

# *Aranimermis giganteus* n. sp. (Mermithidae : Nematoda), a parasite of New Zealand mygalomorph spiders (Araneae : Arachnida)

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## SUMMARY

*Aranimermis giganteus* n. sp. (Mermithidae : Nematoda) is described from New Zealand mygalomorph spiders (Araneae : Arachnida). It has an indirect cycle and infective stage mermithids which are presumed to be *A. giganteus* n. sp. occur free in the hemocoel of a variety of freshwater invertebrates, especially the caddisfly, *Olinga feredayi* (Conoesucidae : Trichoptera). The large size of *A. giganteus* n. sp. (up to 32 cm in length and the largest known mermithid) is associated with its long developmental period in the host. Considering that the present distribution of mygalomorph spiders represents the result of vicariance events in the earth's history, and that both host and nematode groups also occur in North America, it can be inferred that this parasitic association existed some 250 million years ago.

## RÉSUMÉ

*Aranimermis giganteus* n. sp. (Mermithidae : Nematoda)  
parasite d'araignées mygalomorphes (Araneae : Arachnida) de Nouvelle-Zélande

*Aranimermis giganteus* n. sp. (Mermithidae : Nematoda) est décrit chez des araignées mygalomorphes (Araneae : Arachnida) de Nouvelle-Zélande. Le cycle est indirect et des stades infestants de Mermithides, présumés être ceux d'*A. giganteus* n. sp. sont présents, libres, dans l'hémocèle de certains invertébrés d'eau douce et, plus particulièrement d'*Olinga feredayi* (Conoesucidae : Trichoptera). La grande taille d'*A. giganteus* n. sp. — jusqu'à 32 cm, le plus grand des Mermithides connus — correspond à une longue période de développement chez l'hôte. Prenant en considération, d'une part la répartition actuelle des araignées mygalomorphes, résultat des changements qu'a connus l'histoire du globe, d'autre part la présence des deux groupes, hôtes et nématodes, en Amérique du Nord, il peut être inféré que cette association parasitaire existe depuis quelques 250 millions d'années.

While conducting studies on the arthropod fauna from a small area of native bush on Banks Peninsula, South Island, New Zealand, one of us (J.W.E.) discovered mermithids that emerged from mygalomorph spiders. The spiders had fallen into pan traps and drowned and the nematodes had (in most instances) emerged from the body cavity of the spiders and were still living. A study was initiated to investigate this host-parasite association and the results are reported here.

The nematodes belong to a new species of the genus *Aranimermis* Poinar and Benton (1986) and are the first representatives of this genus from the Southern Hemisphere.

## Materials and methods

Parasitized spiders were collected in plastic pan traps (35 cm square and 12 cm deep) that had been placed into

the ground in a small area of native bush in Prices Valley on Banks Peninsula in South Island, New Zealand from January 27-March 29, 1989. The traps contained water, a wetting agent (Triton X) and a preservative (sodium benzoate). The traps were examined every 10-14 days and spiders and mermithids which emerged from the spiders were brought back to the laboratory. Some spiders were recovered with nematodes still inside their body cavities (Fig. 3 A).

The nematodes were washed in tap water and then held in a cabinet at 15 °C with a 14:10 light/dark regime until they molted to the adult stage. They were then killed in hot water, fixed in 3 % formalin and transferred to glycerin for taxonomic studies.

Aquatic invertebrates were collected from November 1988 to January 1989 from three streams in the South Island, New Zealand. These included Prices Valley stream (elevation = 200 m) on Banks Peninsula, which was sampled on January 12, 1989 (water temperature

= 20 °C, air temperature = 21 °C), Cave stream (elevation = 770 m) in Craigieburn Forest which was sampled on November 21, 1988 (water temperature = 12 °C, air temperature = 16 °C) and Fish stream (elevation = 917 m) in Mt. Cook National Park (Ben Ohau Range), sampled on December 6, 1988 (water temperature = 6 °C; air temperature = 15 °C).

*Aranimermis* Poinar & Benton, 1986  
(Mermithidae Braun)

DIAGNOSIS (EMENDED)

Medium to large-sized nematodes; cuticular cross fibers absent in the adults but present in the postparasitic juveniles; six cephalic papillae in one plane; six hypodermal cords at midbody; amphids cup or flask shaped, small to medium in size, located close to the lateral cephalic papillae; mouth opening terminal or shifted ventrally; vagina elongate, flexed three to six times in both vertical and horizontal planes before reaching uterus; spicules paired, long, three or more times body width at cloaca, separated but closely appressed; postparasitic juvenile with or without a small tail appendage or scar.

*Aranimermis giganteus* n. sp.  
(Figs 1 A-H; 3 A-I)

MEASUREMENTS

*Female* (n = 6) : L = 22 (16-32) cm; greatest width = 917 (800-1 000) µm; head to nerve ring = 473 (460-489) µm; thickness of cuticle at nerve ring = 22 (18-25) µm; length amphidial pouch = 22 (20-24) µm; diameter amphidial opening = 9 (8-10) µm; length of vagina = 1 445 (1 268-1 730) µm; vulva = 46 (40-51) µm; end of trophosome from tail tip = 567 (309-756) µm; distance from head to percuton = 504 (485-528) µm; length cephalic peg = 28 (26-31) µm.

*Male* (n = 10) : L = 10 (8-15) cm; greatest width = 736 (608-864) µm; head to nerve ring = 463 (422-504) µm; distance from head to percuton = 530 (504-567) µm; length amphidial pouch = 28 (22-32) µm; diameter amphidial opening = 12 (11-13) µm; tail length = 727 (643-794) µm; body width at cloaca = 518 (410-600) µm; length of spicules = 2 391 (1 575-3 352) µm; greatest width of spicules = 46 (37-63) µm; distance tip of spicule to spicular groove = 2 170 (1 953-2 331) µm; thickness of cuticle at nerve ring = 37 (28-48) µm; length cephalic peg = 40 (32-48) µm; distance genital papillae extend anteriorly from cloacal opening = 2 536 (2 048-3 276) µm.

DESCRIPTION

*Adults* : Large nematodes, females up to 32 cm in

length; color pink, brown or white; six cephalic papillae arranged in a single circle; mouth shifted distinctly to ventral side of head; terminal innervated, cephalic hypodermal peg present; adjacent to cephalic peg and cephalic papillae are numerous nerve fibers emerging from hypodermis and extending through cuticle; amphids flask-shaped, smaller in females; situated at base, on dorsal side, of lateral cephalic papillae; amphidial openings circular; six hypodermal cords at mid-body; small vulvar flap may or may not be present; vagina worm-shaped, with three to six bends in both vertical and horizontal planes; spicules paired, equal, separate, sharply pointed at tips, from three to six times body width at cloaca; proximal portion slightly bifurcated; a groove, accompanied by a change in spicular form, occurs 68-73 % from apex; genital papillae extremely small and numerous, extending from tail tip to over 3 mm up ventral surface of tail; genital papillae arranged in six broken, irregular rows; anterior to cloacal opening, six rows reduced to three rows which continue up tail; protein platelets (1-5 × 1.6-30 µm) occur in body cavity; trophosome often extends into tail region. In the ventral side of the nerve ring can be found a group of nerve fibers which proceed from the nerve ring through the body cavity, adjacent hypodermis and cuticle and extend to the exterior through a small pore. This structure has always been interpreted as an excretory pore in previous descriptions of mermithids but its origin from the nerve ring is clearly distinct here. Since such a structure has not been described in mermithids or nematodes in general, it is proposed to call it a "percuton" (Fig. 2 C) and it will be referred to as such in the remainder of this study.

*Post-parasitic juvenile* (n = 60) : Length and width similar to adults, cuticle with faint cross-fibers; cephalic papillae and amphids reduced; mouth ventral; tail tip lacking projection or scar; cephalic peg absent.

TYPE HOST

*Cantuarina borealis* Forster (Ctenizidae : Araneae). Other spider hosts of *A. giganteus* n. sp. include *Porrhothele antipodiana* (Walckenaer) and *Aparua kaituna* Forster (Dipluridae) and *Migas* sp. (Migidae).

TYPE LOCALITY

Prices Bush, Banks Peninsula, South Island, New Zealand.

TYPE MATERIAL

*Holotype* (male) and *allotype* (female) deposited in the National Museum of New Zealand, Wellington, New Zealand. *Paratypes* deposited in the Division of Nematology, University of California, Davis, California.

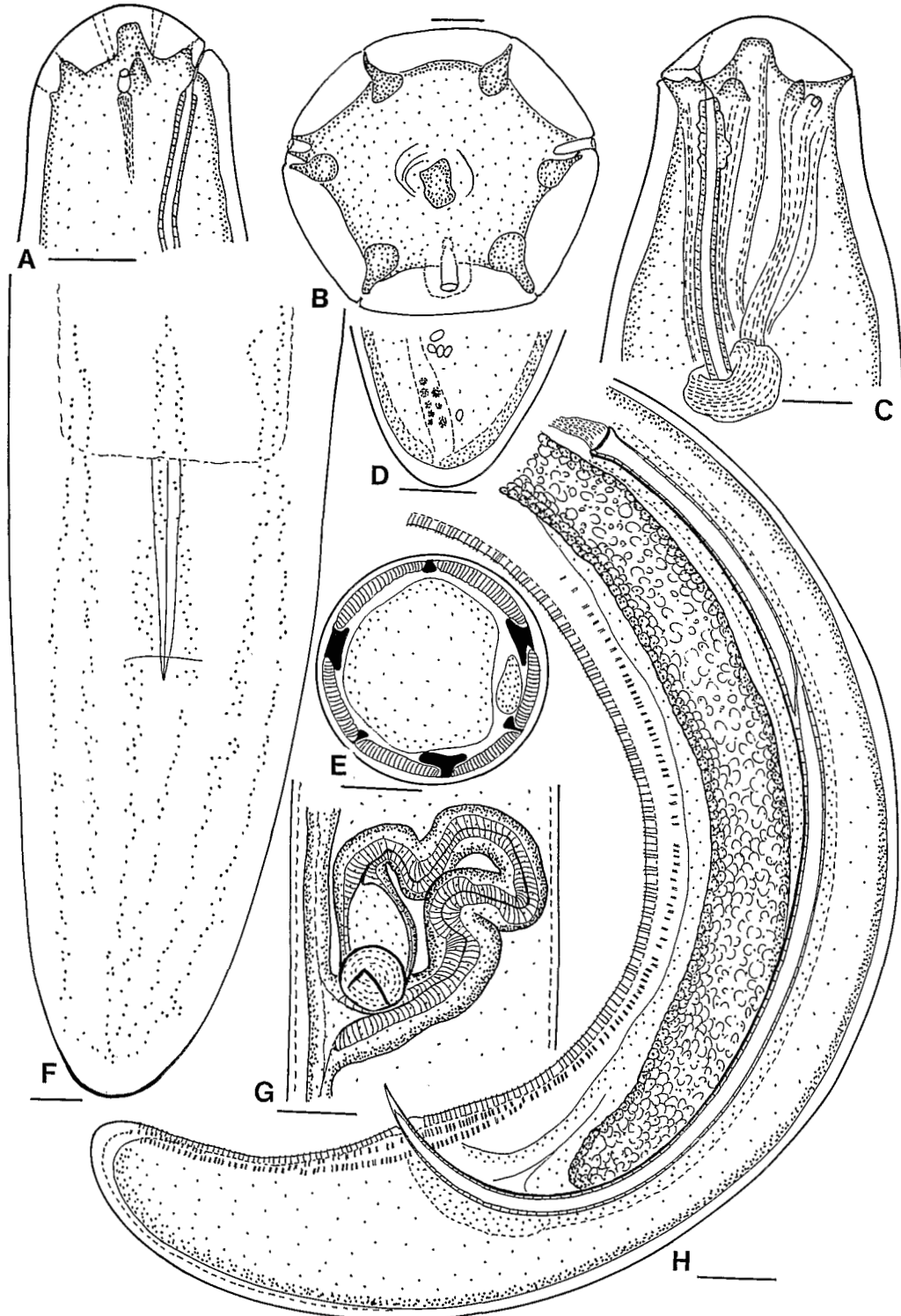


Fig. 1. *Aranimermis giganteus* n. sp. A : Lateral view of male head; B : " En face " view of male; C : Lateral-ventral view of female head; D : Lateral view of postparasitic juvenile female tail; E : Cross section of male mid-body; F : Ventral view of male tail; G : Lateral-ventral view of vulva; H : Lateral view of male tail. (Bars equivalent : A = 100  $\mu$ m; B = 50  $\mu$ m; C = 100  $\mu$ m; D = 200  $\mu$ m; E = 200  $\mu$ m; F = 100  $\mu$ m; G = 200  $\mu$ m; H = 200  $\mu$ m).

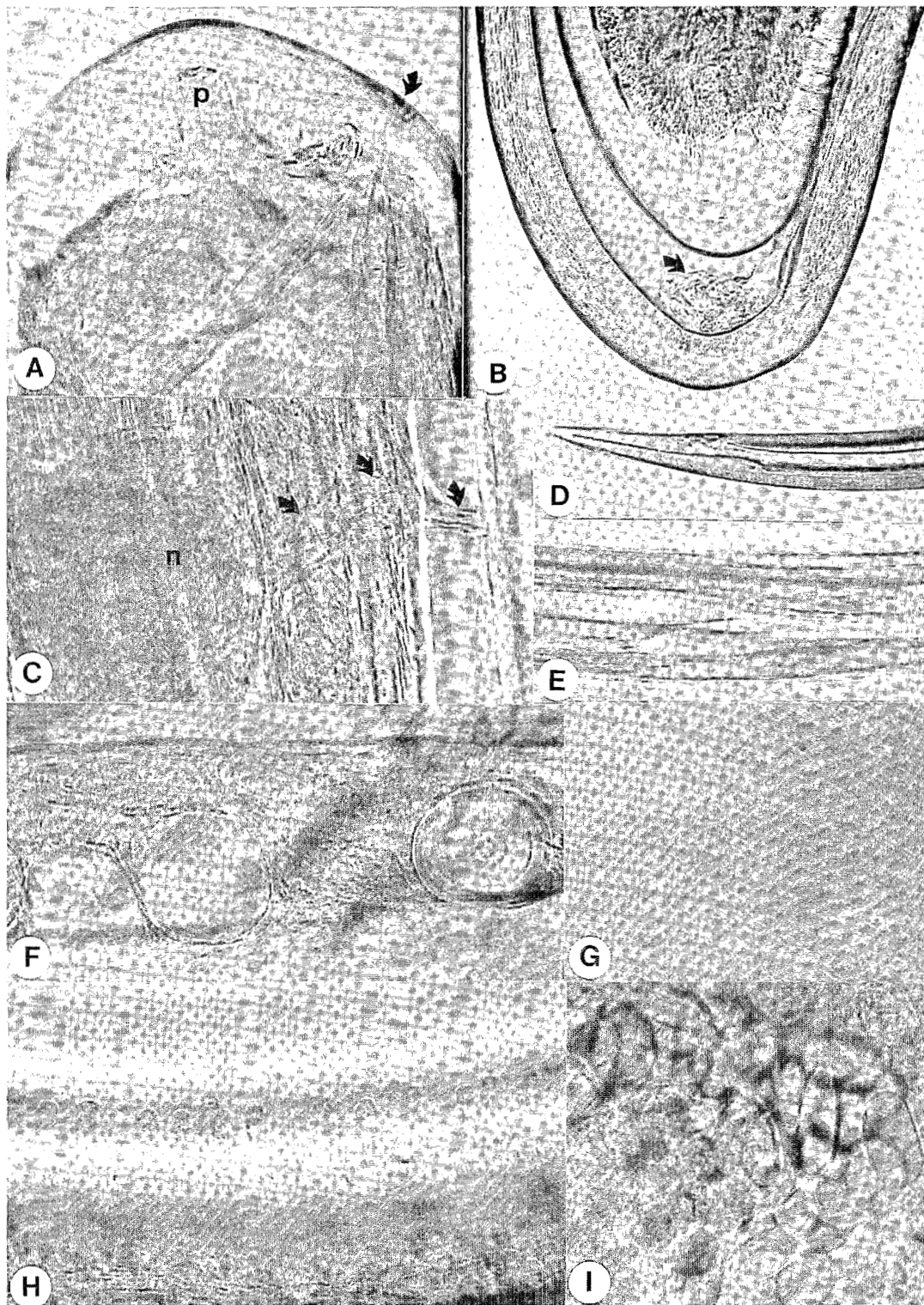


Fig. 2. *Aranimermis giganteus* n. sp. A : Head of male showing terminal cephalic peg (p) and ventral mouth opening (arrow); B : Postparasitic male in process of molting. Note thick postparasitic juvenile cuticle lacking terminal appendage or scar. Arrow shows a portion of the thin, fourth-stage cuticle; C : Percuton (nerve fibers which emerge from the nerve ring and pass through the body cavity, hypodermis and cuticle on the ventral side of the body) n - nerve ring; arrows denote passage of nerve fibers through body cavity, hypodermis and cuticle; D : Tips of the appressed spicules; E : Spicular "groove" or "crossover" area; F : Developing stages of a sporozoan parasite in the lateral nerve cord of a male mermithid; G : Faint cross fibers in cuticle of postparasitic juvenile; H : Ventral-lateral row of male genital papillae; I : Protein platelets in mermithid body cavity.

## DIAGNOSIS

*Aranimermis giganteus* n. sp., the largest mermithid known, is characterized by six cephalic papillae, six hypodermal cords, small amphids, a ventrally displaced mouth, a worm shaped vagina and paired, spicules three or more times body width at cloaca. The terminal cephalic peg, ventrally displaced mouth, more numerous genital papillae and spicular shape separate *A. giganteus* n. sp. from the only other known species in the genus *A. aptispicula* Poinar & Benton, 1986. The postparasitic juveniles of *A. giganteus* n. sp. possess a cuticle with cross fibers (absent in the adult) but lacking a terminal appendage.

## BIOLOGICAL OBSERVATIONS

In the collection site in Prices Valley, *A. giganteus* n. sp. emerged from adult female *Cantuaria borealis* Forster and *Aparua kaituna* Forster. In addition, an adult female *Porrhothele antipodiana*, the Black Tunnelweb Spider, was also found parasitized. In the collection of the Otaga Museum in Dunedin, another parasitized adult female *P. antipodiana* was found (locality unknown). In the North Island, M. J. Meads found two postparasites of *A. giganteus* n. sp. that had emerged from a Tree-Trunk Trapdoor Spider (*Migas* sp.) in Belmont, Lower Hutt on January 27, 1989.

Thus *A. giganteus* is distributed over both the North and South Island and is capable of completing its development in representatives of all three families of mygalomorph spiders in New Zealand. In the State Museums of Victoria and New South Wales in Melbourne and Sydney, Australia, respectively, the senior author examined mermithids that had emerged from Australian spiders. Although he found representatives of *Aranimermis* among these, none were *A. giganteus*. Therefore, it would appear that the latter species is endemic to New Zealand, as are also the spider hosts.

Since mermithids emerged from spiders when the latter entered water in pan traps, it is probable that nematode maturation is completed in an aquatic habitat and that the life cycle involves an aquatic paratenic host. We postulate that this occurs naturally in a stream or pond. After emergence from spiders, nematodes would molt (this took 2.5-3 months at 15 °C in the laboratory), mate and deposit eggs in the water. Eggs would be ingested by aquatic invertebrates where, after hatching in the gut, the infective pre-parasitic juvenile mermithids would penetrate the gut wall and enter the haemolymph. Juveniles would remain inactive throughout the life of the paratenic host until the adult stage was reached and development would not continue until the nematodes were ingested by an adult female mygalomorph spider. A search of aquatic invertebrates that could ingest the eggs of *A. giganteus* was conducted in a small stream that bordered the collection site at Prices

Valley. Mayfly nymphs (Ephemeroptera), annelids, larvae of predatory beetles (Dytiscidae), blackflies (Simuliidae), midges (Chironomidae) and caddisflies (Trichoptera) were collected and dissected. Eight out of nine larvae of the caddisfly, *Olinga feredayi* (McLachlan) (Conoesucidae) (Fig. 3 D) contained one to four infective stage mermithids free in their body cavities (Fig. 3 B). These infective stages were presumed to be those of *A. giganteus* and were characterized by a total length of 534 (440-736) µm, width of 14 (12-16) µm, eight elongate stichocytes and a stylet with a length of 23 (20-26) µm and a medial swollen area. Similar infective stage juveniles were found in the body cavities of nymphs of *Deleatidium* sp. (Ephemeroptera : Leptophlebiidae). No similar mermithid juveniles were recovered from larvae of blackflies, midges or annelids, however a partly melanized infective stage was recovered from the body cavity of a dytiscid larva (Fig. 3 C). Since dytiscid larvae are predaceous, this might represent a secondary paratenic host, which would explain the presence of a defense reaction.

Similar aquatic invertebrates were examined from other streams in the South Island. In Cave stream in Craigieburn Forest near Authur's Pass, trichopteran larvae of *O. feredayi*, *Pycnocentroides* sp. (Conoesucidae) and *Hydrobiosis parumbripennis* (Rhyacophilidae) all contained similar infective stage juveniles free in their body cavities. In Fish Stream at Mt Cook National Park, identical infective stage mermithids were found in the body cavities of *O. feredayi* larvae and nymphs of the stonefly, *Zelandoperla* sp. (Plecoptera : Gripopterygidae).

At this time it is not possible to identify the infective stage mermithids from the stream invertebrates as *A. giganteus*, however several facts suggest that they could well be. The range of the spider hosts and the infected stream invertebrates are widespread and overlap. Mygalomorph spiders are generalists and would feed on the adult stages of the aquatic insects (Forster & Forster, 1973). Also, the preparasitic juvenile mermithids were always recovered free in the hemocoel of the stream invertebrates. This would be ideal for their uptake by spiders, whose mouths are fitted only for the taking of liquid food which is pressed from the victim by means of their chelicerae and pedipalps (Comstock, 1948).

The only other known mermithid genus which has an indirect cycle involving paratenic hosts is *Pheromermis*, a parasite of wasps and ants. The infective stages of these species coil up in the tissues of their paratenic hosts (Poinar, 1976). The young parasites are taken by the worker insects that are searching for solid protein to feed the larvae. Thus, the presence of infective stage mermithids free in the hemolymph of paratenic hosts suggests that the final host is a hemolymph feeder, like spiders.

All infected spiders were females, and these appeared in pan traps from spring (October 1988) through to

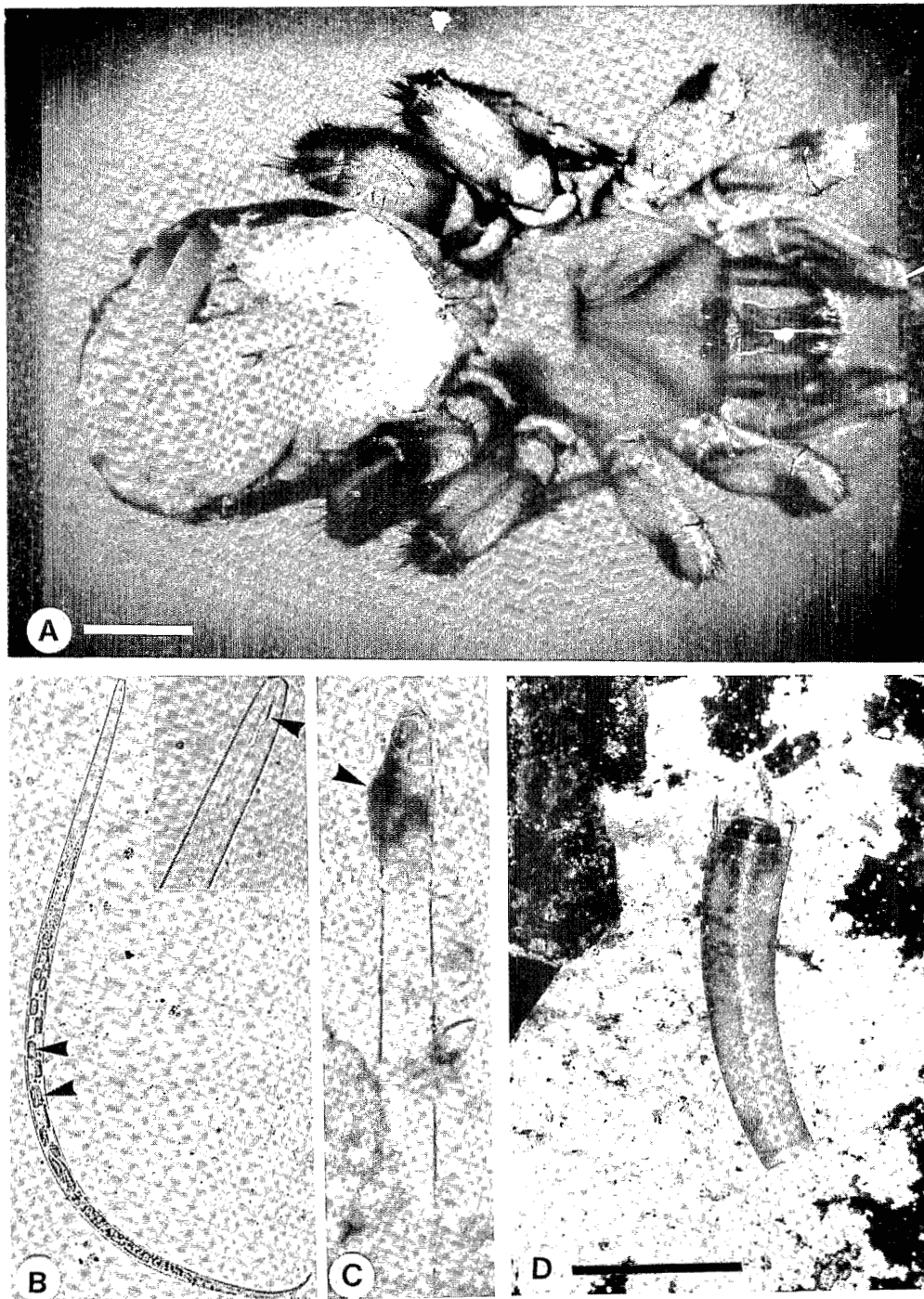


Fig. 3. A : Female *Cantuaria borealis* with a juvenile of *A. giganteus* coiled up in her abdomen; B : Infective stage mermithid (presumably *A. giganteus*) removed from the hemocoel of a larva of *Olinga feredayi* (arrows show characteristic rectangular stichocytes) (insert shows higher mag. of same juvenile with characteristic swelling in middle of stylet); C : Infective stage mermithid (presumably *A. giganteus*) removed from a dytiscid beetle larva (arrow shows deposit of melanin on head); D : Larva of caddisfly (*Olinga feredayi*). (Bars equivalent : A = 3.0 mm; D = 3.5 mm).

autumn (April 1989). Male spiders began to appear in autumn and were found throughout the winter (April-July 1989); this is the time when they mature and wander in search of a mate (Forster & Forster, 1973). No *A. giganteus* emerged from them, and none was found by dissection. *Cantuarina*, like most New Zealand mygalomorphs, are thought to be generalist feeders (Forster & Forster 1973) so both sexes (and possibly late instar juveniles also) are probably at equal risk of infection. Male and female are of similar size and therefore presumably equally adequate to nourish the parasite. Why, then, are males not hosts to *A. giganteus*? Its absence in males suggests that *A. giganteus* requires a long developmental period. Male *Cantuarina* normally survive only 1-3 years, whereas the lifespan of females in captivity may exceed 20 years (R. R. Forster, pers. comm.). If this is so, it is not in the parasite's interest to develop in the relatively short-lived males. *A. giganteus* development may be controlled by host physiology, so that development only proceeds within females as they attain sexual maturity.

It is known that spiders carrying fully developed mermithid parasites are often attracted to water (Poinar, 1985, 1987). This appears to be the case with *A. giganteus*. It is unusual for *Cantuarina* females to leave or move far from their burrows; normally only the males move about in search of mates, and then only in winter (Forster & Forster, 1973) as this study corroborates. This explains why virtually all females trapped were parasitized, and because of this it is not possible to estimate the incidence of parasitism in the spider population. This altered spider behaviour is normally beneficial to the nematode, which requires an aquatic habitat to complete the life cycle.

The search for water by the spider may not always end in an appropriate place for completion of the nematode life cycle as the present study bears out. Other observers have accidentally found the same. In Lower Hutt, M. J. Meads (pers. comm.) collected post-parasites of *A. giganteus* from a water bowl provided for chickens; in Upper Hutt, D. J. W. Cole (pers. comm.) reported mygalomorph cadavers in his swimming pool while the mermithids accumulated on the filter. Others may emerge in temporary rain pools on the forest floor, with no chance of encountering suitable paratenic hosts. There is probably high nematode mortality at this stage of the life cycle.

The number of emerged *A. giganteus* usually exceeded the number of spider cadavers in pan traps, indicating that more than one parasite per host is common. In the few cases where the emerged mermithids could be associated with a single host, it appears that when only one develops it is female, but broods of two or more are all male. The maximum to emerge from a single host was seven.

Several male *A. giganteus* contained cysts (57-63  $\mu\text{m}$  in diameter) in the lateral and ventral nerve cords in the

vicinity of the nerve ring. The cyst walls were thick and composed of concentric layers whereas the center contained from one to three separate cellular bodies (Fig. 2 E). After reviewing the literature on nematode diseases, we consider these cysts to be the developing stages of a sporozoan protozoan parasite (Subphylum Sporozoa) (Poinar & Hess, 1988). Similar bodies were observed by Steiner (1925) in the Indonesian mermithid, *Agameremis paradecaudata*. Steiner considered them to belong to the Order Actinomyxidia (Subphylum Cnidospora). Further studies are necessary to determine their true identity and life cycle.

## Discussion

Mygalomorph spiders are parasitized by *Aranimermis* in California (Vincent, 1986) and so the presence of *Aranimermis* in New Zealand and North America indirectly reveals a minimum geological age for both host and parasite groups. The fossil record of mygalomorphs is sparse, although representatives of the Ctenizidae occur in both Baltic and Dominican amber, thus establishing the group in the Eocene in the Palaearctic and Nearctic regions (Wunderlich, 1986, 1988). Since mygalomorphs disperse only by walking (Decae, 1987) and then only to a very limited extent (Forster & Wilton, 1968), their distribution is a good indicator of historical land patterns and vicariance. If one assumes that North America separated from Gondwana in the Jurassic, some 180 million years ago (Cox & Moore, 1985) then the relationship between mygalomorphs and mermithids was probably established earlier, possibly in the Paleozoic when the first definite fossil record of spiders was recorded (Petrunkevitch, 1955) and Pangaea had formed. This would establish *Aranimermis* or a precursor group of spider mermithids at least some 250 million years ago, much earlier than the presently-known Eocene fossil record of the Mermithidae (Poinar, 1984).

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