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Studies on the genus *Amphimermis* (Nematoda : Mermithidae) : five new species, including four from Orthoptera in southeastern Australia

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Summary – Five new species of *Amphimermis* are designated, of which four are described, namely *A. buraki* n. sp., a parasitoid of the tettigoniid *Conocephalus* sp.; *A. acridiorum* n. sp., *A. mirabinda*, n. sp. and *A. australoelegans* n. sp., parasitoids of acridids including wingless grasshopper, *Phaulacridium vittatum* (Sjöstedt), eastern plague locust, *Oedaleus australis* (Saussure), and Australian plague locust, *Chortoicetes terminifera* (Walker) and, in the case of *A. australoelegans* n. sp., the larval stage of a scarab, *Sericesthis* sp. The males of *A. buraki* n. sp. and *A. acridiorum* n. sp. resemble *A. avoluta* Rubtsov & Koval but differ in size, configuration of spicule twisting and position of amphids. The male of *A. mirabinda* n. sp. resembles *A. bogongae* Welch but is smaller. The male of *A. australoelegans* resembles *A. elegans* (Hagmeier) and *A. tongaensis* Spiridonov, but is larger than both and further differs from *A. elegans* in the morphology of the tail and *A. tongaensis* in the size of the amphids. Material identified as *A. elegans* by Artyukhovski and Kharchenko has been designated *A. artyukhovskii* n. sp. Keys to males and females are provided in which thirteen previously described species are recognised as valid. Species challenged are *A. dolycoris* Rubtsov, *A.* (?) *pardonensis* Rubtsov and *A. elongata* Rubtsov which have been declared *species inquirendae. A. ghilarovi* (Polozhentsev & Artyukhovski) has been synonymised with *A. elegans* (Hagmeier). *A. unka, sensu* Li has been designated *nomen dubium.*

Résumé – *Étude du genre* Amphimermis *(Nematoda : Mermithidae) : cinq nouvelles espèces dont quatre provenant d'Orthoptères du sud-est de l'Australie* – Cinq nouvelles espèces d'*Amphimermis* sont désignées dont quatre sont décrites : *A. buraki* n. sp., parasitoïde de Tettigoniide *Conocephalus* sp., *A. acridiorum* n. sp., *A. mirabinda* n. sp. et *A. australoelegans* n. sp., parasitoïdes d'Acridides dont *Phaulacridium vittatum* (Sjöstedt), *Oedaleus australis* (Saussure) et *Chortoicetes terminifera* (Walker), ainsi que, dans le cas d'*A. australoelegans* n. sp., le stade larvaire d'un carabe, *Sericesthis* sp. Les mâles de *A. buraki* n. sp. et de *A. acridiorum* n. sp. ressemblent à ceux de *A. avoluta* Rubsov & Koval mais en diffèrent par la taille, le type de courbure des spicules et la position des amphides. Les mâles de *A. mirabinda* n. sp. ressemblent à ceux de *A. bogongae* Welch mais sont plus petits. Les mâles de *A. australoelegans* n. sp. ressemblent à ceux de *A. elegans* (Hagmeier) et *A. tongaensis* (Spiridonov) mais ils sont plus longs dans les deux cas et de plus diffèrent de *A. elegans* par la forme de la queue et de *A. tongaensis* par la taille des amphides. Les spécimens identifiés par Artyukhovski et Karchenko comme *A. elegans* sont considérés comme une nouvelle espèce, *A. artyukhovskii* n. sp. Une clé des mâles et une clé des femelles sont proposées dans lesquelles treize espèces déjà décrites sont reconnues valides. Les espèces mises en question sont *A. dolycoris* Rubtsov, *A. (?) pardonensis* Rubtsov et *A. elongata* Rubtsov qui avaient été déclarées *species inquirendae. A. ghilorovi* (Polozhentrev & Artyukhovski) est synonymisé à *A. elegans. A. unka sensu* Li est considéré comme *nomen dubium.*

Key-words : Mermithidae, *Amphimermis,* parasitoids, Acrididae, Scarabaeidae.

The genus *Amphimermis* was previously known in Australia only by *Amphimermis bogongae* Welch, 1963, a parasite of the bogong moth, *Agrotis infusa* (Boisd.) (Lepidoptera : Noctuidae).

The majority of species described in this paper are parasitic on orthopterans. Poinar (1975), in a review of nematode-host associations, lists only one species of the genus, *Amphimermis elegans* (Hagmeier, 1912), parasitising orthopterans, namely *Stenobothrus* sp. (Acrididae) and *Decticus* sp. (Tettigoniidae) in Europe. Since the review by Poinar, *Amphimermis bonaerensis* Miralles & Camino, 1983, has been recorded parasitising *Laplatacris dispar* Rehn (Acrididae) in Argentina. *Amphimermis* spp. appear to be less important as parasitoids of orthopterans as species in the genera *Mermis, Hexamermis* and *Agamermis* whose role in the control of orthopterans has been reviewed (Webster & Thong, 1984; Street & McGuire, 1990). However, recent studies in Australia (Baker, 1986) have indicated that parasitism by *Amphimermis* spp. is a major influence in the population dynamics of grasshoppers in the moist eastern sub-coastal tablelands. Although *Mermis* and *Agamermis* are represented in Australia by species which are also parasitoids of orthopterans (Baker, 1986; Baker & Poinar, 1986, 1988), they are generally less abundant or have a restricted distribution rendering them less effective than species of *Amphimermis* as biological control agents.

The genus *Amphimermis* is here recorded parasitising coleopteran larvae in Australia for the first time. Other mermithid genera, notably *Psammomermis,* appear far more important in the biological control of coleopterans in this region (A. J. Campbell, pers. comm.). *A. elegans* is the only species of *Amphimermis* previously recorded parasitising coleopterans, namely *Melolontha melolontha* (L.) (Scarabaeidae) (Blunck, 1939) and *Leptinotarsa decemlineata* Say (Chrysomelidae) (Kaiser, 1972) in Europe.

Materials and methods

The specimens used in the descriptions in this paper were collected during a study of the population dynamics of the wingless grasshopper, *Phaulacridium vittatum* (Sjöstedt). In order to identify the species of nematodes involved, adult specimens suitable for taxonomic study were obtained by two methods : *i)* natural emergence from host and retention in the laboratory in aerated distilled water until after the final moult; *ii)* sampling from soil in pasturelands with a history of parasitism of acridids by mermithid nematodes. Infective juveniles were obtained when possible by hatching eggs laid in the laboratory. Prior to examination, specimens were gently heat killed, fixed in 3 per cent formalin and processed to glycerin by slow evaporation of Lee's solution (75 % absolute ethyl alcohol, 20 % water and 5 % glycerin).

During the survey, four species of *Amphimermis* new to science were recorded and are herein described. The terminology follows that of Poinar (1983).

Material has been deposited in the Department of Nematology, University of California, Davis, USA (UCD), South Australian Museum, Adelaide, Australia (SAM) and Laboratoires de Biologie Parasitaire, Protistologie, Helminthologie, Muséum National d'Histoire Naturelle, Paris, France (MNHN).

Amphimermis Kaburaki & Imamura, 1932

= *Complexomermis* Filipjev, 1934

DIAGNOSIS (Kaiser, 1991 *emend.*)

Usually medium to long nematodes, 13-260 mm in length. Mouth opening terminal or with slight ventral shift. Amphids large, usually with porelike aperture. Six head papillae lateral and sub-medial in position. Cuticle thick with clearly visible criss-cross fibres. Longitudinal chords in midbody, six. Pharyngeal tube long, in some species reaching 60 % of body length. Pharyngeal tube does not reach the mouth opening but ends behind it with a ringlike thickening. Tail tip in both sexes bluntly rounded and ventrally curved. *Male :* with two long, twisted spicules. Genital papillae in three rows, medial row bifurcates around genital opening. *Female :* vagina elongated, S-shaped, strongly muscularized, often with vulval flap. *Preparasites* do not amputate tail and have extremely high mobility. *Eggs* numerous, medium-sized, without byssi.

TYPE SPECIES

Amphimermis zuimushi Kaburaki & Imamura, 1932.

OTHER SPECIES

A. acridiorum n. sp.
A. artyukhovskii n. sp.
= *A. elegans apud* Artyukhovski & Karchenko, 1965.
A. australoelegans n. sp.
A. avoluta Rubtsov & Koval, 1975.
A. bogongae Welch, 1963.
A. bonaerensis Miralles & Camino, 1982.
A. buraki n. sp.
A. elegans (Hagmeier, 1912) Welch, 1963
= *Mermis elegans* Hagmeier, 1912.
= *Complexomermis elegans* (Hagmeier, 1912) Filipjev, 1934.
= *Complexomermis ghilarovi* Polozhentsev & Artyukhovski, 1958.
= *A. ghilarovi* (Polozhentsev & Artyukhovski, 1958) Welch, 1963 n. syn. (male).
A. lagidzae Rubstsov, 1975.
A. litoralis Artyukhovski & Karchenko, 1971.
A. longiscapus Rubtsov, 1976.
A. maritima Rubstov, 1971.
A. mirabinda n. sp.
A. mongolica Rubtsov, 1976.
A. tinyi Nickle, 1972.
A. tongaensis Spiridonov, 1987.
A. volubilis Rubtsov & Koval, 1975.

SPECIES INQUIRENDAE

A. dolycoris Rubtsov, 1974.
A. elongata Rubtsov, 1978.
A. (?) pardonensis Rubtsov, 1977.

REMARKS

In reviewing the genus, the male of *A. ghilarovi* (= *Complexomermis ghilarovi*) has been designated the lectotype and the species synonymised with *A. elegans :* the male of *A. ghilarovi* is similar to *A. elegans* and the species was differentiated from *A. elegans* on the basis of differences between the females, however given the difference in amphid shape between males and females designated as *A. ghilarovi* (*elegans* like in the male and *bogongae* like in the female) the extreme sexual dimorphism would indicate that males and females have been mistakenly considered conspecific. The females described as *A. ghilarovi* are not regarded as *A. elegans* and as a consequence of the proposed synonymy are unassigned. Artyukhoski (1969) transferred female *Amphimermis ghilarovi* to the genus *Amphibiomermis* Artyukhoski, 1969 as a n. comb. and indicated the male of

Amphibiomermis ghilarovi was unknown. It is not clear if Artyukhovski (1969) intended male *Amphimermis ghilarovi* to be unassigned or to remain as a valid species, the females of which were unknown.

Species have been declared *species inquirendae* on the basis that their descriptions were based on post-parasitic juveniles. *Amphimermis unka, sensu* Li (1981, 1985) is designated *nomen dubium* being either an erroneous reference to *Agamermis unka* Kaburaki & Imamura, or an unidentified species of *Amphimermis* recorded from the same host (*Nilaparvata lugens* Stal.) by Chen and Yang (1985) and Xia (1989). *Agamermis unka* has been recorded parasitising *N. lugens* in China (Wang & Li, 1987) and Korea (Choo *et al.*, 1989).

GROUPS

Males of the described species of *Amphimermis* divide readily into four groups on the basis of the twisting of the spicule and shape of amphids (Fig. 15). Described species and new species described in this paper have been assigned as follows :

volubilis group : spicule twisted entire length; cup shaped amphids; *A. volubilis*.

avoluta group : proximal half of spicule untwisted; cup shaped amphids; *A. avoluta, A. acridiorum* n. sp. and *A. buraki* n. sp.

bogongae group : spicule twisted loosely distal and proximal half, untwisted in middle; cup shaped amphids; *A. bogongae, A. maritima, A. litoralis, A. tinyi, A. bonaerensis, A. mirabinda* n. sp.

elegans group : spicule twisted tightly distal and proximal half, untwisted in middle; thin-walled, pocket-like amphids; *A. elegans, A. zuimushi, A. tongaensis, A. artyukhovskii* n. sp., *A. australoelegans* n. sp.

Summaries of the distribution and host range of *Amphimermis* spp. have been given by Rubstov (1978 *a*) and Kaiser (1991) and are further elaborated in Table 1.

Amphimermis acridiorum n. sp.

(Figs 1-5)

MEASUREMENTS

Holotype (female) : L = 293 mm; mid-body diam. = 340 µm; head width (at level of cephalic papillae) = 75 µm, (at neck) = 80 µm; body diam. at nerve ring = 150 µm; cuticle width (at nerve ring) = 20 µm, (at mid-body) = 50 µm; hypodermis width (mid-body) = 15 µm; amphid aperture = 5 µm; amphid pouch (in dorsal view) = 18 × 12 µm; dist. nerve ring/mouth = 310 µm; V = 50.2; length of vagina (from vulva to junction with uterus in lateral view) = 1.2 mm, (general length in dorsal view) = 670 µm; diam. vagina = 160 µm; length of vulval flap = 250 µm; height of vulval cone = 70 µm; width lateral hypodermal chord = 45 µm; diam. egg in uterus = 100 × 105 µm.

Allotype (male) : L = 107 mm; mid-body diam. = 220 µm; head diam. (at level of cephalic papillae) = 72 µm, (at neck) = 78 µm; body diam. at nerve ring = 120 µm; cuticle width (at nerve ring) = 12 µm, (mid-body) = 15 µm; hypodermis width (mid-body) = 12 µm; amphid aperture = 6 µm; amphid pouch = 20 × 14 µm (in dorsal view), 20 × 20 µm (in lateral view); dist. nerve ring/mouth = 350 µm; spicule length = 2.7 mm; position of twisting = distal 70 % of length; spicule head width = 25 µm; width mid-shaft = 7 µm; tail length = 350 µm; tail diam. at cloaca = 210 µm; position of proximal genital papilla anterior to cloaca = 835 µm; number of genital papillae in medial row (anterior to cloaca) = 35, (posterior to cloaca) = 18.

Paratypes (females and males) : see Tables 2 and 3, respectively.

Juveniles, st. 2 (preparasitic; progeny of holotype; n = 10) : L = 1.401 mm (1.27-1.46); mid-body diam. = 14.6 µm (12-16); head width = 9-10 µm; buccal cavity length = 38.5 µm (32-44); stylet = 24.3 µm (21-26); distance nerve ring mouth = 101 µm (92-107); body diam. at nerve ring = 15.3 µm (14-16); length of stichosome = from 13.03 % (11.8-14.1) to 61.1 % (59.4-66.6) body length; body width mid-stichosome region = 15.4 µm (14-16), mid-trophosome = 10 µm (nil range); tail length = 50-60 µm; tail diam. (50 µm from tip) = 4 µm (nil range).

DESCRIPTION

General : Long nematodes (longest species in the genus, cf. *A. bogongae*), females equal or up to 16 × length of males (males 28-144 mm and females 75-457 mm in length). Cuticle with cross fibres. Head bluntly rounded. Mouth terminal. Four sub-medial cephalic papillae, two lateral cephalic papillae. Opening of lateral cephalic papillae at level of or slightly anterior to level of sub-medial cephalic papillae. Moderate sized amphids, cup shaped, larger in male than female; opening of amphids posterior to opening of lateral cephalic papillae and slightly offset. Six hypodermal chords; lateral hypodermal chord three cells wide. Wall of anterior end of oesophagus thickened to produce a short pharynx.

Females : Opening of vulva a transverse slit. Vulval flap present. Vulval cone present; base not muscular. Horse-shoe shaped build up of vulvar concretion often present in mature specimens. Vagina S-shaped, long, muscular; posterior loop equal to or marginally greater than length of anterior loop; bends rounded. Junction of vagina and uterus at level of or slightly posterior to vulva. Tail conical, slightly flattened on ventral surface. Vestigial anus sometimes present. Eggs in single or double row in uterus and two abreast (four in one plane). Eggs unembryonated when laid.

Males : Tail curled into ring, conoid, bluntly rounded. Spicule paired; tightly twisted for distal two-thirds of length to within one-tenth of length from tip; head flared symmetrically, bulbous; walls thick, especially in head region; spicule length approximately 12 × body width at

Table 1. *Distribution and host range of* Amphimermis *spp.*

Group/species	Distribution	Host	Authority
volubilis group			
A. volubilis	Ukraine	COLEOPTERA : Chrysomelidae *Leptinotarsa decemlineata* Say	Rubtsov & Koval, 1975
avoluta group			
A. avoluta	Ukraine	COLEOPTERA : Chrysomelidae *Leptinotarsa decemlineata* Say	Rubtsov & Koval, 1975
A. acridiorum n. sp.	Australia	ORTHOPTERA : Acrididae *Phaulacridium vittatum* (Sjöstedt) *Oedaleus australis* (Saussure) *Chortoicetes terminifera* (Walker)	Present study
A. buraki n. sp.	Australia	ORTHOPTERA : Tettigoniidae *Conocephalus* sp.	Present study
bogongae group			
A. bogongae	Australia	LEPIDOPTERA : Noctuidae *Agrotis infusa* (Boisd.)	Welch, 1963
A. maritima	Russia (Primorsk Region)	Unknown	Rubstov, 1971
A. litoralis	Russia (Voronezh Region)	Unknown	Artyukhovski & Kharchenko, 1971
A. tinyi	USA	ODONATA : Coenagrionidae *Ischnura posita* (Hagen) *Anomalagrion bastatum* (Say)	Willis, 1971; Nickle, 1972
A. bonaerensis	Argentina	ORTHOPTERA : Acrididae *Laplatacris dispar* Rhen	Miralles & Camino, 1983
A. mirabinda n. sp.	Australia	ORTHOPTERA : ACRIDIDAE *Phaulacridium vittatum* (Sjöstedt)	Presesent study
elegans group			
A. elegans	Germany	ORTHOPTERA : Acrididea *Stenobothrus* sp.	Hagmeier, 1912
	Austria	COLEOPTERA : Chrysomelidae *Leptinotarsa decemlineata* Say	Kaiser, 1972
	Kirgizia	LEPIDOPTERA : Yponomeutidae *Yponomeuta mallinella* (L.) *Yponomeuta padella* (L.)	Kirjanova *et al.*, 1959
	Russia (Kuibyshev region)	COLEOPTERA : Elateridae ? sp.	Shimkina, 1978 (as *A. ghilarovi*)
	Europe	COLEOPTERA : Chrysomelidae *Gastrophysa* sp. *Phyllotreta* sp.	Kaiser, 1991
		DERMAPTERA : Forficulidae *Forficula* sp.	Kaiser, 1991
A. artyukhovskii n. sp.	Russia (Voronesh region)	LEPIDOPTERA : Lymantriidae *Lymantria dispar* (L.) LEPIDOPTERA : Geometridae *Operophtera brumata* (L.)	Artyukhovski & Kharchenko, 1965
A. zuimushi	Japan	LEPIDOPTERA : Pyralidae *Chilo simplex* Butler	Kaburaki & Imamura, 1932
A. tongaensis	Tonga	Unknown	Spiridonov, 1987
A. australoelegans n. sp.	Australia	ORTHOPTERA : Acrididae *Phaulacridium vittatum* (Sjöstedt) *Chortoicetes terminifera* (Walker) COLEOPTERA : Scarabaeidae *Sericesthis* spp.	Present study

Table 2. *Morphometrics of female of new* Amphimermis *species (dimensions of paratypes; mean and range).*

Species	L (mm)	Body width (µm)	Head width µm	Amphid length¹ µm	Amphid width¹ µm	Nerve ring µm	Vagina position (%)	Vagina dia. µm	Vagina length¹ µm	Vagina length² µm	Vest. anus³ µm
A. acridiorum n. sp.	241	329	68.3	18.1	11.7	317	50.2	126	697	1142	278 (5)
n = 27	74-457	225-480	50-85	13-22	8-15	250-400	12.8-59.3	37-200	320-1010	570-1675	140-380
A. buraki n. sp.	30.1	164	51	13.2	7	249	56.6	48.7	210	324	-
n = 5	23-33	130-187	45-54	10-14	-	230-266	54.6-58	40-62	110-282	245-437	-
A. mirabinda n. sp.	161	303	66.8	20.8	14.6	318	50.1	110	628	1063	197 (2)
n = 6	51-331	270-410	48-85	15-23	10-17	312-325	45.6-53.6	62-150	380-850	770-1500	190-205
A. australoelegans n. sp.	139	256	66.6	31.6	15	327	53.4	73	780	1350	180 (1)
n = 3	91-205	220-300	50-85	25-35	-	272-360	48-58	60-100	720-870	1200-1500	-

¹Dorsal view.
²Lateral view.
³Distance of vestigial anus from tail : number in parenthesis.

Table 3. *Morphometric data for male of new* Amphimermis *species (dimensions of paratypes; mean and range).*

Species	L (mm)	Body width (µm)	Head width (µm)	Amphid length¹ (µm)	Amphid width¹ (µm)	Nerve ring (µm)	L spicule (µm)	L tail (µm)	Tail width² (µm)	Proximal papilla³ (µm)	Genital Papillae ant. N	Genital Papillae post. N
A. acridiorum n. sp.	84.3	188	64.5	18.8	10.8	302	2421	279	168	696	28	12
n = 51	28-187	112-262	52-87	12-30	7-17	255-342	1775-3100	192-315	100-225	470-1175	20-41	7-16
A. buraki n. sp.	22.8	115	46.4	14.6	6.4	238	875	144	100	324	14.5	7.5
n = 8	16-31	98-140	39-52	10-19	5-7	211-262	750-975	130-165	87-117	250-375	12-18	4-9
A. mirabinda n. sp.	49.2	169	60.7	20.5	15.7	291	1593	273	145	609	24	10
n = 8	25-102	145-250	52-70	17-25	12-20	250-320	1199-2380	165-310	100-190	470-915	20-40	5-15
A. australoelegans n. sp.	47.4	163	64.8	9	40.7	290	1675	260	138	753	31	99
n = 14	31-75	127-225	60-70	7-10	32-45	255-313	1320-2060	205-315	115-160	575-890	24-37	9-12

¹Dorsal view.
²Tail width measured at cloaca.
³Distance of proximal papilla anterior to cloaca.

cloaca, 7 × tail length. Genital papillae arranged in three rows, medial row marginally longer than sub-medial rows; medial row bifurcate immediately anterior and posterior to cloaca; distance of proximal genital papilla anterior to cloaca = 0.3 × spicule length and 2.4 × tail length. Smaller males (Fig. 4) tend to be aberrant in that the twisted section of the spicule contains a short untwisted portion at about two thirds of the length of the twisted section (Fig. 3 F).

Juvenile, st. 2 (preparasitic) : Short, slender larvae. Proximal half of body broader than distal half. Cephalic papillae distinct. Stylet barbed on one side; distal end with slight terminal swelling. Oesophagus terminates mid-stichosome; sixteen stichocytes present in stichosome. Trophosome interspaces indistinct and well spaced (approx. 40-50 µm). Tail attenuated to a fine point with tip tending to hook shape in life. A moult occurs within the host during the early stages (5-10 days) of parasitic development when larvae are 2-12 mm long (Fig. 5 B, C). A moult during parasitic development has been described for *Romanomermis culicivorax* Ross & Smith (Poinar & Otieno 1974; Vyas-Patel, 1992), and Hominick *et al.* (1982) suggested the presence of a stylet in some parasitic juveniles of *Hexamermis glossinae* Poinar, Mondet, Gouteux & Laveissier indicated a moult within the host. The postparasitic juvenile undergoes a double moult.

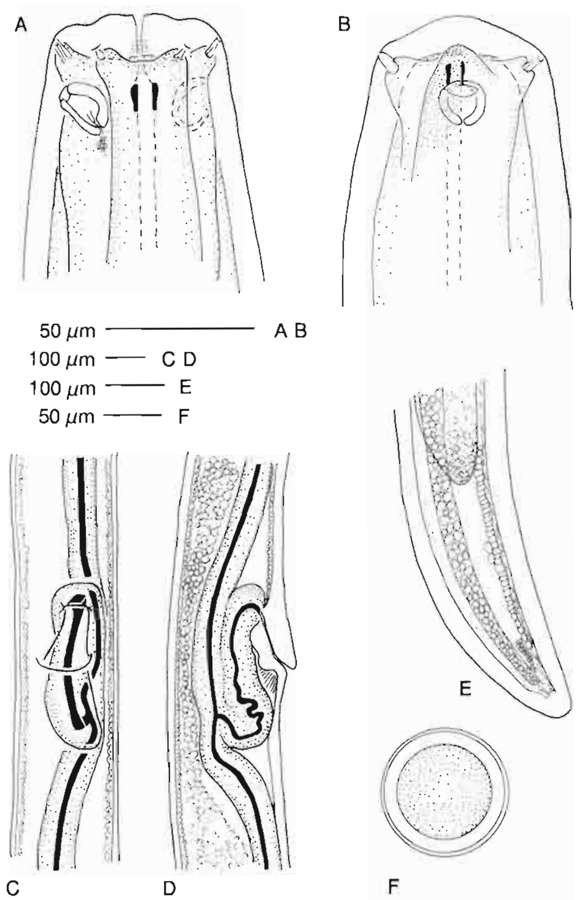

Fig. 1. Amphimermis acridiorum *n. sp. Female. A : Head, dorsal view; B : Head, lateral view; C : Vagina, ventral view; D : Vagina, lateral view; E : Tail, lateral view; F : Uterine egg.*

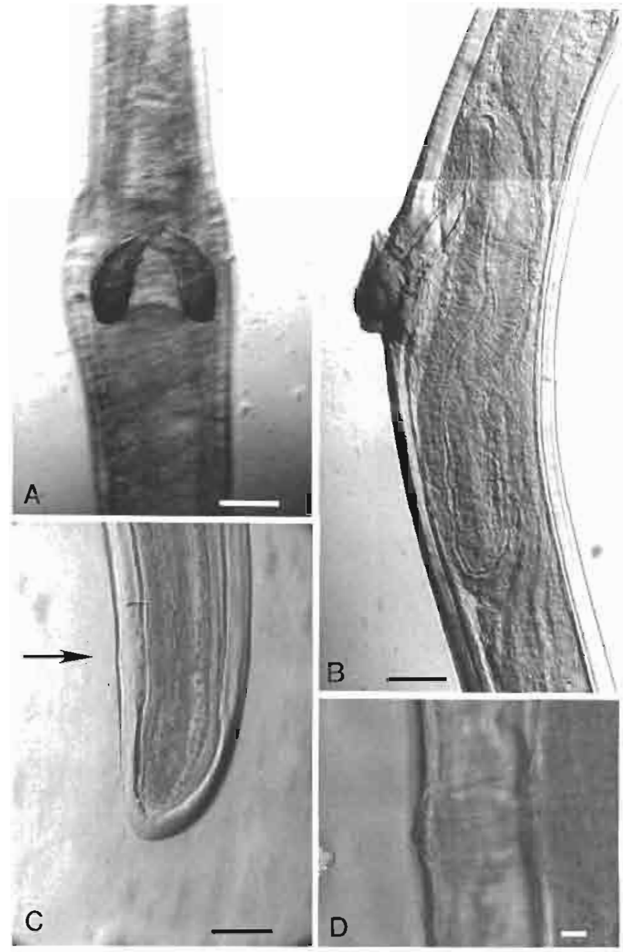

Fig. 2. Amphimermis acridiorum *n. sp. Aberrant females. A : Vagina with cloacal concretion, ventral view; B : Same, lateral view* (Bar : 100 μm); *C : Tail with vestigial anus (arrow), lateral view; D : Vestigial anus, lateral view* (Bar equivalent : A, B, C = 100 μm; D = 10 μm).

TYPE HOST AND LOCATION

Phaulacridium vittatum (Sjöstedt) (Orthoptera : Acrididae). " Ambleside "[33° 43′ S, 149° 46′ E], Oberon, Central Tablelands, New South Wales, Australia.

TYPE MATERIAL

Holotype (female) and *allotype* (male) in UCD. *Paratypes* (one male and one female) deposited in SAM and MNHR.

DIAGNOSIS AND RELATIONSHIPS

A. acridiorum n. sp. males belong to the *avoluta* group (Table 1) in having the proximal section of the spicule untwisted.

Male *A. acridiorum* n. sp. differs from *A. avoluta* in the position of the amphidial opening in relation to the opening of the lateral cephalic papillae (amphidial opening posterior to lateral cephalic papillae *vs* at same level); *A. buraki* n. sp. in being longer (28-187 *vs* 16-31 mm), in having a short spicule in relation to body length (2.4 and 87 mm (i.e. 1 : 36) *vs* 0.8 and 22 mm (i.e. 1 : 27) and in the position of the spicule twisting (distal 62-76 *vs* distal 51-58 %); relative position of the openings of the lateral and sub-medial head papillae (level *vs* submedial anterior to lateral) and having proportionally smaller amphids (30 *vs* 35 % head width).

Female *A. acridiorum* n. sp. can be distinguished from all described species except *A. bonaerensis* and *A. bogongae* on the basis of the form of the vagina; loops anterior and posterior to vulva of equal length (Fig. 16). *A. acridiorum* n. sp. differ from *A. bonaerensis* having a generally shorter vagina in relation to body (320-1010 μm and 75-457 mm *vs* 400 μm (measured from illustration in Miralles & Camino, 1983) and 100-120 mm) and *A. bongongae* in having a generally longer

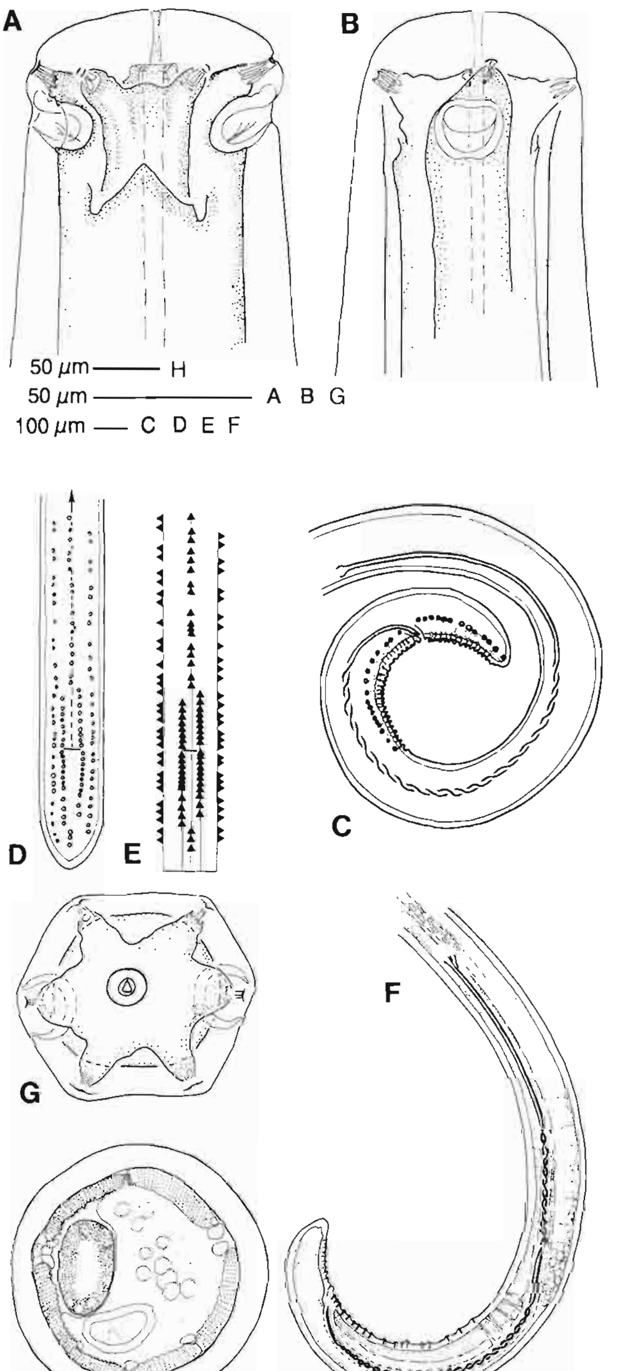

Fig. 3. Amphimermis acridiorum *n. sp. Male. A : Head, dorsal view; B : Head, lateral view; C : Tail, lateral view; D : Tail, ventral view; E : Schematic representation of genital papillae; F : Tail, lateral view (aberrant form); G : Head,* en face *view; H : Mid-body, cross section.*

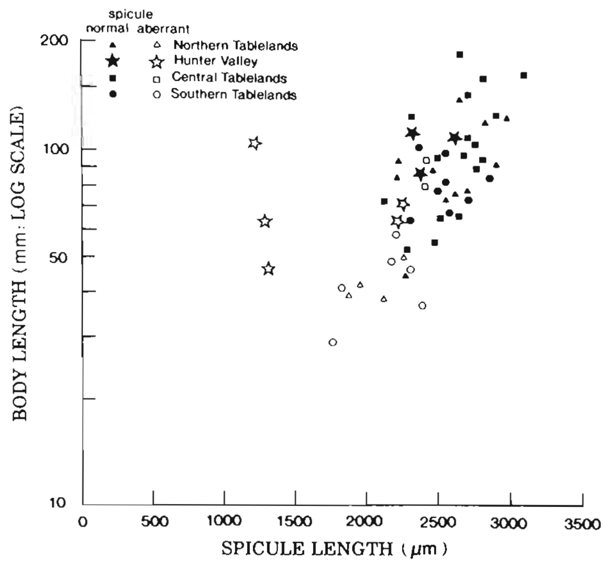

Fig. 4. Amphimermis acridiorum *n. sp. Male. Scatter diagram of spicule length regressed against body length.*

vagina (in one plane) in relation to body length (320-1010 µm and 75-457 mm *vs* 380 µm and 160-205 mm for *A. bogongae*). The uterine egg is of comparable size to *A. bogongae* but the st. 2 juvenile is only two thirds the length (1.4 mm *vs* 1.9 mm).

Host range

Oedaleus australis (Saussure) (Acrididae) : two males and one female reared from adults, Upper Rouchell, March 25, 1987, K. England.

Chortoicetes terminifera (Walker) (Acrididae) : three males and one female reared from nymphs. Laboratory culture, Rydalmere, NSW, M. Davison; three males reared from adults, " Westbrook ", Singleton, March 16, 1992, R. Pigott; one male reared from adult, " Longarm ", Barraba, February 26, 1992, R. Pigott.

Distribution

In addition to the type location, *A. acridiorum* n. sp. has been reared from *P. vittatum* collected in the Northern Tablelands (Stonehenge, Hernani, Walcha), Central Tablelands (Oberon : " Cormark ", " Ambleside ") and Southern Tablelands (Jerangle, Braidwood, Dalgety) and South West Slopes (Tumbarumba). *A. acridiorum* n. sp. has also been reared from *C. terminifera* collected on the North West Slopes and Hunter Valley districts of New South Wales. *A. acridiorum* n. sp. appears to be widely distributed throughout the tablelands

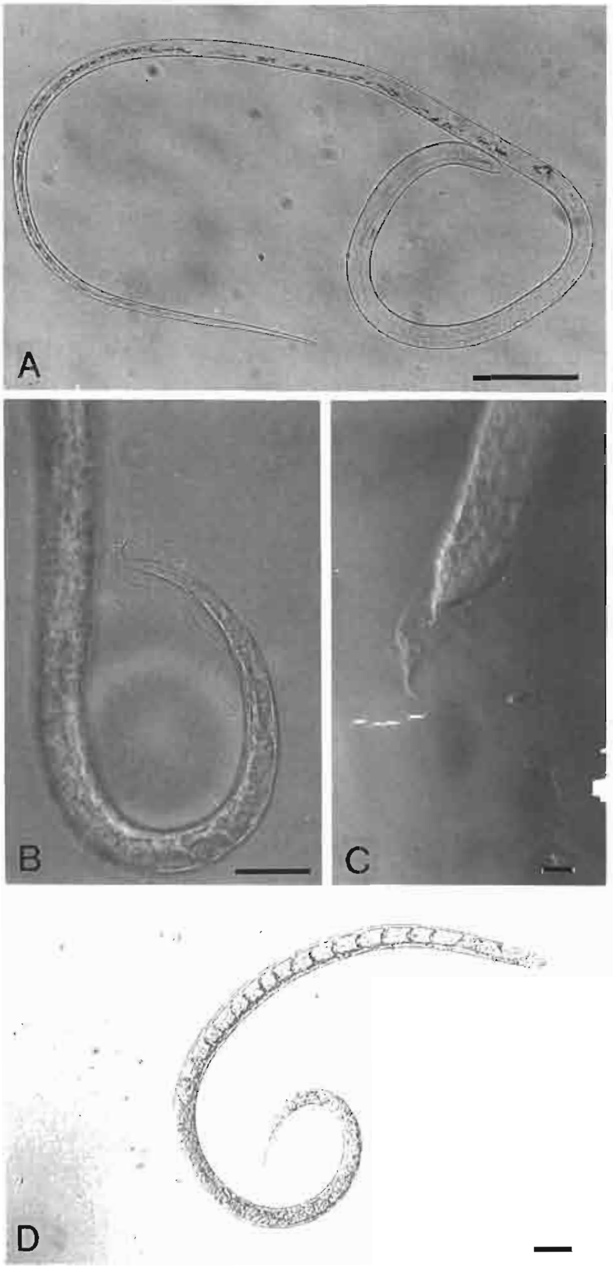

Fig. 5. Amphimermis acridiorum *n. sp. Parasitic juveniles. A : St. 2 (infective), whole body; B : St. 2 (parasitic) tail with ecdysed cuticle; C : Late stage St. 2 (parasitic) tail with ecdysed cuticle; D : St. 3 (parasitic). All from host* Phaulacridium vittatum. (Bar equivalent : A, D : 100 μm; B, C : 100 μm).

and western slopes of New South Wales in districts receiving both high summer rainfall and districts with marginal summer rainfall and an autumn maximum.

Amphimermis buraki * n. sp.

(Figs 6, 7)

MEASUREMENTS

Holotype (female) : L = 33 mm; mid-body diam. = 167 μm; head diam. (at level of cephalic papillae) = 53 μm, (at neck) = 54 μm; body diam. at nerve ring = 92 μm; cuticle width (at nerve ring) = 7 μm, (at mid-body) = 15 μm; hypodermis width (mid-body) = 6 μm; amphid aperture = 2 μm; amphid pouch (in dorsal view) = 13 × 8 μm; dist. nerve ring/mouth = 230 μm; V = 56.1; length of vagina (from vulva to junction with uterus) = 265 μm, (in dorsal view) = 200 μm; diam. vagina = 62 μm; length vulval flap = 95 μm; height of vulval cone = 25 μm; width of lateral hypodermal chord = 20 μm; diam. of uterine egg = 75-80 μm.

Allotype (male) : L = 16 mm; mid-body width = 89 μm; head width (at level of cephalic papillae) = 39 μm, (at neck) = 42 μm; body width at nerve ring = 70 μm; cuticle width, (at nerve ring) = 13 μm, (mid-body) = 15 μm; hypodermis width (mid-body) = 5 μm; amphid aperture = 6 μm; amphid pouch = 15 × 7 μm (in dorsal view), 17 × 20 μm (in lateral view); dist. nerve ring/mouth = 245 μm; spicule length = 810 μm; position of twisting = distal 69 per cent of length; spicule head width = 12 μm; width mid shaft = 5 μm; tail length = 142 μm; tail width at cloaca = 92 μm; position of proximal genital papilla anterior to cloaca = 307 μm; number of genital papillae = 58.

Paratypes (Females and males) : see Tables 2 and 3, respectively.

DESCRIPTION

General : Short nematodes, female 1.3 × length of male. Cuticle with cross fibres. Head bulbous. Cuticle anterior to head protoplasm extremely broad. Mouth terminal. Four submedial cephalic papillae; two lateral cephalic papillae. Opening of sub-medial cephalic papillae anterior to opening of lateral cephalic papilla, more pronounced in male than female. Large cup shaped amphids, larger in male than female; opening of amphids posterior to opening of lateral cephalic papillae and slightly offset. Six hypodermal chords. Wall of anterior end of oesophagus thickened to produce a short pharynx.

Females : Opening of vulva a transverse slit. Vulval flap present, rim thickened. Vulval cone present; base muscular and fused with terminal segment of vagina. Vagina S shaped, short, muscular; posterior loop × 1.5 length of anterior loop; bends extremely sharp. Junction of vagina and uterus well posterior to vulva. Tail conical, slightly curved ventrally. Tail bluntly rounded. No vestigial anus. Eggs in double row in uterus. Eggs unembryonated when laid.

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* *buraki,* aboriginal (Yarrowitch dialect) = hidden valley, alluding to limited distribution.

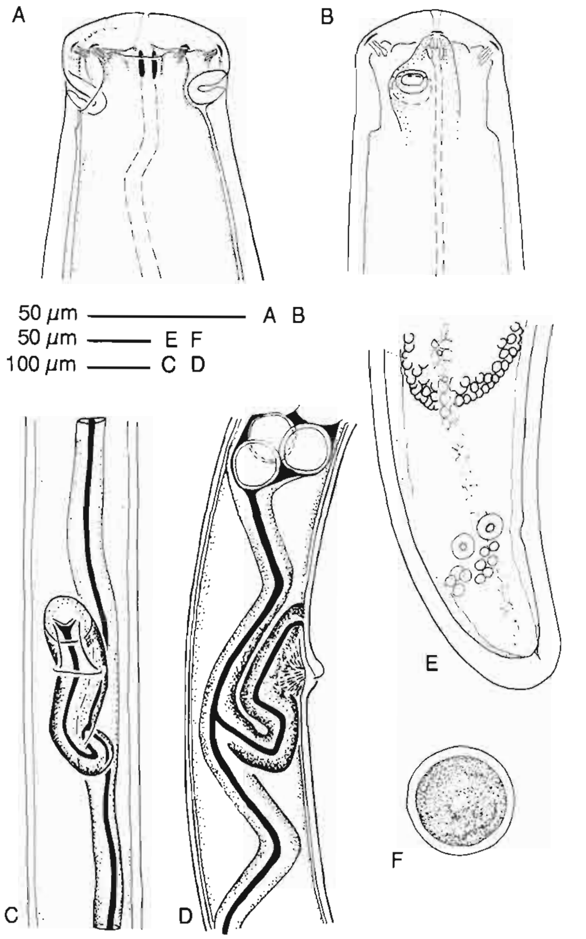

Fig. 6. Amphimermis buraki *n. sp. Female. A : Head, dorsal view; B : Head, lateral view; C : Vagina, ventral view; D : Vagina, lateral view; E : Tail, lateral view; F : Uterine egg.*

Males : Tail tightly curled into ring, conoid, bluntly round. Spicules paired; loosely twisted for distal two thirds of length (70 %); fused at tip, attenuated to fine point; head gently flared with pincer like terminus; wall thick proximal third, thin distal two thirds (twisted section); spicule length × 9 body width at cloaca, × 6 tail length. Genital papillae arranged in three rows, medial row marginally longer than submedial rows; distance of proximal genital papillae from cloaca × 0.4 length of spicule and × 2.2 tail length. Head more bulbous than female. Wall of amphid thin relative to that in female. Ducts of submedial cephalic papillae at acute angle to long axis of body, ducts of lateral cephalic papillae transverse.

TYPE HOST AND LOCATION

Conocephalus sp. (Orthoptera : Tettigoniidae). Kangaroo Flat, [31° 11′ S, 152° 07′ E], Yarrowitch, Northern Tablelands, New South Wales, Australia.

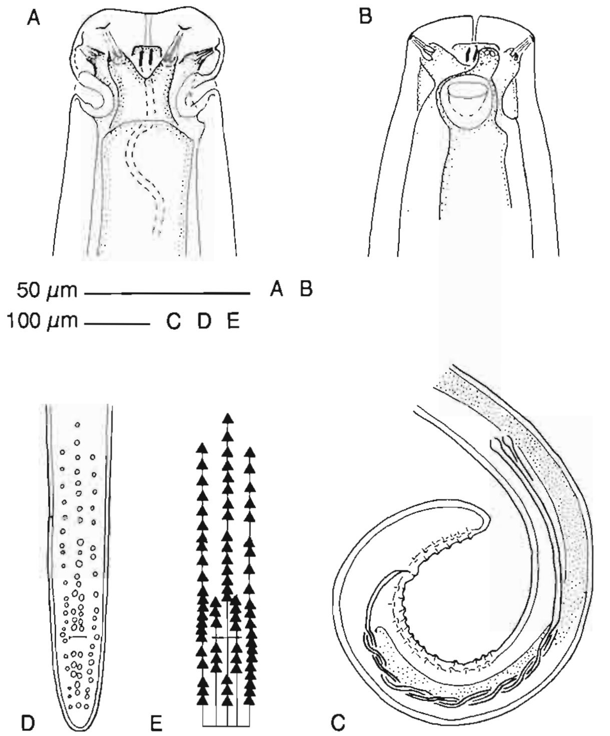

Fig. 7. Amphimermis buraki *n. sp. Male. A : Head, dorsal view; B : Head, lateral view; C : Tail, lateral view; D : Tail, ventral view; E : Schematic representation of genital papillae.*

TYPE MATERIAL

Holotype (female), *allotype* (male) in UCD. *Paratypes* (one female and one male) deposited in SAM and MNHN.

DIAGNOSIS AND RELATIONSHIPS

Male *A. buraki* n. sp. is distinguished from all previously described species of *Amphimermis* except *A. avoluta and A. acridiorum* n. sp. on the basis of the twisting configuration of the paired spicules, being twisted for the distal two thirds only, the proximal third being straight. *A. buraki* n. sp. differs from *A. avoluta* in that the body length is shorter (16-31 mm *vs* 57 mm); the spicule length is shorter (750-975 µm *vs* 2000 µm); the distal twisted portion of the spicules is a greater proportion of the total spicule length (70 *vs* 45 %); the spicule head is pincer-shaped rather than flared; the head is bulbous rather than bluntly rounded; the opening of the amphids is a substantial distance posterior to the lateral cephalic papillae rather than adjacent and *A. acridiorum* n. sp. in being shorter (16-31 mm *vs* 28-187 mm), the spicule length is shorter (750-975 µm *vs* 1775-3100 µm); the head is bulbous rather than bluntly rounded.

The female of *A. buraki* n. sp. is distinguished from all previously described species except *A. elongata, A. maritima* and *A. mongolica* on the lack of vestigial anus (excluding intersexuals) and form of the vagina : loop of vagina posterior to vulva greater length than anterior loop and junction of vagina and uterus posterior to vulva greater length than anterior loop and junction of vagina and uterus posterior to level of vulva. *A. buraki* n. sp. differs from *A. maritima* and *A. elongata* in having a relatively long vagina (greater than body width) and *A. mongolica* in having thick-walled amphids and the opening of the lateral cephalic papillae in close proximity to the opening of the submedial cephalic papillae.

Female *A. buraki* n. sp. differ from other species in the *avoluta* group in the following respects : *A. avoluta* in that body length is shorter (31-36 mm *vs* 125 mm); the head is bulbous rather than bluntly rounded; the opening of the amphids is well posterior to the lateral cephalic papillae rather than adjacent; the vagina is shorter (265-350 µm *vs* 950 µm); the junction of the vagina with the uterus is posterior to the vulva rather than anterior; uterine eggs generally smaller (75 × 80 µm *vs* 65 × 100 µm) : *A. acridiorum* n. sp. in being shorter (33 mm *vs* 241 mm); the form of the head (bulbous *vs* bluntly rounded); the length of the vagina (0.26 mm *vs* 1.2 mm); and differing in the relative length of the anterior and posterior loops (approximately equal *vs* anterior loop 1.3 × posterior loop).

The openings of the submedial and lateral cephalic papillae are on the same level in the females of both *A. buraki* and *A. avoluta* yet in the male of both species the opening of the lateral cephalic papillae is well posterior to the submedial cephalic papillae. This sexual dimorphism in regard to arrangement of cephalic papillae is not shared by other species of *Amphimermis*.

Amphimermis mirabinda * n. sp.
(Figs 8, 9)

MEASUREMENTS

Holotype (female) : L = 113 mm; mid-body diam. = 270 µm; head diam. (at level of cephalic papillae) = 65 µm, (at neck) = 78 µm; body diam. at nerve ring = 120 µm; cuticle width (at nerve ring) = 10 µm, (at mid-body) = 27 µm; hypodermis width (mid-body) = 12 µm; amphid aperture = 7 µm; amphid pouch 23 × 14 (in dorsal view); dist. nerve ring/mouth = 312 µm; V = 49.5; length vagina (from vulva to junction with uterus) = 975 µm, (in dorsal view) = 540 µm; length vulval flap = 75 µm; height vulval cone = 45 µm; width lateral hypodermal chord = 25 µm; diam. egg in uterus = 77-82 × 100-102 µm.

Allotype (male) : L = 36 mm; mid-body diam. = 117 µm; head diam. (at level of cephalic papillae) = 52 µm, (at neck) = 55 µm; body diam. at nerve ring = 87 µm; cuticle width (at nerve ring = 15 µm), (mid-body) = 25 µm; hypodermis width (mid-body) = 14 µm; amphid aperture = 8 µm; amphid pouch = 20 × 15 µm (in dorsal view), 21 × 21 µm (in lateral view); dist. nerve ring/mouth = 255µm; spicule length = 1199 µm; position of twisting from tip = 10.4 to 54.2 and 80.2 to 97.1 % spicule length; spicule head width = 14 µm; spicule width mid-shaft = 5µm; tail length = 165 µm; tail diam. at cloaca = 100 µm; position of proximal genital papilla anterior to cloaca = 587 µm; number of genital papillae = 62.

Paratypes (Females and males) : see Table 2 and 3, respectively.

Juvenile, st. 2 (pre-parasitic) (n = 5) : L = 1.44 mm (1.40-1.53); mid body diam. = 15 (nil range); head diam. : 12 µm (nil range); buccal cavity length = 20 µm (nil range); stylet = 26 µm (25-28); dist. nerve ring/mouth = 108 µm (100-115); body diam. at nerve ring =

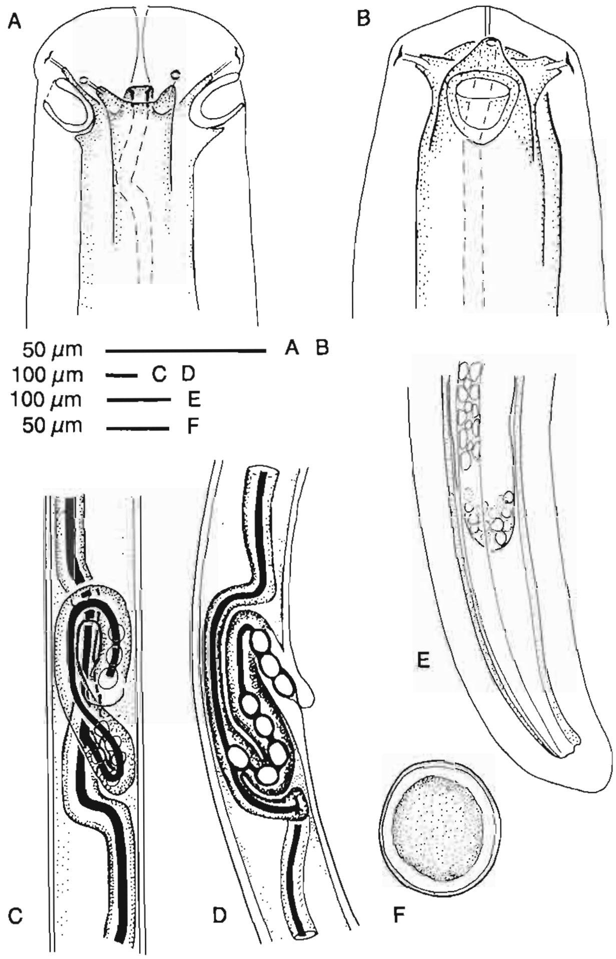

Fig. 8. Amphimermis mirabinda *n. sp. Female. A : Head, dorsal view; B : Head, lateral view; C : Vagina, ventral view; D : Vagina, lateral view; E : Tail, lateral view; F : Uterine egg.*

* *mirabinda,* aboriginal (Nembo dialect) = place with running water, alluding to habitat.

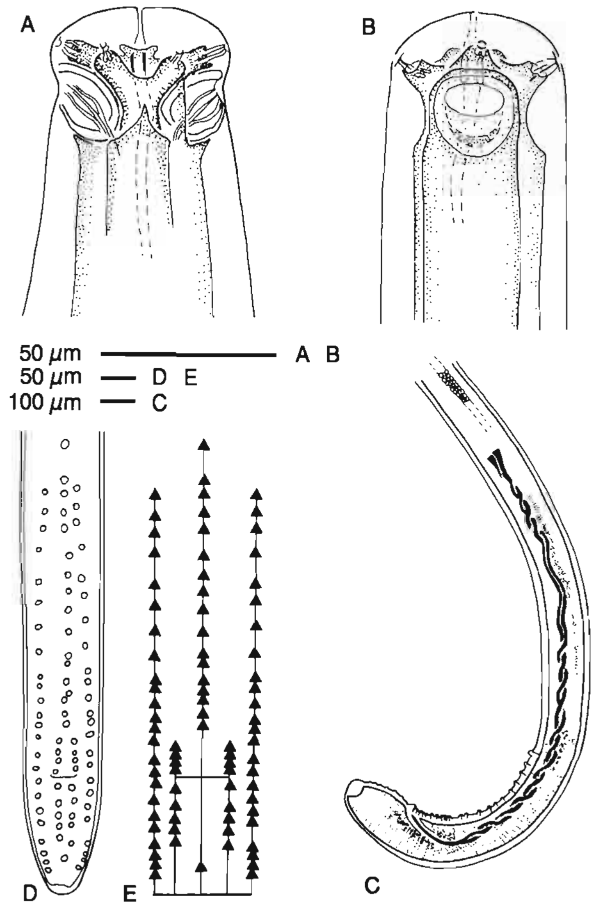

Fig. 9. Amphimermis mirabinda *n. sp. Male. A : Head, dorsal view; B : Head, lateral view; C : Tail, lateral view; D : Tail, ventral view; E : Schematic representation of genital papillae.*

15 (nil range); position of stichosome : proximal end = 13.7 % (13.3-14.8), distal end = 62 % (60-63) body length; body diam. mid-stichosome = 17 µm (nil range); mid-trophosome = 15 µm (nil range); length of tail = 56.6 µm (44-70); tail diam. (50 µm from tip) = 6 µm (nil range).

DESCRIPTION

General: Medium length nematodes, females 1.2-3.1 × length of male. Cuticle with cross fibres. Mouth terminal. Four submedial cephalic papillae; two lateral cephalic papillae. Opening of submedial cephalic papillae posterior to opening of lateral cephalic papillae in both males and females. Enormous amphids, larger in male than female; opening of amphids posterior to opening of lateral cephalic papillae. Six hypodermal chords. Wall of anterior end of oesophagus thickened to produce a short pharynx.

Females : Opening of vulva a transverse slit. Vulval flap large, rim thickened to appear bulbous in lateral view. Vagina S-shaped, anterior and posterior loops of equal prominence. Junction of vagina and uterus posterior to vulva. Distal uterus with transversely looped segment immediately posterior to vagina. Tail conoid, slightly curved ventrally. Uterine eggs in double row. Eggs unembryonated when laid.

Males : Tail-shaped (a feature shared with *A. bogongae*), conoid, terminus bulbous. Spicules long, fine, paired; loosely twisted for proximal fifth of length and distal half of length; tips fused, attenuated to a fine point; head gently flared with pincer like terminus; spicule length 12 × body width at cloaca, 7-9 × tail length. Genital papillae arranged in three rows, medial row marginally larger than submedial rows; distance of proximal genital papillae from cloaca 0.3-0.48 × length of spicule and 2.6-3.5 × tail length.

Juvenile, st. 2 (preparasitic) : Short, slender. Proximal half of body broader than distal half. Cephalic papillae distinct. Stylet barbed on one side. Trophosome interspaces indistinct. Tail attenuated to a fine point. Similar to *A. acridiorum* n. sp. preparasitic juvenile in many respects differing in the slightly greater length of the stylet, a more pronounced thickening of the tip of the stylet and elongated stichocytes.

TYPE HOST AND LOCATION

Phaulacridium vittatum (Sjöstedt) (Orthoptera : Acrididae). Jingera [35° 45′ S, 149° 26′ E], Southern Tablelands, New South Wales, Australia.

TYPE MATERIAL

Holotype (female) and *allotype* (male) in UCD. *Paratypes* (one female and one male) deposited in SAM and MNHN.

DIAGNOSIS AND RELATIONSHIPS

Male *A. mirabinda* n. sp. differs from all species in the *bogongae* group *(A. bogongae, A. tinyi, A. maritima, A. litoralis, A. bonaerensis)* by having enormous amphids (width approximately half head diameter). The body length of *A. mirabinda* is comparable to that of *A. maritima* and *A. litoralis*. However, the spicule is considerably shorter (1199-2380 *vs* 2200 and 3400 µm, respectively) and position of proximal papilla as a proportion of spicule length (30-48 *vs* 19 %). *A. mirabinda* n. sp. also differs from *A. bogongae* in having larger amphids and a more bulbous tail.

Female *A. mirabinda* n. sp. can be distinguished from all other species except *A. bonaerensis* and *A. bogongae* by the form of the vagina (anterior and posterior loops of equal prominence and junction of vagina and uterus posterior to level of vulva). *A. mirabinda* n. sp. differs from *A. bonaerensis* in lacking a vulval flange, though this may not be a good diagnostic character (see discussion), and from *A. bogongae* in length (51-113 *vs* 160-

205 mm), egg diameter (102 *vs* 140 μm) and width of lateral hypodermal chord (25 *vs* 100 μm).

DISTRIBUTION

Apart from the type location, *A. mirabinda* n. sp. has been reared from *P. vittatum* collected in the Central Tablelands (Oberon) and has been collected ex soil in the Hunter Valley (Gundy, April 1989, R. Pigott).

***Amphimermis australoelegans* n. sp.**
(Figs 10-11)

MEASUREMENTS

Holotype (female) : L = 123 mm; mid-body diam. = 250 μm; head diam. (at level of cephalic papillae) = 85 μm, (at neck) = 83 μm; body diam. at nerve ring = 117 μm; cuticle width, (at nerve ring) = 10 μm, (at mid-body) = 12 μm; hypodermis width, mid-body = 25 μm; amphid aperture = 8 μm; amphid pouch : (in lateral view) = 35 × 5 μm, (in dorsal view) = 35 × 25 μm; dist. nerve ring/mouth = 350 μm; V = 48.8 length vagina (from vulva to junction with uterus) = 1500 μm, (in dorsal view) = 870 μm; length vulval flap = 105 μm; height vulval cone = 50 μm; width lateral hypodermal chord = 37 μm; diam. uterine egg = 65-70 μm.

Allotype (male) : L = 62 mm; mid-body diam. = 165 μm; head diam. (level of cephalic papillae) = 63 μm, (at neck) = 65 μm; body diam. at nerve ring = 100 μm; cuticle width (at nerve ring) = 18 μm, (mid-body) = 23 μm; hypodermis width (mid-body) = 8 μm; amphid aperture = ill defined; amphid pouch = 43 × 12 μm (in dorsal view), 43 × 32 μm (in lateral view); dist. nerve ring/mouth = 295 μm; spicule length = 1711 μm; position of twisting = 15.3-59.1 and 69.4-94.9 % of length; spicule head width = 23 μm; width mid-shaft = 9 μm; tail length = 260 μm; tail at cloaca = 155 μm; position of proximal genital papilla anterior to cloaca = 887 μm; number of genital papillae in medial row (anterior to cloaca) = 37, (posterior to cloaca) = 10.

Paratypes (Females and males) : see Tables 2 and 3, respectively.

DESCRIPTION

General : Medium sized nematodes, female 2 × length of males. Cuticle with cross fibres. Head bluntly rounded. Mouth terminal. Head with four submedial cephalic papillae and two lateral cephalic papillae. Opening of submedial cephalic papillae posterior to opening of lateral cephalic papillae. Amphids large, thin walled, irregular shaped cuticular incursion into head protoplasm. Opening of amphids indistinct. Six hypodermal chords.

Females : Opening of vulva a transverse slit. Vulval flap thickened to form a semicircular rim anterior to vulva and extending posteriorly around edge of vulva. Post laying, cytoplasmic extrusions may modify the form of the ring to produce a flange. Vagina S-shaped and relatively long in relation to body width; posterior loop 4 × length of anterior loop; walls uniformly thin. Junction of vagina and uterus slightly posterior to the position of the vulva. Tail tapered to a point. No vestigial anus. Eggs in up to four rows in uterus. Eggs relatively small, unembryonated when laid.

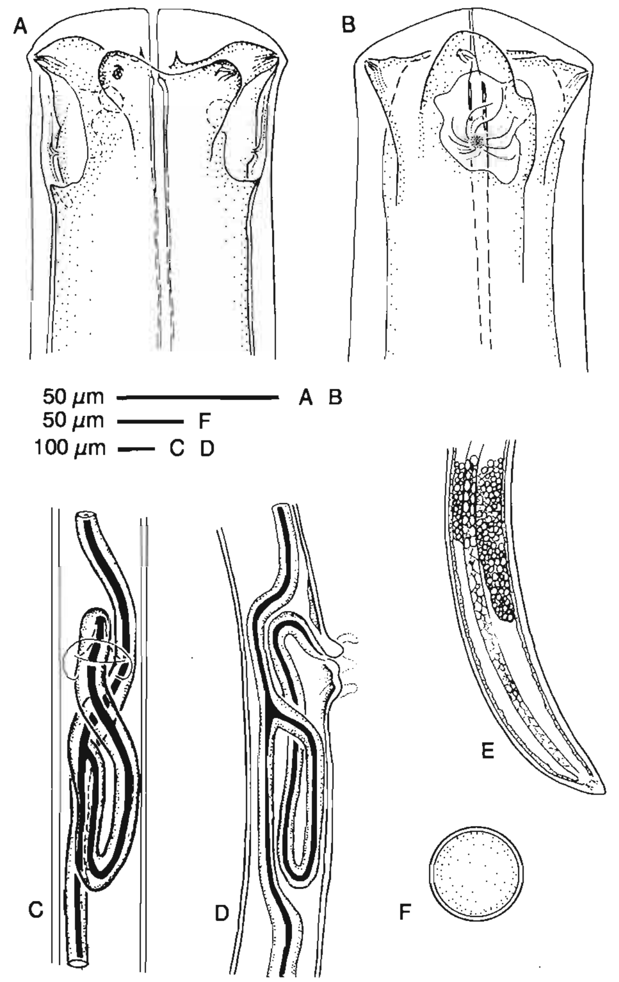

Fig. 10. Amphimermis australoelegans *n. sp. Female. A : Head, dorsal view; B : Head, lateral view; C : Vagina, ventral view; D : Vagina, lateral view; E : Tail, lateral view; F : Uterine egg.*

Males : Tail curled into a ring, flat ventrally, pointed. Spicules paired, tightly twisted except for one sixth of length from tip and a small section at one third of length from proximal end; head flared, ventral flare shorter than dorsal flare; walls thick uniformly along length; spicule length approximately 11 × body width at cloaca, 6.5 × tail length, 27 % body length. Genital papillae arranged in three rows median row marginally longer than sub-medial rows; medial row bifurcate anterior and

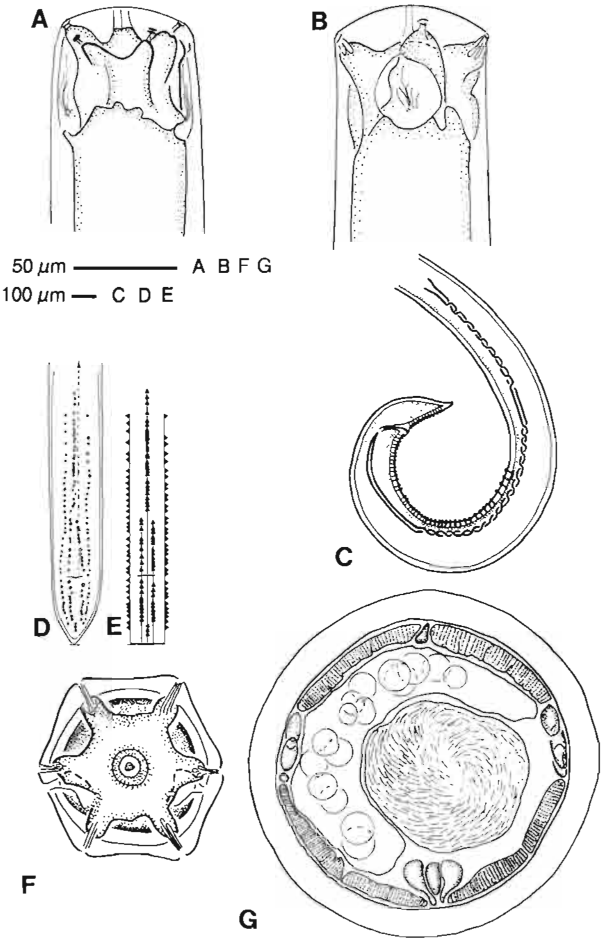

Fig. 11. Amphimermis australoelegans *n. sp. Male. A : Head, dorsal view; B : Head, lateral view; C : Tail, lateral view; D : Tail, ventral view; E. Schematic presentation of genital papillae; F : Head,* en face; *G : Mid-body, cross section.*

posterior to cloaca; distance of proximal genital papilla anterior to cloaca = 0.5 × spicule length and 3.4 × tail length.

Type host and location

Phaulacridium vittatum (Sjöstedt) (Orthoptera : Acrididae). Kangaroo Flat [° 11′ S, ° 07′ E], Yarrowitch, Northern Tablelands, New South Wales, Australia.

Type material

Holotype (female) and *allotype* (male) and 3 paratype males in UCD. *Paratypes* (one female and two males) deposited in SAM and MNHN.

Diagnosis and relationships

Male *A. australoelegans* n. sp. has characteristic amphids and twisting of the spicule which separates it from all species except *A. elegans, A. zuimushi, A. tongaensis* and *A. artyukhovski* n. sp. *A. australoelegans* n. sp. differs from *A. elegans* in regard the form of the tail (conoid with pointed terminus in *A. australoelegans vs* bluntly rounded in *A. elegans*), having greater number of anal papillae anterior to cloaca (24-37 *vs* 13), in form of spicule twisting (proportionally short straight section mid-spicule *vs* long straight section mid-spicule) and spicule tip (attenuated to a fine point *vs* relatively blunt); *A. zuimushi* in having a relatively short body length in relation to spicule length (× 23-30 *vs* 40-60) and with regard to the position of the proximal anal papilla (approximately 30 % of spicule length in *A. australoelegans* n. sp. *vs* approximately 60 % in *A. zuimushi*); *A. tongaensis* in greater body length (31-64 mm *vs* 20-32 mm) and form of the amphids (sensilla core centrally placed *vs* on outer rim) and size of the amphids in lateral view (one third diameter of head *vs* two thirds diameter of head) and *A. artyukhovskii* n. sp. in the shape of the tail (pointed *vs* bluntly rounded).

The female of *A. australoelegans* n. sp., like the male, has characteristic amphids which separate it from all species except *A. elegans, A. zuimushi* and *A. artyukhovskii* n. sp. The female of *A. tongaensis* is unknown. *A. australoelegans* n. sp. differs from *A. elegans* with regard to range of body length (91-205 mm in *A. australoelegans* n. sp. *vs* 145-260 mm in *A. elegans* (Hagmeier, 1912; Kirjanova *et al.* 1959); *A. zuimushi* with regard to vagina length in relation to body width (780 and 256 µm respectively in *A. australoelegans* n. sp. *vs* 800 and 350 µm respectively in *A. zuimushi*) and thickness of wall of anterior loop of vagina (thin *vs* thick) and *A. artyukhovskii* n. sp. in relative thickness of vagina wall (thin *vs* thick).

Host range

In addition to the type host, *A. australoelegans* n. sp. has been recorded from the following hosts : *Chortoicetes terminifera* (Walker) (Orthoptera : Acrididae) : one male and one female reared from adult host, Weldon Lane, Moree, May 10, 1988, R. Pigott, and *Sericesthis* sp. (Coleoptera : Scarabaeidae) : Melolonthinae) : one female reared from late instar host larva, Hernani, March 14, 1985, A. J. Campbell.

Distribution

Apart from the type locality *A. australoelegans* n. sp. has been recorded from Hernani (ex *Sericesthis* sp.) and Moree (ex *C. terminifera*). The species would appear to be restricted to relatively warm districts with high summer rainfall.

Amphimermis artyukhovskii n. sp.

= *A. elegans apud* Artyukhovski & Kharchenko, 1965.

A. elegans, sensu Artyukhovski & Kharchenko (1965), is considered a distinct species on the basis of the high number of genital papillae anterior to cloaca, and the more rounded (bulbous) tail. The hosts also differ significantly (Lepidoptera *vs* Orthoptera). The material is assigned the new name *artyukhovskii* n. sp. The male of *A. australoelegans* n. sp. differs from *A. artyukhovskii* n. sp. in having fewer genital papillae anterior to cloaca, and a tail with a more pointed terminus. The female of *A. australoelegans* n. sp. differs from *A. artyukhovskii* n. sp. in the form of the vagina (long and thin walled *vs* relatively short and thick walled). The male of *A. artyukhovskii* n. sp. most closely resembles *A. zuimushi* differing from this species only in the relative length of the spicule in relation to body length. The male *A. elegans* illustrated in Kiryanova *et al.* (1959) has a rounded tail similar to that illustrated for *A. elegans* in Artyukhovski and Kharchenko (1965), which is much more rounded than that illustrated by Hagmeier (1912) for *A. elegans*. However, it is similar to *A. elegans* in respect to number of genital papillae and position of proximal genital papillae, differing from the material of Artyukhovski and Kharchenko (1965) and *A. australoelegans* n. sp. in both these respects. The differences are not considered sufficient to erect a new species as has been done for the material of Artyukhovski and Kharchenko (1965).

Key to males of the genus *Amphimermis* (Figs 12-15)

1. – Spicule twisted entire length (= *volubilis* group) .... *volubilis*
   – Spicule twisted for only part of length 2
2. – Proximal half of spicule untwisted (= *avoluta* group) 3
   – Spicule twisted distal and proximal ends with straight section in middle 5
3. – Body short (< 30 mm), spicule length 750-975 μm, terrestrial .... *buraki* n. sp.
4. – Amphid opening at level of lateral cephalic papilla .... *avoluta*
   – Amphid opening posterior to lateral cephalic papilla .... *acridiorum* n. sp.
5. – Amphid indistinct, amphidial pore (opening) small : a thin walled pocket in cuticle (= *elegans* group) 6
   – Amphid distinct, amphidial pore medium-large : a thick walled, cup-shaped incursion into head cytoplasm (= *bogongae* group) 10
6. – Amphid diameter greater than two thirds head width .... *tongaensis*
   – Amphid diameter less than half head width 7
7. – Distance proximal anal papillae to cloaca > 60 % spicule length 8
   – Distance proximal anal papillae to cloaca < 60 % spicule length 9
8. – Spicule 1020-1450 μm. Body 42-88 mm .... *zuimushi*
   – Spicule 1600-1800 μm. Body 26-53 mm. Tail conoid, rounded .... *artyukhovskii* n. sp.
9. – Tail bluntly rounded .... *elegans*
   – Tail conoid, pointed terminus .... *australoelegans* n. sp.
10. – Body short (11-17 mm), spicule 700-860 μm, aquatic .... *tinyi*

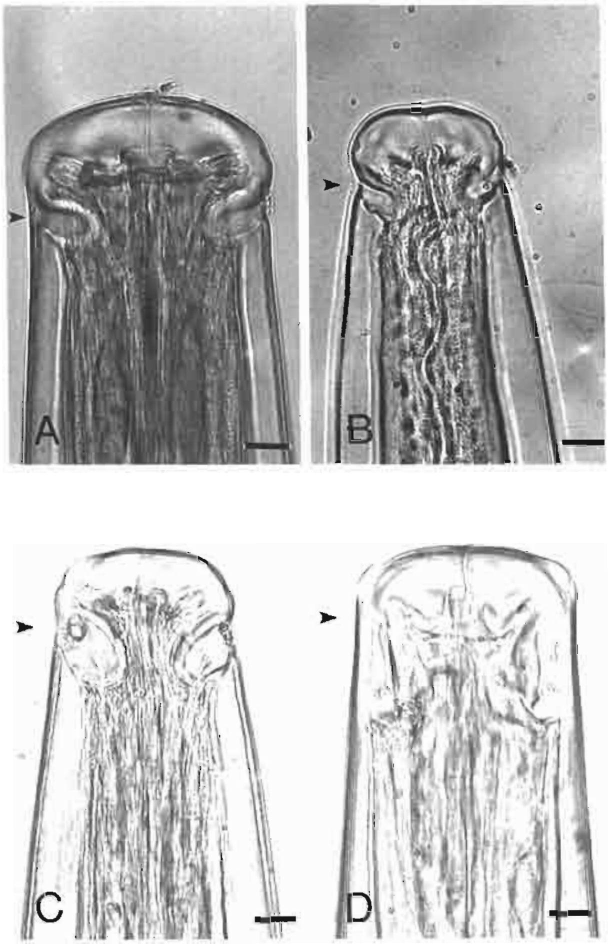

Fig. 12. Amphimermis *spp. Males; Head, dorsal view showing form of amphid and position of amphidial pore (arrow). A :* A. acridiorum *n. sp.; B :* A. buraki *n. sp.; C :* A. mirabinda *n. sp.; D :* A. australoelegans *n. sp.* (Bar = 10 μm).

   – Body medium-long (30-123 mm), terrestrial 11
11. – Body short (30-70 mm) 12
   – Body long (70-123 mm) 13
12. – Spicule long (2900-3600 μm) in relation to body length (45-70 mm) .... *litoralis*
   – Spicule medium (1200-2200 μm) 14
13. – Tail bluntly rounded, distance of proximal papillae from cloaca = 20 % of spicule length .... *bogongae*
   – Tail pointed, distance proximal papillae to cloaca ≥ spicule length .... *bonaerensis*
14. – Spicule 1200-1500 μm. Body 35-42 mm *mirabinda* sp. n.
   – Spicule 2,200 μm. Body 53 mm .... *maritima*

Key to females of the genus *Amphimermis*
(Figs 1 B; 10 B, C, D; 16)

1. – Amphids indistinct, thin-walled pear shaped pocket in cuticle 2

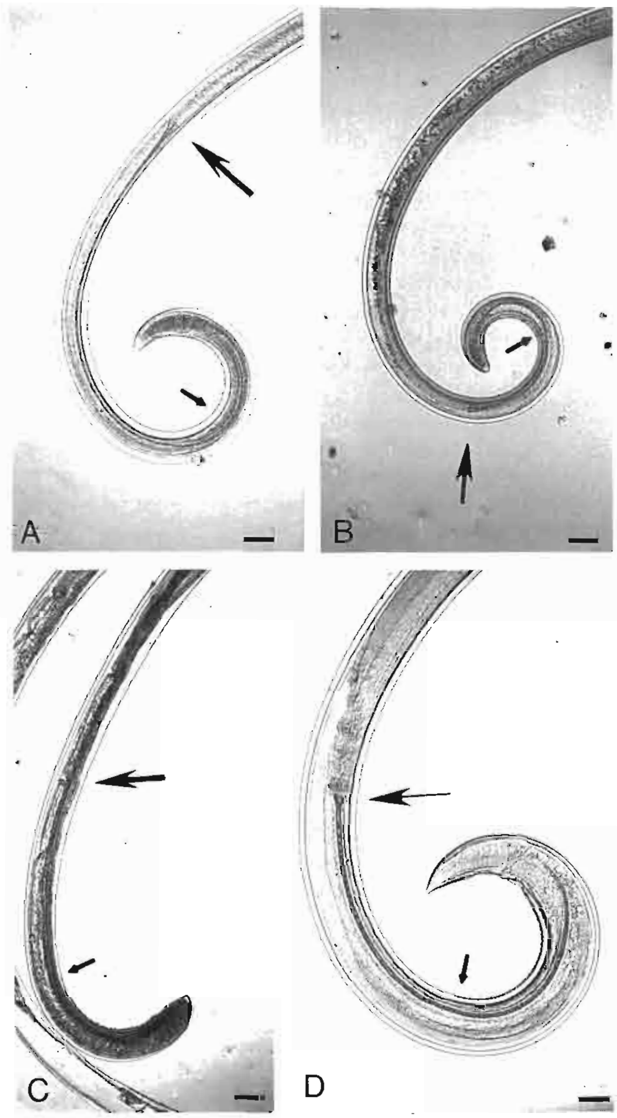

Fig. 13. Amphimermis *spp. Males; Proximal tips of spicules (large arrow) in relation to position of proximal genital papillae (small arrow). A :* A. acridiorum *n. sp.; B :* A. buraki *n. sp.; C :* A. mirabinda *n. sp.; D :* A. australoelegans *n. sp.* (Bar = 100 μ).

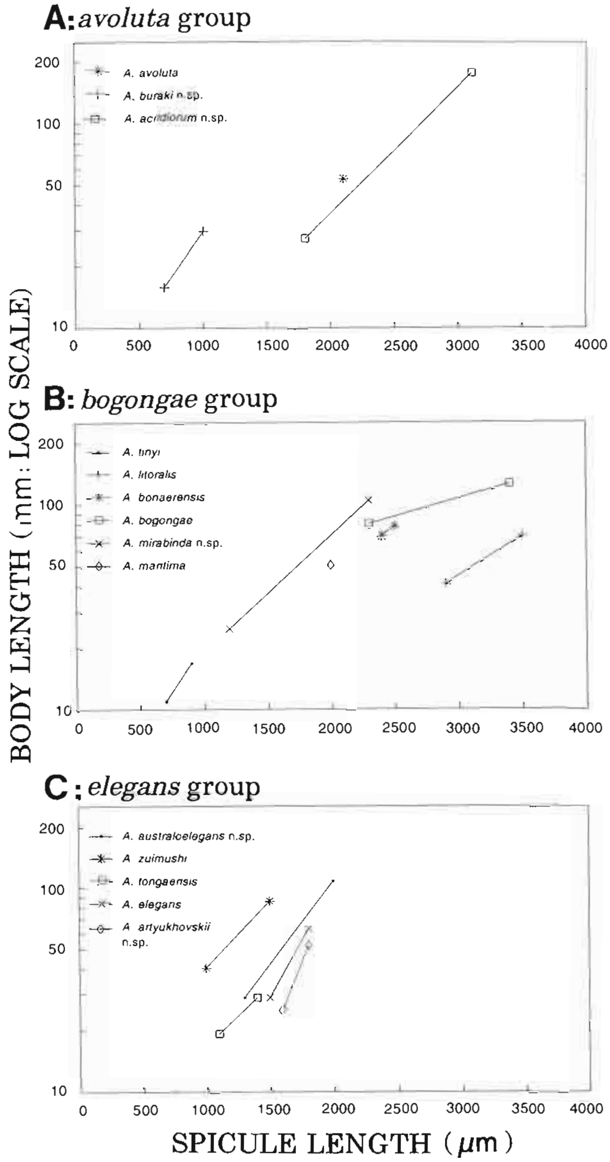

Fig. 14. The relationship between body length and spicule length for male Amphimermis *spp. A :* avoluta *group; B :* bogongae *group; C :* elegans *group.*

– Amphids distinct, thick-walled cup shaped incursion into head protoplasm 4

2. – Vagina long (1.5 mm), thin walled .... *australoelegans* n. sp.
– Vagina short-medium length (0.5-0.9 mm), thick walled 3

3. – Vagina medium length (0.9 mm) .... *zuimushi*
– Vagina short (0.5 mm) 15

4. – Anterior loop of vagina of equal or greater length than posterior loop 5
– Anterior loop of vagina shorter than posterior loop . 8

5. – Anterior loop greater length than posterior loop 6
– Anterior loop equal to posterior loop 7

6. – Vagina medium (0.5 mm) .... *avoluta*
– Vagina long (0.7 mm) .... *volubilis*

7. – Vagina short and broad (in lateral view) 16
– Vagina long and narrow (in lateral view) *acridiorum* n. sp.

8. – Posterior loop of vagina less than or equal to 3 fold length of anterior loop 9
– Posterior loop of vagina greater than 3 fold length of anterior loop 14

9. – Junction of vagina and uterus at level of vulva 10
– Junction of vagina and uterus posterior to level of vulva 11

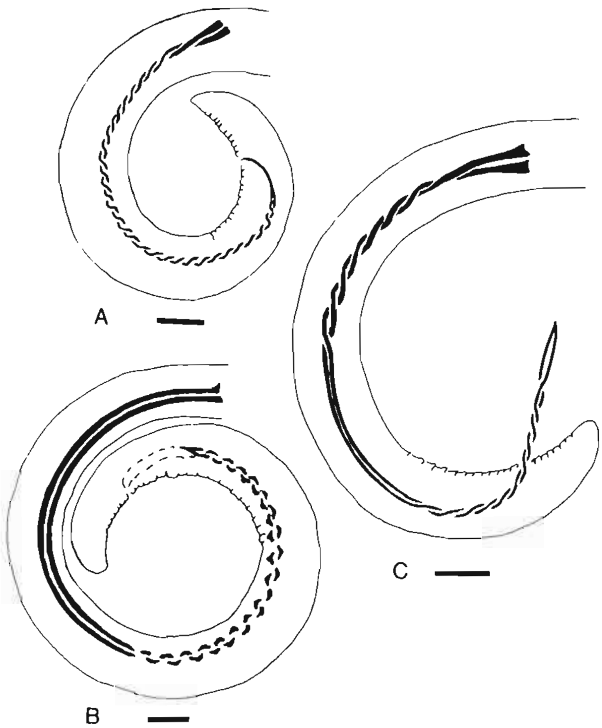

Fig. 15. Variations in the form of the spicule in Amphimermis *males. A :* A. volubilis *(after Rubtsov and Koval, 1975); B :* A. avoluta *(after Rubtsov and Koval, 1975); C :* A. elegans *(after Hagmeier, 1912)* (Bars = 100 μm).

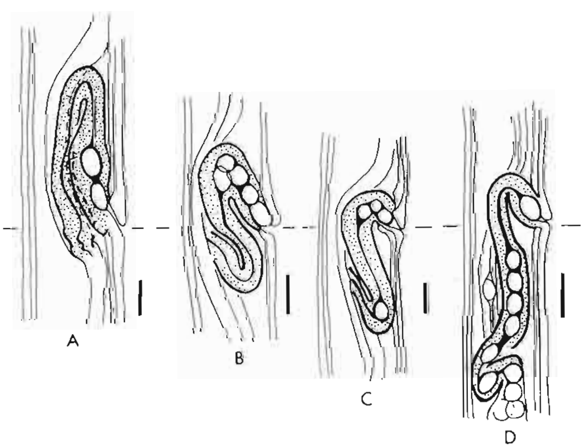

Fig. 16. Variations in the form of the vagina in Amphimermis *females. A :* A. avoluta *(after Rubtsov and Koval, 1975); B :* A. bogongae *(after Welch, 1963); C :* A. mongolica *(after Rubtsov, 1976* b*); D :* A. longiscapus *after Rubtsov, 1976* a*)* (Bars = 100 μm).

10. – Body length 30 mm, aquatic .... *tinyi*
   – Body length 110 mm, terrestrial .... *litoralis*
11. – Vagina length equal to mid-body width 12
   – Vagina length greater than mid-body width 13
12. – Junction of vagina and uterus at an acute antero-ventral angle .... *elongata*
   – Junction of vagina and uterus at an obtuse antero-ventral angle .... *maritima*
13. – Amphids thin-walled, situated in neck region with opening well posterior to lateral head papillae ..... *mongolica*
   – Amphids thick-walled, situated anterior to neck region with opening immediately posterior to lateral head papillae .... *buraki* n. sp.
14. – Amphids situated anterior to neck region with opening immediately posterior to lateral head papillae. Body 43 mm .... *longiscapus*
   – Amphids situated in neck region with opening well posterior to lateral head papillae. Body 74 mm ... *lagidzae*
15. – Body length 36-190 mm .... *artyukhovskii* n. sp.
   – Body length 195-260 mm .... *elegans*
16. – Vulva with flanges .... *bonaerensis*
   – Vulva without flanges 17
17. – Medium sized amphids in relation to head diameter, thick-walled .... *bogongae*
   – Large amphids in relation to head diameter, thin-walled .... *mirabinda* n. sp.

Discussion

Stage and sex of the host may have a substantial impact on subsequent adult length (Herron & Baker, 1991) even within a single host species. Similarly, the physical environment may have an indirect impact on development (Baker & Holmes, 1986). Such plasticity impacts on many aspects of morphology and reduces the availability of stable diagnostic characters. Given the intraspecific variation which may occur, the species described in this paper are further discussed.

The body and spicule length of *A. buraki* n. sp. is at the low extremity of a continuum which includes all species in the *avoluta* group (Fig. 14). As such this species could be regarded simply as small specimens of *A. acridiorum* n. sp., the small size induced by development in a small alternative host. *A. buraki* n. sp. was only recorded in the 1984-85 season which received above average rainfall resulting in rank pastures which favoured grass-seed feeding tettigoniids such as *Conocephalus* sp. but was coincident with very low densities of acridids following the collapse of the 1979-1982 outbreak of *P. vittatum* (Baker, 1992). The coincidence of a temporal change in abundance with an inversion in the relative abundance of two potential alternative hosts implies a host induced change in size of a single species. However, *A. buraki* n. sp. has only been recorded from the Kangaroo Flat area of the Northern Tablelands. If simply a host induced aberrant sized *A. acridiorum* n. sp. then both forms would be expected to have a similar distribution. However, despite equally exhaustive sampling at other sites within the distribution of *A. acridiorum* n. sp. the smaller *A. buraki* n. sp. has not been recorded. Differences possessed by *A. buraki* n. sp. which are not readily attributable to host size are the much steeper slope of the relationship between spicule length and body length and morphological characters such as head form and relative position of head papillae openings.

A. acridiorum n. sp. is closely related to *A. buraki* n. sp. and represents the upper limit of a continuum in regard many morphological features. However, the configuration of the spicule in the aberrant form of *A. acridiorum* n. sp. tends towards that of *A. bogongae* and the aberrant form of *A. acridiorum* n. sp. may represent a sibling species which is the phylogenetic precursor of both *A. bogongae* and *A. bonaerenis* as well as being the phylogenetic link between the *avoluta* and *bogongae* groups of *Amphimermis*.

Three specimens designated as *A. acridiorum* n. sp. in Fig. 4, which were collected from soil in the Hunter Valley, have not been included in the range of dimensions given in Table 3. Their extremely short spicules sets them apart from other specimens of *A. acridiorum* n. sp. and they may represent a new species.

In many respects, the difference between *A. mirabinda* n. sp. and *A. bogongae*, both males and females, is one of size only, *A. bogongae* being the larger species. However, *A. mirabinda* n. sp. is considered as a distinct species as the width of the lateral hypodermal chord is disproportionately broad in *A. bogongae*. Also, the head protoplasm in *A. bogongae* is more extensive and the head papillae much less pronounced.

The size difference between *A. mirabinda* n. sp. and *A. bogongae* could be attributed to development of *A. bogongae* in a smaller host. However, mitigating against their being conspecific in the fact that differences in host size, although affecting female length is rarely a limiting factor in determining the length of males.

A. mirabinda n. sp. is restricted to the Southern Tablelands and Hunter Valley, both districts which have relatively low summer rainfall. In *A. mirabinda* n. sp. the relationship between the body length and spicule length is at the lower end of the range for *A. bogongae* and overlaps to some extent. However, the species are separated by habitat, *A. bogongae* being found in hibernating moths occuring only in rock crevices and caves at high altitudes. In May 1990 the acridid *Kosiuscola cognatus* Rehn was collected at the type locality of *A. bogongae* (Mt Gingara, ACT, Australia) and found to be parasitised by a species of *Amphimermis* which unfortunately was not reared to the adult stage. Comparison of the DNA of the parasitic juveniles with that of *A. bogongae* and *A. mirabinda* n. sp. adults should confirm if *A. bogongae* has acridids as alternative hosts of if *A. mirabinda* n. sp. has a wide geographic range or a further undescribed species of *Amphimermis* occurs at high altitude and has an acridid host (J. Curran pers. comm.).

The genus *Amphimermis*, as with the majority of mermithid genera, is ubiquitous being represented on all continents except Africa and Antarctica.

The apparent discontinuity in the distribution of the closely related *A. elegans* and *A. australoelegans* n. sp. with dissimilar species in the intervening geographic regions (*A. artyukhovskii* n. sp. in Central Asia, *A. zuimushi* in South-East Asia and *A. tongaensis* in Tonga) may indicate that *A. australoelegans* n. sp. represents convergent host adaptation by a formerly widespread *elegans* group progenitor in the Asian region. No species belonging to the *elegans* group have been recorded from North and South America or Africa and it is likely the group originated in Central Asia and spread to Australia after the fusion of the Australian and Indonesian tectonic plates in the mid Miocene period. As *A. australoelegans* n. sp. is distributed in temperature regions with a summer rainfall maxima, colonisation of Australia by the species progenitor was most likely from the north and may have coincided with invasion of large tropical Acridinae (i.e. *Locusta, Gastrimargus*) and Crytacanthacridinae (i.e. *Nomadacris*) which took place in recent (Pleistocene) times (Key, 1959).

Of the species groups erected in this paper, endemicity is greatest in the primitive *avoluta* group. The *avoluta* group is considered the most primitive group because of the relatively simple arrangement of the spicule twisting. The coincidence of both primitiveness and a high level of speciation in this group in Australia could indicate an Australian origin. The *bogongae* group is only slightly more evolved than the *avoluta* group but again shows a high level of speciation and specialisation of host and habitat in Australia. Two species in this group, *A. bonaerensis* and *A. mirabinda* n. sp. are parasitoids of Orthopterans in South America and Australia respectively. This could again indicate origin in Australia with a spread from Australia during the Upper Cretaceous period as far as Eurasia with adaptation to Orthoptera taking place prior to this spread with more recent adaptation to alternative hosts in Eurasia.

The speciation of both the *avoluta* and *bogongae* groups in Australia may have been in response to conditions favouring both host and nematode during the Tertiary period. There was a proliferation of grasslands during the Eocene and Oligocene epochs of the Tertiary period and it was during this period that the acridid fauna proliferated, especially the subfamily Catantopinae (Key, 1959). The Catantopinae today are represented by species restricted to moist, alpine habitats (Key, 1986) coincident with the distribution of *Amphimermis* spp.

The increasing aridity during the Pliocene, Pleistocene and Holocene epochs would be expected to have restricted the distribution of both the acridid and mermithid fauna to refugia. The high level of speciation in the *avoluta* group in Australia with orthopterans as host was most probably the result of disparate evolution in the few isolated grasslands present in the moist, upland areas of south eastern Australia. The currently evident sympatry between endemic *Amphimermis* spp. may have been achieved post-European settlement, following the creation of contiguous grasslands through the extensive clearing of forest for grazing. Under this scenario, competition between formerly allopatric species may ultimately reduce species richness. The implicit associated loss of biological diversity could reduce the capability of residual *Amphimermis* spp. to adapt to changing climatic conditions and consequently impair their ability to suppress acridid host populations.

Acknowledgments

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