1981.

*Comments*

The condition of unequal spicules appears to have evolved independently in this genus and in at least two terrestrial mermithids from Europe. In 1883, von Linstow described *Mermis paludicola* as possessing a pair of long spicules and a short gubernaculum. Unfortunately, only a single entire male was available and few additional characters were provided. The two long spicules of *M. paludicola* was a character noted by both Polozhentsev & Artyukhovsky (1959) and Rubstov (1972), both of whom moved the species to *Bathymermis* Daday. Later, Rubstov (1978) transferred the species again to a new genus, *Linstowimermis* Rubstov, 1978, characterised by two long spicules and a gubernaculum. However, with the absence of additional characters and until further material is found, *M. paludicola* should be considered a *species inquirenda*. The characters of this species which separate it from *Thaumamermis* are two long spicules (as well as a gubernaculum), a brown colour, a terminal mouth, cross-fibres in the adult cuticle and four rows of caudal papillae.

Based on a single adult male, Ipatjeva & Pimenova (1985) described the terrestrial mermithid *Gubernaculimermis paradoxus*, characterized by a small and a large spicule. The male of this species is considerably smaller than the two *Thaumamermis* species recognised here (L = 10.3mm) and the long spicule is only 2.6 times longer than the short spicule. In *T. zealandica* n. sp. (see below), it is 12 times longer than the shorter spicule and in *T. cosgrovei* Poinar, 1981 it is 20 times longer. In addition to these differences, the male of *G. paradoxus* has only a single row of caudal papillae, consisting of six pre-anal and five post-anal. In his treatment of soil mermithids, Artyukhovsky (1990) treated *Gubernaculimermis* as a *genus inquirendum* in the absence of additional characters.

***Thaumamermis zealandica* n. sp.**

*Description* (Figures 1-10)

*Females* (n = 7). L, 12.2 (10.5-15.0) cm; greatest body width 176 (158-189); distance from head to nerve-ring 286 (265-315); length of amphidial pouch 14 (11-16); diameter of amphidial opening 10 (8-13); length of vagina 383 (346-410); % vulva, 55 (52-57); eggs in uteri elliptical, 60 (54-64) ×44 (40-48); rudimentary anal opening 177 (174-190) from tail tip.
*Males* (n = 3). L, 48 (40-55) mm; greatest body width 113 (100-126); distance from head to nerve-ring 246 (235-252); length of amphidial pouch 14 (10-19); diameter of amphidial opening 10 (6-13); length of small spicule 76 (72-80); greatest width of small spicule 18 (17-19); length of long spicule 898 (882-914); width in middle of long spicule 8 (7-9); width at base of long spicule 14 (13–16); length of tail 139 (136-143); width of body at cloacal opening 92 (82-101).
*Post-parasitic juveniles* (n = 4). Same length as adults; tail with appendage 16-29 long; cuticle bearing very fine cross-fibres (absent on adult cuticle); moults twice to adult stage.
*Pre-parasitic juvenile* (n = 1). L, 444; stylet length 18.
*Adults*. Large white nematodes with mouth shifted slightly to ventral side of head; amphids goblet-shaped, not connected by commisure, opening anterior to cephalic papillae; spicules paired, separate and unequal; one relatively thick and shorter than body width at cloaca; other thin and slender and extending > 9 times body width at cloaca; longer spicule with thick walls enclosing partly filled cavity; short spicule with straight shaft and upward-curved capitulum; essentially 3 single rows of caudal papillae, 7-11 in post-cloacal region of each row and 15-16 in pre-cloacal region of each row; vagina of medium length, flexed once near vulva and with or without another flexure when connecting with oviducts; percuton (probably a tactoreceptor) present just posterior to nerve-ring on ventral side of both sexes; females with rudimentary anal opening on ventral side of tail; vulvar opening slit-like; vulval lips sometimes project upwards; 6 hypodermal cords at mid-body; final moult double, representing third and fourth moults; tails of both sexes bluntly rounded; body-cavity contains plate-like crystals.

*Type-host*: *Talorchestia quoyana* Milne-Edwards (Talitridae: Amphipoda).
*Type-locality*: Long Beach, just north of Dunedin,

South Island, New Zealand.
*Type-material*: Deposited in the Museum of New Zealand Te Papa Tongarewa, Wellington, New Zealand: holotype (male) ZW 1509; allotype (female ZW 1510. Paratypes in the authors' collections.

*Remarks*

The genus *Thaumamermis* exhibits the unusual character of unequal spicules to an extreme degree, which separates it from all others known to parasitize amphipods, as shown by the following key (see also Table 1):

1a. Male with two spicules . . . . . 3
1b. Male with single spicule . . . . . 2

2a. Spicule short, less than twice body width at cloaca . . . . . *Limnomermis* Daday, 1911
2b. Spicule medium to long, more than twice body width at cloaca . . . . . *Gastromermis* Micoletzky, 1923

3a. Spicules unequal in size . . . . . *Thaumamermis* Poinar, 1981
3b. Spicules equal in size . . . . . 4

4a. Four cephalic papillae; vagina straight; no cross-fibres in adult cuticle . . . . . *Pseudomermis* de Man, 1903
4b. Six cephalic papillae; vagina S-shaped or curved; cross-fibres in adult cuticle . . . . . *Gammaromermis* Rubstov & Bekman, 1979

The new species can be easily separated from the only other member of *Thaumamermis* (*T. cosgrovei*) by the anterior position of the amphids, the greater length and considerably smaller vagina of the females and the smaller long spicule in the male. In *T. cosgrovei*, the length ratio between the small and large spicule is 0.04, while in *T. zealandica* it is 0.08. Also, the tip of the small spicule is pointed in *T. cosgrovei*, but blunt in *T. zealandica*. The three rows of caudal papillae divide in two around the cloacal opening in *T. cosgrovei* but remain essentially single in *T. zealandica*.

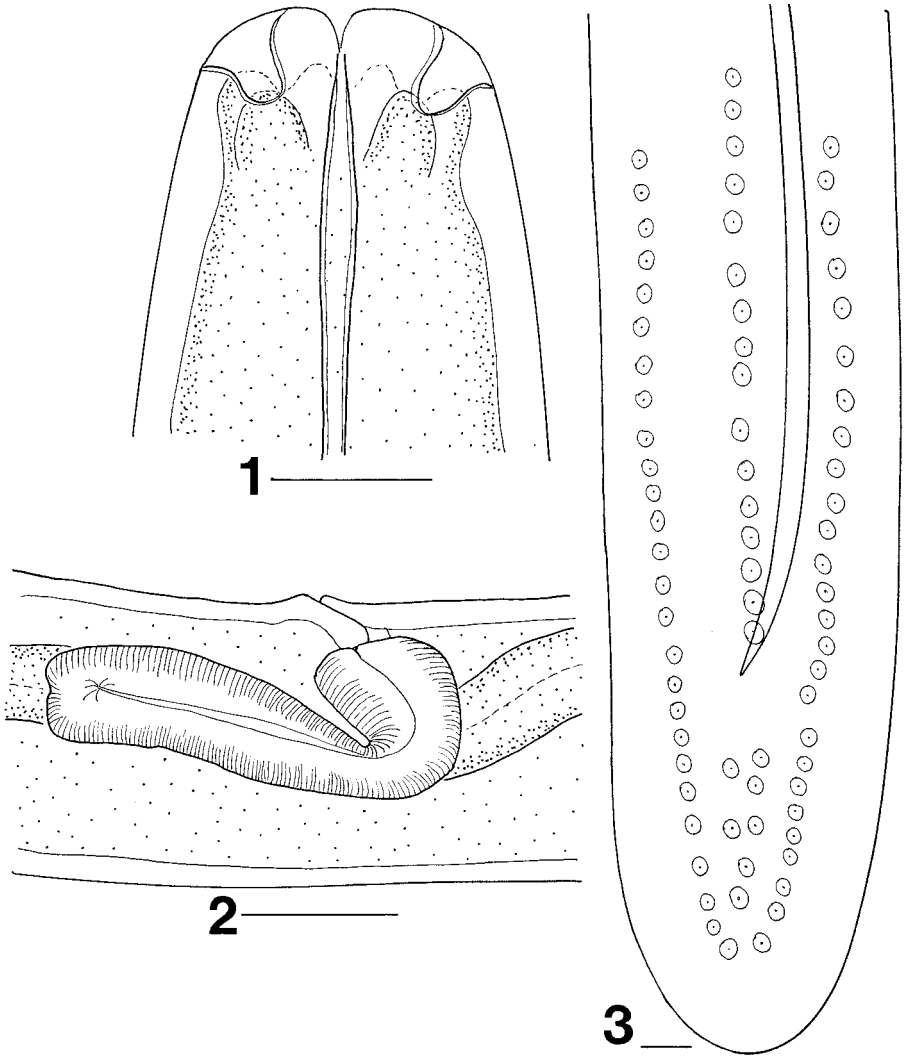
In *T. zealandica*, it is clearly the left spicule which is the longer of the two. This is obvious by its left-sided position in the body. Whether the small spicule is really a true spicule or a modified gubernaculum can perhaps be determined by a detailed study of the number and position of associated muscles. In the present case, a single muscle mass that runs to the body wall is attached to the lateral side of the small spicule. If both are true spicules, their position is modified from that of most mermithids (and nematodes). Instead of lying adjacent to each other, the tip of the longer spicule rests on the top of the smaller one, with the latter functioning as a gubernaculum.

The presence of a percuton (nerve-fibres originating from the nerve-ring, passing through the body-cavity, hypodermis and cuticle on the ventral side of the body) has been noted and described in the mermithid *Aranimermis giganteus* Poinar & Early, 1990 from spiders (Poinar & Early, 1990). This structure has been called a ventral pore or an excretory pore by previous authors but is clearly associated with the nervous system and not the excretory system. It is similar in structure to the deirids, which are paired lateral tactoreceptors in the vicinity of the nerve-ring.

*Biology and ecology*

The prevalence of infection ranged from 2 to 14% of amphipods over separate kelp patches on the beach in November, 1999 (Poulin & Rate, 2001), but reached an overall value of 31% in November, 2000 (Poulin & Latham, 2002a). Amphipods harbouring mermithids were on average longer than unparasitised individuals and in general, mermithid length showed a positive correlation with host length (Poulin & Rate, 2001). The number of parasites per amphipod host varied from a single mermithid per host, which was the normal condition, to a single case of 33 nematodes in a single amphipod (Poulin & Latham, 2002b). Ecological studies on the spatial distribution of healthy and mermithid-parasitised amphipods (Poulin & Rate, 2001), variability in body sizes of the mermithid parasites in their amphipod hosts (Poulin & Latham, 2002b) and the effect of mermithid-parasitism on the burrowing depth of *Talorchestia quoyana* (see Poulin & Latham, 2002a) have been conducted. In the latter study, the authors noted that mermithid-parasitised beach hoppers burrowed deeper than healthy ones.

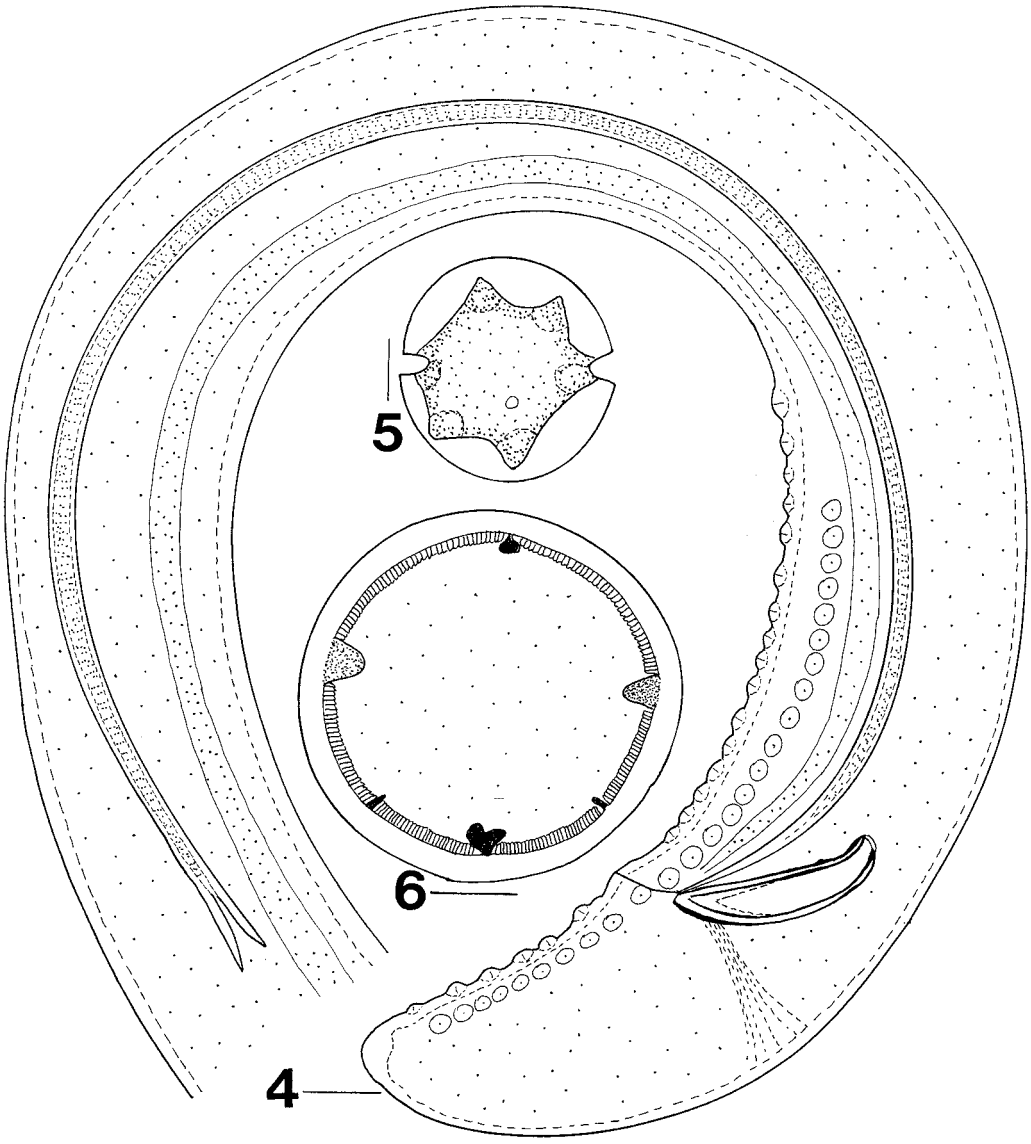
Most amphipods died when the nematodes made their exit into the sand. Post-parasites of *T. zealandica* n. sp. maintained in sand with fresh water moulted in approximately 6 weeks and mated immediately afterwards. The newly-moulted adults formed mating balls, where presumably the eggs were deposited. Several post-parasitic worms were infected with an unidentified fungus, which spread from its point of attack in the mid-body area of the nematode towards both ends. Eventually only the head and tail ends of the nematode




*Figures 1-3. Thaumamermis zealandica* n. sp. 1. Ventral view of adult female head. 2. Lateral view showing curved vagina (modified S-shape). 3. Ventral view of male tail showing left positioned long spicule and arrangement of caudal papillae. *Scale-bars*: 1, 32 $\mu$m; 2, 95 $\mu$m; 3, 16 $\mu$m.

*Table 1.* Mermithid parasites of amphipods.

| Host | Mermithid | Reference |
|---|---|---|
| *Carinogammarus rhodophthalmus* (Dyb.) | *Gammaromermis carinogammari* (Rub.) | Rubstov, 1976 |
| *C. rhodophthalmus* (Dyb.) | *G. longicaudata* Rub. & Bek. | Rubstov & Bekman, 1979 |
| *Corophium* sp. | *Pseudomermis cazanica* Băc. | Băcesco, 1948 |
| *Echiuropus morawitzi* (Dyb.) | *G. baikalensis* Rub. & Bek. | Rubstov & Bekman, 1979 |
| *Gammarus pulex* (L.) | *Agamomermis gammari* (von Linstow) | von Linstow, 1892 |
| *Hyalella curvispina* Shoe. | *Limnomermis bonaerensis* Cam. | Camino, 1989 |
| *Micruropus ivanowi* Bazik. | *Agamomermis gammari* (von Linstow) n. comb. | von Linstow, 1892 |
| *M. semenowi* Bazik. | *A. gammari* (von Linstow) | von Linstow, 1892 |
| *Talorchestia quoyana* M.-E. | *Thaumamermis zealandica* n. sp. | Present study |
| Unknown | *Gastromermis* sp. | Garcia & Camino, 1987 |



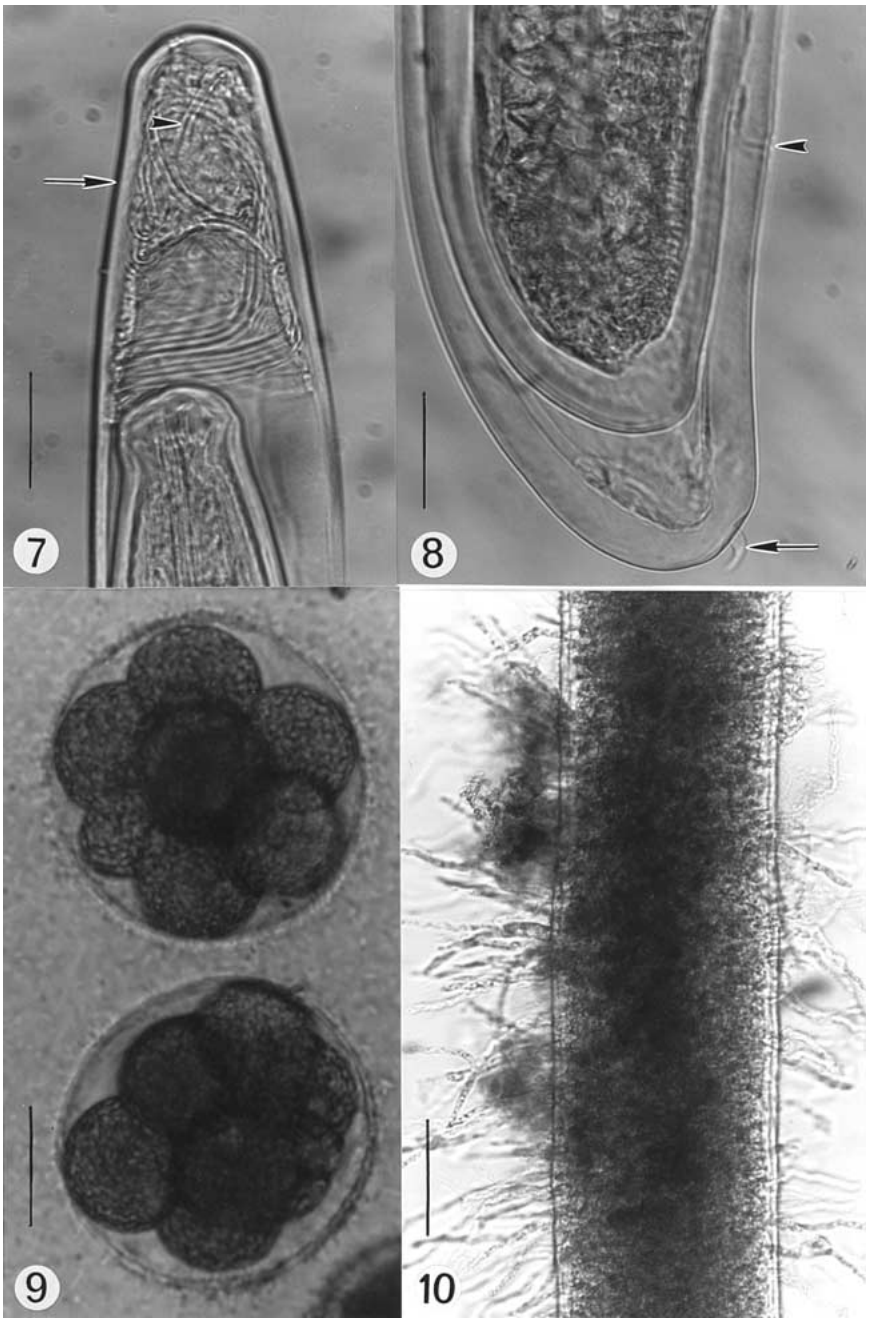

*Figures 4-6. Thaumamermis zealandica* n. sp. 4. Lateral view of male tail showing long and short spicules and genital papillae. 5.' En face' view of adult female. 6. Cross-section of female at mid-body showing six hypodermal cords and six muscle fields. *Scale-bars*: 4, 32 $\mu$m; 5, 21 $\mu$m; 6, 48 $\mu$m.

were mobile, while the mid-portion was destroyed and filled with fungal mycelium (Figure 10). At the time of oviposition, the mermithid eggs were either undivided or showed initial development up to the tetrad stage. Further development occurred as the eggs rested on the bottom of the container (Figure 9). Hatching occurred in c. 50 days at 16 °C. It is presumed that the infective stage of these mermithids enter young amphipods by directly penetrating through the body wall, although this has not been confirmed.

## Discussion

This is the first record of a member of the Mermithidae attacking a marine invertebrate and the first record of a mermithid parasitising a talitrid amphipod. All previous records of mermithids parasitising amphipods occurred in freshwater habitats (Table 1).

*Thaumamermis* contains two species, one of which, *T. cosgrovei*, parasitises terrestrial isopods (Poinar, 1981) and *T. zealandica* n. sp., which parasitises marine amphipods. This genus may be re-




*Figures 7-10. Thaumamermis zealandica* n. sp. 7. Anterior end of moulting female showing thick fourth-stage cuticle (arrow) and membraneous third-stage cuticle associated with the lining (arrowhead) of the pharyngeal tube. 8. Posterior end of moulting female showing bluntly rounded tail, partly shed fourth-stage cuticle with caudal papilla (arrow) and vestigial anus (arrowhead). 9. Two eggs in the early stages of development. 10. Mid-section of body of post-parasitic juvenile showing mid-section destroyed by a fungus infection (both anterior and posterior ends were normal and still moving). *Scale-bars*: 7, 62 $\mu$m; 8, 49 $\mu$m; 9, 20 $\mu$m; 10, 80 $\mu$m.

stricted to crustacean hosts, much like *Aranimermis* Poinar & Benton is restricted to arachnid hosts and contrasts with most other genera of mermithid parasites of amphipods (Table 1), such as *Pseudomermis, Gastromermis* and *Limnomermis*, where insects are the normal hosts. Exceptions may be *Gammarimermis*, which appears to be restricted to amphipods, and the species *Mermis gammari* (von Linstow, 1892), which was described based on juvenile characters, cannot be assigned to any known genus and herewith is placed in the group *Agamomermis* Stiles, 1903 (indicating that its status is in question) as *A. gammari* n. comb.

The two known species of *Thaumamermis*, one in California and the other in New Zealand, pose several biogeographical questions. Can we assume that both species are endemic to their respective geographical locations? Since the New Zealand species is a beach inhabitant and the Californian specimens were found in two localities, both close to the Pacific Ocean, were specimens dispersed from one geographical location to the other by some unknown means of transportation, possibly in ship-ballast? Could the morphological differences observed between the two species be the effect of environmental and host differences? While *T. cosgrovei* is from an isopod in California and *T. zealandica* from an amphipod in southern New Zealand, could either develop in the other host group and if so, would certain morphological features be modified? Further experimental studies could shed light on this interesting topic.

If both species are truly endemic, then the genus would have to extend back in time at least to when the continents were joined, since the natural migratory powers of both hosts and parasites are quite limited. Separation of Gondwanaland from Laurasia occurred some time in the Jurassic, some 170-160 million years ago (Smith et al., 1994) and, in order to achieve a wide pre-separation distribution, *Thaumamermis* would have had to exist long before. It is possible that *Thaumamermis* occurs in other parts of the world as well, which would alter the above dates to some degree.

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