Mermis quirindiensis n. sp. (Nematoda : Mermithidae), a parasite of locusts and grasshoppers (Orthoptera : Acrididae) in south-eastern Australia

Graeme L. BAKER and George O. POINAR, Jr.

Entomology Branch, Biological and Chemical Research Institute, Department of Agriculture, New South Wales, PMB 10, Rydalmere, NSW, 2116, Australia and Division of Entomology and Parasitology, University of California, Berkeley, Ca 94720, USA.

SUMMARY

Mermis quirindiensis n. sp. is the first species of *Mermis* Dujardin recorded on mainland Australia, where it has a coastal and sub-coastal distribution within central and northern New South Wales. Hosts include the wingless grasshopper, *Phaulacridium vittatum* Sjöstedt, the yellow-bellied grasshopper *Praxibulus* sp. and the Australian plague locust, *Chortoicetes terminifera* (Walker). The eggs of *M. quirindiensis* n. sp. bear polar knobs and byssi, the species being closely related to *M. nigrescens* Dujardin and *M. mirabilis* von Linstow but readily differentiated from the former by having colourless eggs and the latter by having a thick, rough outer layer of chorion on the egg. The description of *M. quirindiensis* n. sp. brings the number of species in the genus *Mermis (sensu stricto)* to eight.

RÉSUMÉ

Mermis quirindiensis *n. sp. (Nematoda : Mermithidae), parasite des criquets et sauterelles (Orthoptera : Acrididae) de la région sud-est de l'Australie*

Mermis quirindiensis n. sp. constitue la première espèce de *Mermis* Dujardin rencontrée sur le continent australien, essentiellement dans les régions côtières ou proches de la côte, relativement limitées, du nord et du centre du New South Wales. Les hôtes comprennent *Phaulacridium vittatum* Sjöstedt, *Praxibulus* sp. et *Chortoicetes terminifera* (Walder). Les œufs de *M. quirindiensis* n. sp. comportent des boules polaires et des byssus; l'espèce est ainsi apparentée à *M. nigrescens* Dujardin et à *M. mirabilis* von Linstow, mais diffère toutefois de la première par les œufs non colorés et de la seconde par la couche épaisse et rugueuse du chorion entourant l'œuf. La description de *M. quirindiensis* n. sp. porte à juit le nombre d'espèces du genre *Mermis sensu stricto.*

The mermithid fauna of Australia has been little studied. The sole taxonomic reference is a paper by Welch (1963) in which he describes the two terrestrial mermithids *Amphimermis bogongae* Welch, 1963 and *Hexamermis cavicola* Welch, 1963 parasitising Noctuidae on mainland Australia, and a record by Crowcroft (1948) of *Mermis nigrescens* Dujardin parasitising Dermaptera on the island of Tasmania.

During extensive sampling of terrestrial mermithid nematodes in pasturelands of New South Wales between 1982-1985 *M. quirindiensis* was the only species of *Mermis* recorded. However, in February 1986, *Mermis athysanota* Steiner, 1921 was recorded on the Northern Tablelands of New South Wales bringing to two the number of species of *Mermis* occurring on mainland Australia. A description of the male and a redescription of the female of *M. athysanota* is in preparation.

The following description of *Mermis quirindiensis* n. sp. is based on three females and two males from a soil sample beneath an improved pasture in the Northern Tablelands of New South Wales. Other adults collected between 1979 and 1984 from this and other locations were kept in the laboratory for studies of their biology and behaviour until death, and were afterwards unsuitable for descriptive purposes.

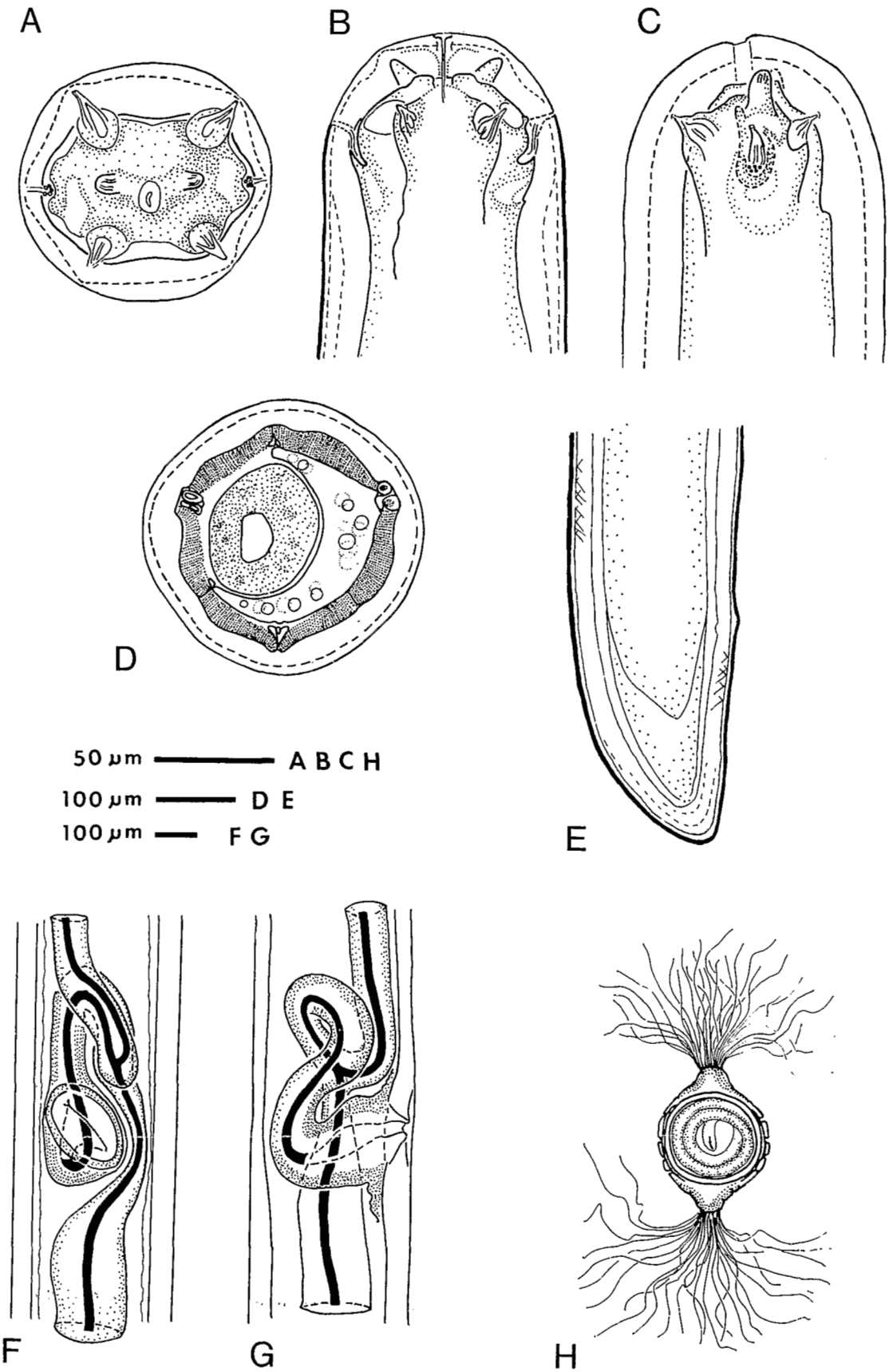

Fig. 1. *Mermis quirindiensis* n. sp. Female. A : Head, *en face* view. B : Head, dorsal view. C : Head, lateral view. D : Cross section, mid-body. E : Tail, lateral view. F : Vagina, ventral view. G : vagina, lateral view. H : Egg.

Specimens were placed in water and heat-killed at time of collection, fixed in 3 % formalin solution and then processed to glycerin.

Mermis quirindiensis n. sp.
(Figs 1-6)

Mermis Dujardin, 1842 (emended by Poinar, Rémillet & van Waerebeke, 1978). Mermithidae Braun, 1883.

MEASUREMENTS*

Females (n = 3) : L = 52 mm (60-103); mid-body width = 280 µm (299-418); head width (at level of cephalic papillae) = 82 µm (85-99), (at neck) = 94 µm (88-114); body width at nerve ring = 137 µm (143-176); cuticle width (at nerve ring) = 13 µm (24-28) (at mid-body) = 14 µm (40-55), (at terminus) = 46 µm (76-80); hypodermis width (mid-body) = 15 µm (26-27); amphid aperture = 2-3 µm; amphid pouch = 15 × 10 µm (nil range); distance of nerve ring from mouth = 301 µm (364-399); position of vulva = 49.0 per cent of body length (51.6-58.3); length of vagina (from vulva to junction with uterus) = 465 µm (864-1 043); diameter of vagina = 150 µm (186-210); width of lateral hypodermal chord = 42 µm (42-45); distance of vestigial anus from tail = 285 µm (285-357); tail width at vestigial anus = 207 µm (228-304); diameter of eggs in uterus = 35 × 25 to 48 × 62 (paratype material within range of that exhibited by holotype).

Males (n = 2) : L = 33.2 mm (46.5); width mid-body = 240 µm (205); head width (level of cephalic papillae) = 85 µm (85), (at neck) = 92 µm (92); body width at nerve ring = 124 µm (122); cuticle width at nerve ring = 14 µm (11), mid-body = 20 µm (13), hypodermis mid-body = 15 µm (12); amphid aperture = 3 µm; amphid pouch 10 × 8 µm; distance of nerve ring from mouth = 329 µm (261); spicule length = 216 µm (245); spicule head width = 35 µ m (23); mid-shaft width 28 µm (20); tail length = 212 µm (237); tail width at cloaca = 148 µm (176); position of proximal genital papillae anterior to cloaca = 231 µm (263); number of genital papillae = 71 (76).

Juvenile, st. 2 (ovic; n = 10) : L = 170-180 µm; width mid-body = 6-8 µm; position of node (junction of stichosome and trophosome) as proportion of body length = 40-45 per cent; stylet length = 14-16 µm; position of stylet crossbar as proportion of length = 45-50 per cent.

Juvenile, st. 3 (early parasitic; n = 5) : L = 0.63-1.26 mm; mid-body width = 10.6-16.1 µm; tail width (100 µm from tip) = 3.1-3.7 µm; length of stylet = 27-29 µm; distance of nerve ring from mouth = 110-116 µm.

DESCRIPTION

General : Long nematodes, females 1.5-2 × length of males. Cuticle with cross fibres. Head rounded. Mouth with slight ventral shift. Head protoplasm rectangular in face view, lateral axis longer than dorso-ventral axis. Paired prominent lateral lip papillae (15-18 µm high); four submedial head papillae; paired amphids posterior to level of submedial papillae. Opening of amphid duct small (2-3 µm), posterior to opening of submedial papillae; duct indistinct when traversing cuticle; amphid pouch a hook-shaped pocket, appearing as a largely opensided indentation of the protoplasm of the lateral lobe; amphid pouch richly endowed with nerve endings; some errant nerves terminating at level of lateral lip papillae. Six hypodermal chords; lateral hypodermal chord located at 20 % of circumference from dorsal hypodermal chord; sub-ventral 16 % from lateral, and ventral 14 % from sub-ventral; sub-ventral chords indistinct. Cuticle of medium thickness (13-14 µm) in recently moulted specimens (i.e. with large fat reserves), but much thicker (20-55 µm) in older specimens (i.e. with depleted fat reserves).

Females : Vulva an oblique slit at 60° to long axis of body; cuticle surrounding cuticular canal, unmodified, walls thin; muscular vagina a modified S-shape, twisted in two planes; transverse region of vagina below vulva horn-shaped turning cephalad to a ventrally arched longitudinal section; return loop half length of longitudinal section and contiguous with posterior uterus; anterior uterus ventrally located, joining vagina by sharp dorsal turn immediately anterior to vulval region. No pigment in neck region in live or recently fixed material despite oviposition above ground (Baker, 1983). Gravid females white (lacking dark colouration of *M. nigrescens*). Tail conoid, flattened ventrally, convex dorsally without any terminal projections. Vestigial anus well developed as both a cuticular and hypodermal structure. Head conforming to general description above. Cuticular incursion into lateral lobe (situated between lateral lip papillae and amphidial pouch) larger than in male.

Eggs : Embryonated in uterus; with nipple-shaped polar knobs and long (60-70 µm) unbranched byssi; colourless; chorion composed of two layers : outer layer thick, rough, composed of overlapping plates, inner layer thin and clear, spherical or slightly ovoid; when ovoid its long axis at right angles to long axis of egg. Inner layer 35-37 (35) µm × 35-39 (39) µm. Outer layer 5 µm thick at equator and 10-15 µm at poles, outer dimensions of egg 40-48 (48) × 53-63 (62) µm.

* In the following description, the first figure refers to the holotype (female) or allotype (male) and the figures in parentheses refer to the allotype (s).

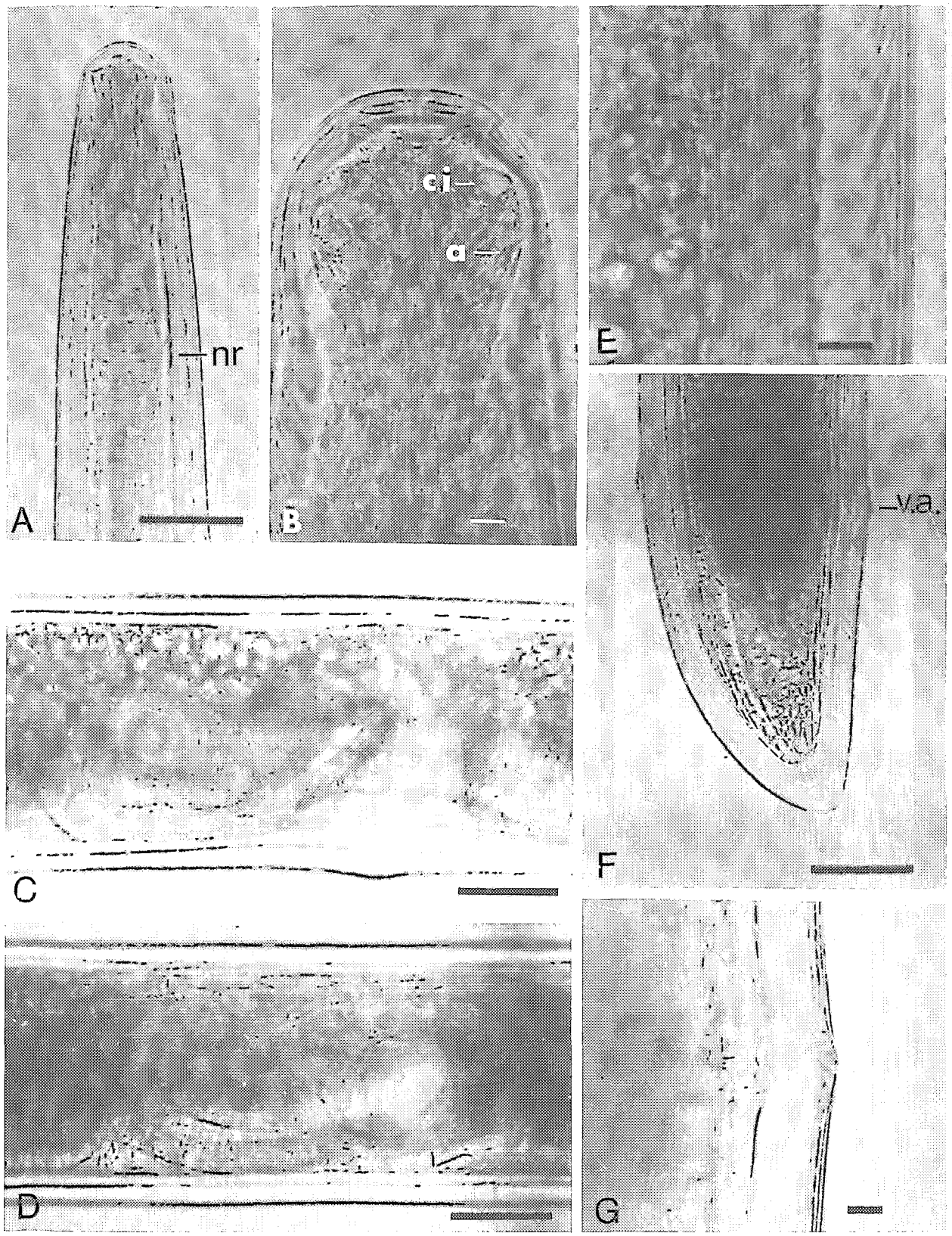

Fig. 2. *Mermis quirindiensis* n. sp. Female. A : Head, lateral view; *nr* equals nerve ring (Bar : 100 μm). B : Head, dorsal view; *ci* equals cuticular incursion of lateral lobe. *a* equals amphidial pouch (Bar : 10 μm). C : Vagina, lateral view (Bar : 100 μm). D : Vagina, ventral view (Bar : 100 μm). E : Cuticle, mid-body (Bar : 10 μm). F : Tail. *va* equals vestigial anus. G : Vestigial anus (Bar : 10 μm).

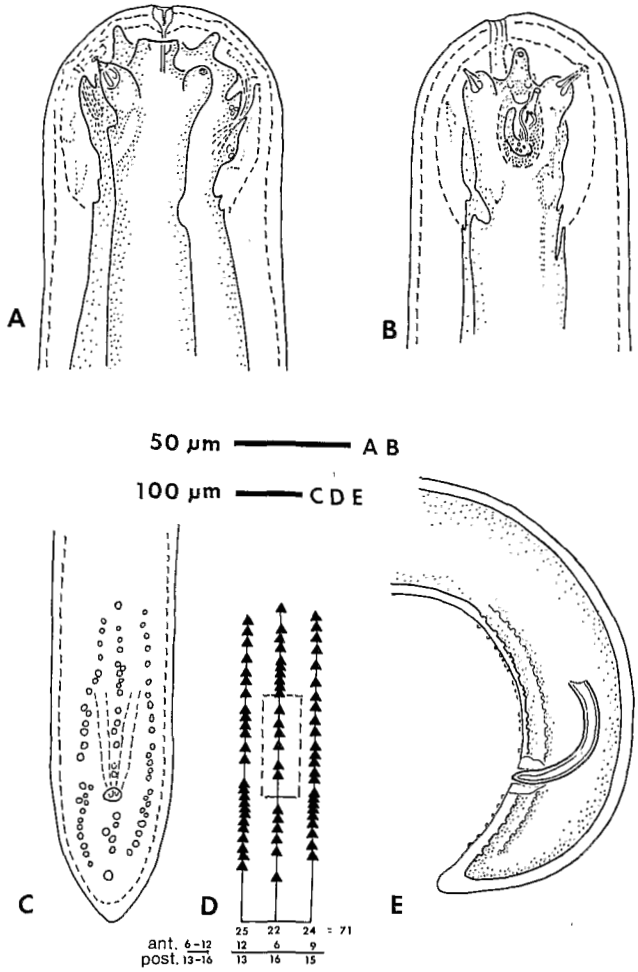

Fig. 3. *Mermis quirindiensis* n. sp. Male. A : Head, dorsal view. B : Head, lateral view. C : Tail, ventral view showing arrangement of genital papillae. D : Schematic arrangement of genital papillae. E : Tail, lateral view.

Unembryonated eggs with single layer of clear chorion 2-3 µm thick. During development surface of the egg becoming covered by discontinuous layer of amorphous gelatinous material of variable thickness, but lacking differentiation into polar regions. During embryonation outer layer of the chorion thickening to twice that of the inner layer followed by further thickening in the region of the poles, giving rise to polar knobs. Basal width of polar knob variable (10-15 µm) but generally no wider than maximum thickness of the outer layer of cuticle at poles. Thread-like byssi visible only in late stage eggs and then only as they issue from the polar knob. Shape of polar knobs of uterine eggs occasionally with striking superficial resemblance to those of *M. mirabilis*. Polar knob narrow and full extent of byssi becomes apparent in laid eggs.

Males : Tail tightly curled, conoid with small terminal projection. Spicules paired, separate, strongly curved; head slightly flared on ventral wall, walls thick (7-10 µm); length greater than (× 1.5) body width at cloaca; length approximately equal (× 1.02) tail length; spicule tip rounded, plain; canal constricted before terminal expansion at tip; genital papillae arranged in three rows, medial row marginally longer than lateral submedial rows; distance of proximal genital papillae from cloaca 1.1 × length of spicule and 1.1 × tail length. Structure of head similar to that of female, however cuticular incursion into lateral lobe smaller than in female but lateral lip more sharply defined.

Juvenile, st. 2 (ovic) : Larvae ruptured from naturally oviposited eggs short; stichocytes not clearly differentiated; stylet with characteristic cross bar midlength. Stylet form similar to that illustrated for *M. nigrescens* (Christie, 1937).

Juvenile, st. 3 (early parasitic) : Short; body broad cephalad, tapered caudad; tail attenuated curled; stylet laterally compressed, characteristic ring-like thickening of stylet wall at two thirds of length from anterior end; stylet tip pointed in dorsal view, ventral wall thicker than dorsal wall in lateral view. Form of stylet similar to that of *M. nigrescens* figured by Baylis (1944, 1947).

Juvenile, st. 3 (late parasitic and postparasitic) : Long; lacking distinctive morphological characters; tail lacking any appendage.

Type host

Phaulacridium vittatum Sjöstedt (Orthoptera : Acrididae).

Type location

Kangaroo Flat, Northern Tablelands, New South Wales, Australia.

Type material

Holotype (female) and allotype (male) in Department of Nematology, University of California, Davis, USA. Paratypes (one female and one male) deposited in South Australian Museum, Adelaide, Australia (Nos. U 3968 and U 3969, respectively).

Diagnosis and relationships

The form of the egg with polar knobs and byssi, its colourless appearance, and the rough outer coating differentiate *M. quirindiensis* n. sp. from all described species of *Mermis* listed by Poinar, Rémillet and van Waerebeke (1978). The egg of *M. quirindiensis* n. sp. resembles in form the egg of *M. nigrescens* Dujardin, 1842 (= *M. subnigrescens* Cobb, 1926, = *M.*

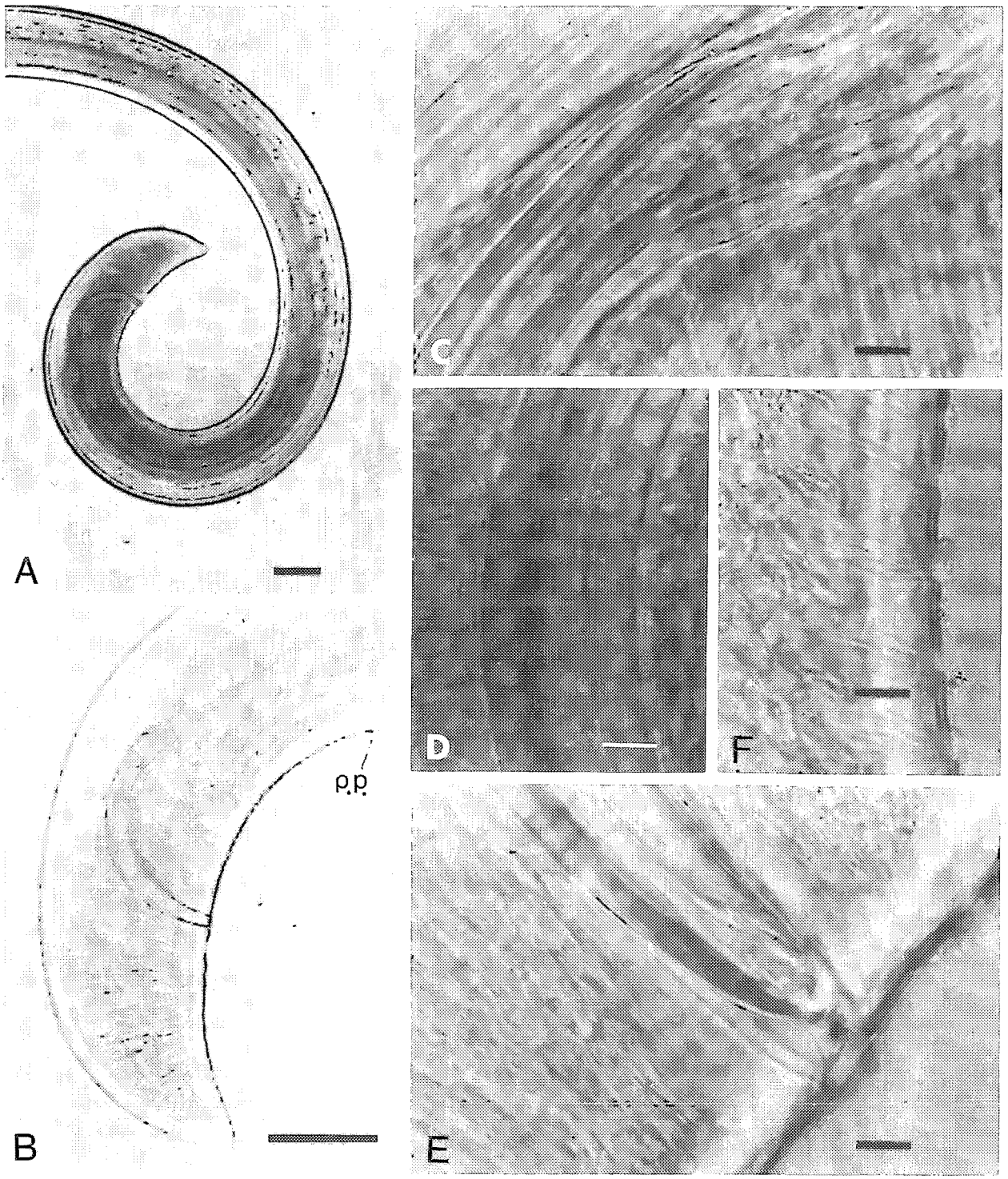

Fig. 4. *Mermis quirindiensis* n. sp. Male. A : Tail (Bar : 100 µm). B : Tail (*p.p.* equals proximal anal papilla). (Bar : 100 µm). C : Spicule head (Bar : 10 µm). D : Spicule mid-shaft (Bar : 10 µm). E : Spicule tip (Bar : 10 µm). F : Anal papillae (Bar : 10 µm).

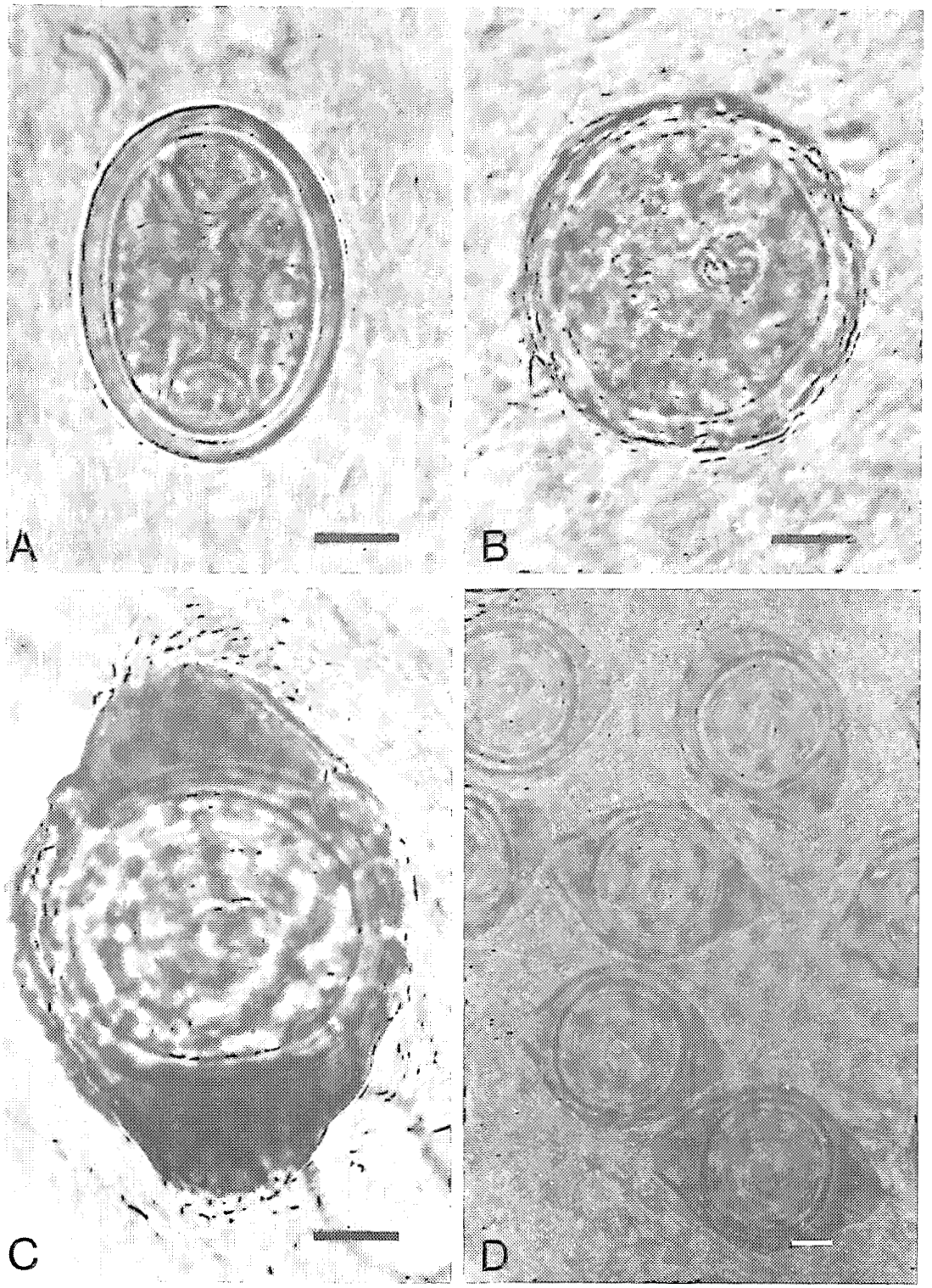

Fig. 5. *Mermis quirindiensis* n. sp. eggs (uterine). A : Unembryonated, with single inner layer of chorion. B : Partially embryonated, with formation of rough outer layer. C : Embryonated, with exceptionally well developed (broad) polar knobs. D : Embryonated, with typical development of polar knobs and byssi (Bars : 10 µm).

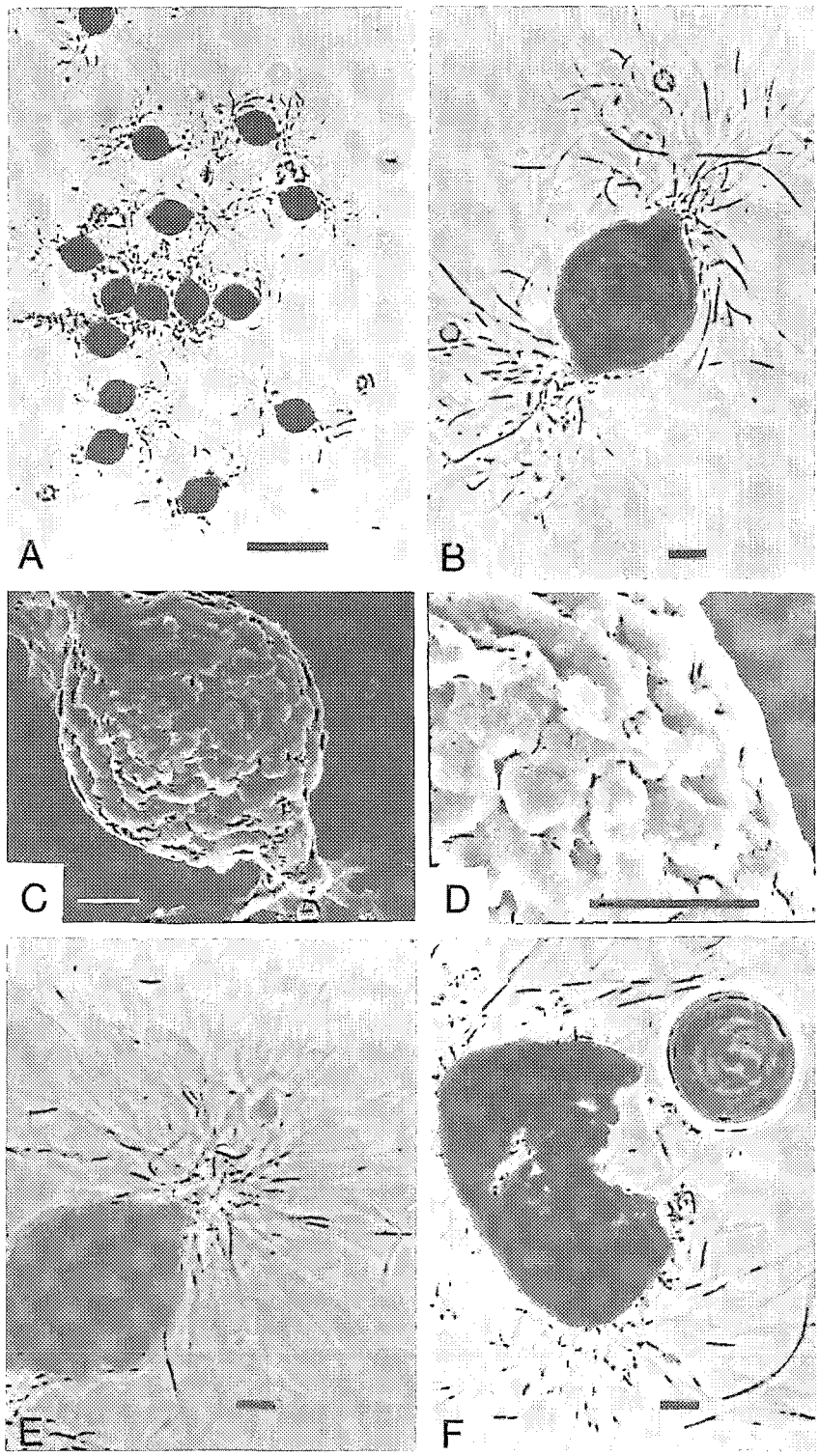

Fig. 6. *Mermis quirindiensis* n. sp. eggs (oviposited). A : Egg cluster (Bar : 100 µm). B : Typical form showing polar knobs and byssi (Bar : 10 µm). C-D : SEM of outer coating (Bars : 10 µm). E : Unbranched fan shaped arrangement of byssi (Bar : 10 µm). F : Ruptured egg showing plate-like structure of outer coating (Bar : 10 µm).

meissneri Cobb, 1926; Poinar, Rémillet & van Waerebeke, 1978), and *M. mirabilis* von Linstow, 1903 (= *M. tahitiensis* Baylis, 1944; Poinar, Rémillet & van Waerebeke, 1978), however it is easily distinguished from the former by the lack of pigment and the latter by the rough outer coating of the chorion and long byssi. The egg of *M. athysanota* Steiner, 1921 (= *M. nigrescens* Dujardin, 1842 var. *athysanota* Steiner, 1921; Baylis, 1944) also has a thick roughened outer coating but lacks polar knobs and byssi. The egg of *Mermis* sp. (Artyukhovski & Kharchenko, 1965) has polar knobs yet byssi are apparently absent or at least not visible on the uterine egg.

Both sexes of *M. quirindiensis* n. sp. have a mouth shifted slightly ventrad, differentiating it from all species in the genus except *M. changodudus* Poinar, Rémillet & van Waerebeke, 1978 from which the female differs in the length of the vagina (77-133 µm *vs.* 465-1 043 µm) and the form of the egg, and the male in the length of the spicule (169-200 µm *vs.* 212-237 µm).

Since the publication of a key to the genus *Mermis* by Poinar, Rémillet and van Waerebeke (1978), only three species of *Mermis* have been described. *Mermis* (?) *pterostichiensis* Rubzov, 1977 is based on postparasitic juvenile material and is assigned by the authors to the genus *Agamomermis* on the basis of criteria outlined by Poinard and Welch (1981). *M. paranigrescens* Rubzov, 1976 and *M. savaiiensis* Orton Williams, 1984 differ from *M. quirindiensis* n. sp. by having their mouth terminal, and round and smooth eggs. The authors acknowledge the designation by Orton Williams (1984) of *M. marocana* Baylis, 1935, as *species inquirenda.*

The form of the egg of *M. quirindiensis* n. sp. and *M. mirabilis* is similar. However, *M. quirindiensis* n. sp. can be readily distinguished from *M. mirabilis* by its (the former) ventrad shift in the mouth, greater length of the spicule in the male (212-237 µm *vs.* 120 µm) and greater number of genital papillae (22-25 per row *vs.* 12-15 per row). Male characters of *M. mirabilis* are only known from a hermaphrodite (von Linstow, 1903).

Host range

Eggs oviposited by a field collected *M. quirindiensis* n. sp. female (Kangaroo Flat, 20 January, 1982) on agar gel, were fed to ten *P. vittatum* adults in the laboratory. Five were dissected three weeks after infection and five were held until natural death. Two late parasitic juveniles of *M. quirindiensis* n. sp. were recovered from dissected material confirming development in *P. vittatum.*

No adults could be reared from specimens emerging from hosts. However, since *M. quirindiensis* was the only member of the genus *Mermis* recorded during the study, any postparasitic juveniles reared from orthopteran insects which lacked the tail appendage of *Hexamermis* and *Amphimermis*, or lacked the wart-like scar of *Agamermis*, were accepted as being *M. quirindiensis* n. sp. Such parasitic juveniles were obtained from the following hosts :

Phaulacridium vittatum Sjöstedt (Acrididae) : Oberon, February 1978, GLB, dissected from field-collected hosts (2 stage 3 (parasitic) juveniles); Kangaroo Flat, NSW, Australia, 20th January, 1982, GLB, dissected from field-collected hosts (moulting stage 2 juvenile, 11 stage 3 juveniles (early parasitic) from 4 hosts and 3 stage 3 juveniles (late parasitic) from 3 hosts).

Praxibulus sp. (Acrididae) : Hernani NSW 22nd March, 1985, A. J. Campbell, emerged from field-collected host (stage 3 (postparasitic) juvenile). *M. athysanota* has since been recorded at this site and this host association is uncertain.

Chortoicetes terminifera (Walker) (Acrididae) : Laboratory culture, Rydalmere, NSW, December 1979, M. Davison, emerged from caged laboratory-reared hosts (postparasitic) (stage 3 juveniles) : infection believed to be by *M. quirindiensis* n. sp. eggs on field grown kikuyu grass collected and fed to laboratory culture; Croft's, Uralla, NSW, December 1981, GLB and R. Pigott, emerged from field collected 4th instar nymphs (postparasitic) (stage 3 juveniles).

In the Australasian region mermithid nematodes designated as *Mermes* sp. (= *Mermis*) were recorded from *C. terminifera* in central western New South Wales by Farrow (1982) but as all postparasitic material examined from this region during the current study bore a tail appendage Farrow's material was probably either *Hexamermis* sp. or *Amphimermis* sp. rather than *Mermis* sp.

The generic status of *Mermis* sp. recorded from *Locusta migratoria* (L.) in Papua New Guinea (Baker, 1975; Young, Dori & Gorea, 1984) is unknown as the genus was designated in the broad sense of a nominal genus for mermithid parasites of acridids.

Distribution

In addition to the type location, adult *M. quirindiensis* n. sp. have been collected from the soil in the Central Tablelands of New South Wales (" Ambleside ", Oberon). Postparasitic juveniles have been reared from acridid hosts from these and other Northern and Central Tableland localities and from the coast. No specimens were found in soil or have emerged from acridid hosts during extensive sampling in the Southern Tablelands of New South Wales and areas west of the Great Dividing Range.

Discussion

This description of *M. quirindiensis* n. sp. brings the number of *Mermis (sensu stricto)* species to eight.

M. quirindiensis n. sp. females ascend vegetation during rainy periods to oviposit (Baker, 1983). *M. nigrescens* is the only other species of mermithid known to display this behaviour. However, *M. mirabilis* may behave in a similar way as its eggs have byssi, presumably for attachment to vegetation. *M. athysanota* (Steiner, 1921) and *Mermis* sp. (Artyukhovski & Kharchenko, 1965) females might also show similar behaviour. Although the eggs of both *M. athysanota* and *Mermis* sp. A.. & K. are described as lacking byssi, females have pigment in their head region, which is believed to be photosensitive (Cobb, 1929) and this indicates aboveground oviposition.

Throughout their development, the eggs of *M. quirindiensis* n. sp. resemble several previously described *Mermis* spp. recorded in the South Pacific area : the unembryonated egg of *M. quirindiensis* n. sp. (Fig. 5 A) resembles that of *M. savaiiensis* Orton Williams, 1984 in both shape and size; the early embryonated egg of *M. quirindiensis* n. sp. (Fig. 5 B) has a rough gelatinous outer coating resembling the egg of *M. athysanota* (Steiner, 1921); the fully embryonated egg (Fig. 5 C-D) has short byssi and well developed polar knobs superficially resembling those of *M. mirabilis* (von Linstow, 1903). The embryonic development of *M. quirindiensis* perhaps indicates the phylogenetic relationship between the above named species and *M. quirindiensis.*

ACKNOWLEDGEMENTS

M. quirindiensis n. sp. was collected during a study of the population dynamics of the acridid *P. vittatum* supported by an Australian Meat Research Committee Grant (DAN 19 S). A travel grant to finalize the taxonomic aspects of the study was provided by the Tablelands Wingless Grasshopper Committee.

REFERENCES

ARTYUKHOVSKI, A. K. & KHARCHENKO, N. A. (1965). [On knowledge of mermithids of the Streletskaya steppe]. *Trudy Tsentral'nongo-Chernozemnogo Gosudarstvennogo Zapouednika,* 9 : 159-185.

BAKER, G. L. (1975). The locust outbreak in the Markham and Ramu Valleys, 1973-1975. *Bubia Inform. Bull. Dept. prim. Ind. Lae, Papua New Guinea,* 15 : 8 p.

BAKER, G. L. (1983). Parasites of locusts and grasshoppers. *Agfact AE 2, NSW Dept. Agric., Sydney :* 16 p.

BAYLIS, H. A. (1935). Four new species of nematodes. *Ann. Mag. nat. Hist.,* 16 : 370-382.

BAYLIS, H. A. (1944). Observations on the nematode *Mermis nigrescens* and related species. *Parasitology,* 36 : 122-132.

BAYLIS, H. A. (1947). The larval stages of the nematode *Mermis nigrescens. Parasitology,* 38 : 10-16.

CHRISTIE, J. R. (1937). *Mermis subnigrescens,* a nematode parasite of grasshoppers. *J. agric. Res.,* 55 : 353-364.

COBB, N. A. (1926). The species of *Mermis,* a group of very remarkable nemas infesting insects. *J. Parasitol.,* 13 : 66-72.

COBB, N. A. (1929). The chromatropism of *Mermis subnigrescens. J. Wash. Acad. Sci.,* 19 : 159-166.

CROWCROFT, P. W. (1948). Notes on the occurrence of the nematode *Mermis nigrescens* Dujardin and its effect on the common earwig in Tasmania. *Pap. & Proc. roy. Soc. Tasmania,* 1947 : 59-62.

DUJARDIN, F. (1842). Mémoire sur la structure anatomique des *Gordius* et d'un autre Helminthe, le *Mermis,* qu'on a confondu avec eux. *Annls Sc. nat., Zool.,* 18 : 129-151.

FARROW, R. A. (1982). Population dynamics of the Australian plague locust *Chortoicetes terminifera* (Walker) in Central Western New South Wales. II. Factors influencing natality and survival. *Aust. J. Zool.,* 30 : 199-222.

ORTON WILLIAMS, K. J. (1984). *Mermis savaiiensis* n. sp. (Nematoda : Mermithidae) from Western Samoa. *Syst. Parasitol,* 6 : 257-260.

POINAR, G. O., RÉMILLET, M. & VAN WAEREBEKE, D. (1978). *Mermis changodudus* sp. n. (Mermithidae) a nematode parasite of *Heteronychus* beetles (Scarabaeidae) in Madagascar. *Nematologica,* 24 : 100-104.

POINAR, G. O. & WELCH, H. E. (1981). Parasites of invertebrates in the terrestrial environments. In Slusarski, W. (Ed.) *Review of Advances in Parasitology.* Warszawa, PWN-Polish Scientific Publ. : 947-954.

RUBZOV, I. A. (1976). [New species of mermithids]. *Zool. Zh.,* 55 : 1 292-1 298.

RUBZOV, I. A. (1977). [New species of mermithids from the Far East. In the series, *Entomofauna of the Far East : Works of the Biological Soil Institute (new series), Vladivostok] :* 149-154.

STEINER, G. (1921). Beitrage zur Kenntnis der Mermithiden. *Zentbl. Bakt. ParasitKde,* 87 : 451-465.

VON LINSTOW, V. (1903). Helminthologische Beobachtungen. *Zentbl. Bakt. ParasitKde,* 34 : 526-531.

WELCH, H. (1963). *Amphimermis bogongae* sp. nov. and *Hexamermis cavicola* sp. nov. from the Australian bogong moth, *Agrotis infusa* (Boisd.), with a review of the genus *Amphimermis* Kaburaki and Imamura, 1932 (Nematoda : Mermithidae). *Parasitology,* 53 : 55-62.

YOUNG, G. R., DORI, F. M. & GOREA, K. G. (1984). A plague of *Locusta migratoria* (L.) (Orthoptera : Acrididae) in the Markham and Upper Ramu Valley of Papua New Guinea, March 1975-November 1976. *Dept. prim. Ind. Port Moresby, Res. Bull.,* 34 : 42 p.

Accepté pour publication le 17 février 1986.