Agamermis catadecaudata n. sp. (Nematoda : Mermithidae), a parasitoid of Orthoptera in south-eastern Australia

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Accepted for publication 22 April 1994.

Summary - Agamermis catadecaudata n. sp. is a parasitoid of the acridids Phaulacridium vitatum (Sjöstedt), Praxibulus exculpitus Rehn and Brachyexarna lobipennis Sjöstedt, the tetrigid Paratettix australicus Walker, the katydid Conocephalus sp. and the cricket Bobilla victoriae Otte & Allexander in the Northern Tablelands of New South Wales. In the laboratory A. catadecaudata n. sp. infected and developed in the acridid Chortoicetes terminifera (Walker). A. catadecaudata n. sp. is distinguished from all previously described species by the length of the infective juvenile and the position of the node. The infective is decaudate. Adult A. catadecaudata n. sp. are similar to A. decaudata but the egg is smaller and the male has a shorter spicule. Throughout its range there are two forms of preparasitic juvenile the relative abundances of which are variable. An undescribed species, Agamermis sp. aff. sinuosa Kaiser, was recorded in the Southern, Central and Northern Tablelands and was sympatric with A. catadecaudata n. sp. in the Northern Tablelands. The host of A. sp. aff. sinuosa is unknown.

Résumen - Agamermis catadecaudata n. sp. (Nematoda : Mermithidae), un parasitode des Orthoptères du sud-est de l'Australie - Agamermis catadecaudata n. sp. est un parasitode des acridiens Phaulacridium vitatum (Sjôstedt), Praxibulus exculpitus Rehn et Brachyexarna lobipennis Sjôstedt, du Théridide Paratettix australicus Walker, du Katydid Conocephalus sp. et du grillon Bobilla victoriae Otte & Allexander dans le nord des Tablelands en Nouvelle Galle du Sud. Au laboratoire, Agamermis catadecaudata n. sp. se distingue de toutes les espèces déjà connues du genre par la longueur des juvéniles infestants et la position du nœud. Ces juvéniles infestants perdent leur queue. Les adultes de Agamermis catadecaudata n. sp. sont semblables à ceux de A. decaudata, mais les œufs sont plus petits et le spicule plus court. Il existe deux types de juvéniles préinfestants dont l'abondance relative est variable. Une espèce non encore décrite, Agamermis sp. aff. sinuosa Kaiser, a été rencontrée dans les régions sud, centrale et nord des Tablelands; elle est sympatrique d'Agamermis catadecaudata n. sp. dans la région nord; ses hôtes sont inconnus.

Key-words : Entomophilic nematodes, Mermithidae, Agamermis, Acrididae.

During sampling of terrestrial mermithid nematodes as part of a study of nematode parasitism in acridids (Orthoptera) in the tablelands of New South Wales by G. L. B., mermithid adults, eggs and infectives of an Agamermis type similar to A. sinuosa Kaiser, 1977, were occasionally recorded. The species had a wide distribution from latitude 28°-32° S. Attempted infection of third instar stage Australian plague locust nymphs, Chortoicetes terminifera (Walker), using L2 larvae hatched from field collected eggs failed. No decaudate parasitic juveniles were recovered from acridids during an extensive parasite sampling program conducted between 1979-1983 (Baker, 1986) and the host of the species remained unknown.

In March 1985 A. J. Campbell, NSW Agriculture, Armidale, collected a large series of conspecific adult material of a second species of Agamermis from soil at Beaumont's Road, Hernani (32°22' S 152°28' E). Orthopteran insects collected from the pasture at the sampling site were heavily parasitised by parasitic juveniles of an Agamermis species. Infection of C. terminifera in the laboratory using L2 larvae hatched from eggs was successful.

The species is new to science and is herein described. The description is based solely on material from the Hernani area. However, a detailed comparison is made of eggs and L2 infectives from other locations. Specimens were heat killed, fixed in 3 % formaldehyde and then processed to glycerine. In the description the first figure is the dimension of the holotype (female) and allotype (male) and the figures in parentheses the range of paratype specimens. In addition to those specimens used in the description a further large series of females, eggs and progeny were measured.

Morphometric data were analysed using regression analysis and analysis of variance.

The species of Agamermis described in this paper has been the subject of studies on behaviour (Robinson et al., 1990) and parasitic development (Baker et al., 1988).
**Agamermis Cobb, Steiner & Christie, 1923**

**Diagnosis** (Kaiser, 1991, *emend.*).


**Type Species**

Agamermis decaudata Cobb, Steiner & Christie, 1923  
= A. decaudata var. paraguayensis Steiner, 1924 n. syn.  
= A. angusticephala Steiner, 1924 n. syn.  
= A. pachycephala Steiner, 1928 n. syn.

**Other Species**

A. unka Kaburaki & Imamura, 1932  
A. cobbi Schuurmans-Stekhoven & Mawson, 1955  
A. sinuosa Kaiser, 1977  
A. changshaensis Bao, Lou & Lou, 1992  
A. cata decaudata n. sp.

**Species inquirenda**

A. parva Rubtsov, 1976

**Species formerly placed in the genus**

Aganomermis dubia (Steiner, 1924) n. comb.  
= Aganermis dubia Steiner, 1924  
Aganomermis hangaica (Rubtsov, 1976) n. comb.  
= Aganermis hangaica Rubtsov, 1976  
Aganomermis saldulae (Rubtsov, 1969) n. comb.  
= Aganermis saldulae Rubtsov, 1969  
Hexamermis microamphidis Steiner, 1925  
= Aganermis paradecaudata Steiner, 1925 n. syn. (male)  
Oesophagomeris terricola (Hagmeier, 1912) Artyukhovski, 1969  
= Aganermis terricola (Hagmeier, 1912) Kiryano-va, Karavaev & Romanenko, 1959  
= Mermis terricola Hagmeier, 1912  
Schuurmanmermis couturieri (Schuurmans Stekhoven & Mawson, 1955) Rubtsov, 1978  
= Aganermis couturieri Schuurmans Stekhoven & Mawson, 1955

**Remarks**

A. decaudata var. paraguayensis, A. angusticephala and A. pachycephala are here synonymised with A. decaudata. A. decaudata var. paraguayensis is distinguished from A. decaudata in having a ventral cleft between the ventral sub-medial head papillae (Steiner, 1924). This cleft is not a good diagnostic character being also present in A. decaudata as figured in Kaiser (1991) and is also present in A. cata decaudata n. sp. between both the dorsal and ventral submedial head papillae. The description of A. decaudata var. paraguayensis by Steiner (1924) is regarded as the first description of A. decaudata, which was subsequently illustrated by Nickle (1972), Camino et al. (1986) and Kaiser (1991). A. angusticephala is most probably the postparasitic juvenile of A. decaudata var. paraguayensis, having the same host and locality data. A. pachycephala is described from juvenile specimens with a head which is holoccephalic while A. decaudata is described as hemicephalic (Steiner, 1928) as is the head of A. decaudata var. paraguayensis (Steiner, 1924) and the differences could be attributed to their being different stages of a single species. The fact that Leidy's material, on which the description of A. pachycephala is based, was from the grasshopper Dissosteira carolina (L.) and apparently common throughout Philadelphia would further indicate the species to be A. decaudata.

A. parva is described species inquirenda on the grounds that the adults were inadequately described for assignment to the genus Agamermis being described from an immature female and the egg and preparasitic juvenile are unknown (Rubtsov, 1976 a). The unusually shaped vagina is not characteristic of Agamermis and it may represent a new genus.

A. terricola was designated by Artyukhovski (1969) as the type species of the genus Oesophagomeris. A. couturieri was considered to be a species of Amphimermis by Kaiser (1977) and was subsequently designated by Rubtsov (1978) as the type species of the genus Schuurmanmermis. A. dubia, A. saldulae and A. (?) hangaica were described from juvenile material and are assigned to the genus Aganomermis on the basis of criteria outlined by Poinar and Welch (1981). A. saldulae has a scab on the terminus of the tail and is probably Aganermis. However, A. dubia and A. (?) hangaica do not have a scab on the terminus of the tail (Steiner, 1924; Rubtsov, 1976 a) and do not belong to the genus Aganermis.

A. paradecaudata is considered a junior synonym of Hexamermis microamphidis because of the dubious assignment of material from the same host. Of the 28 nematode specimens ex Helopeltis antonii Sign (Hemiptera: Miridae), all the parasitic juveniles and females were assigned to a new species H. microamphidis, and all the males and a parasitic juvenile based on a sketch, to A. paradecaudata. The authors consider it probable that Steiner's material was the male and female of a single species of Hexamermis. Steiner (1925) gives no reason for linking a sketch of the parasitic juvenile, which is a typical Aganermis parasitic juvenile, with all the male material. The meagre description of H. microamphidis by Steiner (1925) is accepted as valid as convention would otherwise name the species Hexamermis para...
Agamermis catadecaudata n. sp.

(Figs 1-4)

Measurements

Female (n = 16): L = 154 (56-200) mm; diam. mid-body = 326 (242-326) μm; head diam. (at level of cephalic papillae) = 62 (55-72) μm; body diam. at nerve ring = 148 (120-150) μm; cuticle width at nerve ring = 21 (5-21) μm; at mid-body = 12 (6-21) μm; width hypodermis, at mid-body = 10 (7-20) μm; amphid aperture (residual); amphid pouch (residual); distance of nerve ring from mouth = 319 (300-380) μm; V = 51.29 (51.2-58.0); length of vagina = 318 (187-318) μm; diameter of vagina = 156 (80-162) μm; width of lateral hypodermal chord = 32 (17-45) μm; distance of vestigial anus from tail = 199 (150-232) μm; diameter of eggs, in uterus = 118 (110-130) μm, laid = 130 (110-130) μm.

Male: (n = 12): L = 16.2 (5.4-24.0) mm; diam., mid-body = 121 (88-185) μm; head diam. at level of cephalic papillae = 54 (42-58) μm; at neck = 52 (52-62) μm; body diam. at nerve ring = 80 (67-105) μm; cuticle width at nerve ring = 12 (3-12) μm, mid-body = 14 (3-30) μm; hypodermis width mid-body = 10 (5-10) μm; amphid aperture = 1 μm; amphid pouch 3 x 5 μm; distance of nerve ring from mouth = 275 (187-280) μm; spicule length = 97 (77-137) μm; spicule head width = 13 (7-20) μm; spicule width mid-shaft = 9 (5-10) μm; tail length = 124 (102-150) μm; tail width = 103 (75-124) μm; position of proximal papillae anterior to cloaca = 84 (45-120) μm; number of genital papillae = 34 (34-48).

Preparasitic juvenile (n = 25): L = 2.6 mm (2.3-3.3 mm); mid-body diam. = 15 μm (11-18); head diam. = 7 μm (7-8); buccal cavity length = 30 μm (30-32); stylet length = 28 μm (25-30); distance of nerve ring from mouth = 98 μm (98-140); body width at nerve ring = 12 μm (12-19); position of stichosome = 150 μm (150-210) to 220 μm (220-400); position of node as per cent of body length = 12.6 (12.2-17.2).

Description

General: Body length exhibiting extreme sexual dimorphism, females being 2-20 x the length of males. This is greater than for any other species of Agamermis for which both sexes have been described. Mouth terminal. Amphids poorly developed and making no incursion into the lateral cephalic papillae; simply forming void in cuticle with very indistinct connection to outer cuticle.

Female: Amphids less distinct than in males, reduced to rudimentary duct in close association with second errant nerve ending in neck region. Amphid not visible in en face view or in lateral view. Vagina, though horn-shaped, closely opposed to uterus with junction in same transverse plane. Vaginal opening oblique slit. Vestigial anus well developed with cone-shaped external pore and filamentous tubes within hyaline cuticular body, base of which lies in depression or pocket in hypodermis. Eggs undeveloped when laid.

Male: Head rounded, slightly set off from body (neck diameter sometimes less than width at level of cephalic papillae). Bilateral symmetry of head pronounced, large dorsal and ventral cuticular incursions separating paired submedial papillae. Lateral papillae broader than submedial papillae. Amphids indistinct, set posterior (approx. 10 μm) and slightly lateral to sub-medial papillae. Spicule relatively narrow, evenly curved, head slightly flared due to prolongation of ventral wall; ventral wall slightly greater length than dorsal wall. Spicule length approximately equal to body width at cloaca. Tail length greater than spicule length (x 1.1-1.5). Proximal genital papillae less than spicule length anterior to cloaca (x 0.6-0.9). Genital papillae in three rows of unequal length, median row bifurcate in region of cloaca. Medial and lateral papillae in 2-3 rows, abdominal papillae in 2 rows. Vulva operculated with laterally compressed oviporus opening at mid-body. Eggs very thin, roughly spherical, laid in lateral oviporus.

caudata (Steiner, 1925) n. comb which would unfortunately provide a species of Hexamermis with a specific name indicating a decaudate preparasitic juvenile.
cytes distinct during early development, either paired or single, numbering fourteen to fifteen.

Postparasitic juveniles with rounded tail. Stub retained. Pharynx thickened at proximal end. Double moult to adult stage.

**TYPE HOST AND LOCALITY**

*Praxibulus exsculptus* Rehn (Orthoptera : Acrididae). Beaumont Road, Hernani (32° 22' S 152° 28' E), New South Wales, Australia.

**HOST RANGE**

In addition to the type host, *P. exsculptus*, *A. caladecaudala* n. sp. has been reared from *Phaulacridium vitatum* (Sjostedt), *Brachyexama lobipennis* Sjostedt (Orthoptera : Acrididae), *Paraleuix australicus* Walker (Orthoptera : Tetrigidae), *Conocephalus* sp. (Orthoptera : Tettigoniidae) and *Bobilla vicloriae* Otte & Alexander (Orthoptera : Gryllidae). In the laboratory *A. caladecaudala* n. sp. readily infected and developed in *Chortoicetes terminifera* (Walker) (Orthoptera : Acrididae).

**TYPE SPECIMENS**

Holotype (female) and allotype (male) in Department of Nematology, University of California, Davis, USA (UCD). Paratypes (one male and one female) deposited in South Australian Museum, Adelaide, Australia (acquisition numbers AHC 18807-18809) and Laboratoire de Biologie Parasitaire, Protistologie, Helminthologie, Muséum National d'Histoire Naturelle, Paris, France.

**DIAGNOSIS AND RELATIONSHIPS**

*Agamermis caladecaudala* n. sp. differs from all described species of *Agamermis* in regard to the diameter of the egg in relation to body length in the female; body length and position of the node in the preparasitic juvenile; and spicule length in relation to body length in the male.

The original description of *A. decaudata* contained no dimensions and in the following study of relationships the dimensions are from a redescription by Nickle (1972). Further dimensions given by Camino et al. (1986) fall within the range given by Nickle (1972) unless otherwise indicated.

**Female**

*Agamermis caladecaudata* n. sp. differ from *A. decaudata* in the generally shorter body length: 56-200 vs 50-465 mm (30-465 mm in Camino et al., 1986) and smaller eggs, especially in relation to body length (110-130 vs 150-180 μm) and narrower mid-body width (approx. 300 vs 500 μm); *A. unka*, *A. sinuosa* and *A. changshaensis* in the greater body length (56-200 vs 24-34, 30-37 and 23-41 mm respectively) and relatively larger eggs in relation to female length (110-130 vs 70-75, 95-110 and 105-140 μm respectively) and *A. cobbi* in the shorter body length (56-200 vs 213-323 mm) and smaller eggs (110-130 vs 150-200 μm).

**Male**

*Agamermis caladecaudata* n. sp. differ from *A. decaudata* in having a generally smaller body length (5.4-24 vs 10-120 mm in Nickle, 1972) and smaller spicule length,
Agamermis catadecaudata n. sp.

Fig. 3. Agamermis catadecaudata n. sp., egg and parasitic juvenile. A: Egg; B: Head of parasitic juvenile with skin of st. 1 attached; C: Node; D: Whole body; E: Anterior region. (Bar equivalents: A, D, E = 50 µm; B, C = 10 µm.)
especially in relation to body length (77-137 vs 150-180 \(\mu\text{m}\)); from *A. unka* and *A. changshaensis* in much smaller spicule length (77-137 vs 190-230 and 170-267 \(\mu\text{m}\) respectively), especially significant given the similarity of the body length of the three species (5.4-24 vs 11-22 and 13-28 mm, respectively); from *A. sinuosa* in arrangement of the genital papillae (three rows, median row bifurcate in region of cloaca vs six rows). The male of *A. cobbi* is unknown.

Preparasitic juveniles differ from *A. decadaudata* (based on paralektotype material from Falls Creek, Virginia collected by Christie and held in UCD), in generally short-
Agamermis catadecaudata n. sp.

Biology and ecology

Extensive collections of Agamermis spp. were made at two sites in the Northern Tablelands of New South Wales, Hernani and Black Mountain between 1983-1985.

There were no apparent differences between adults from both sites. However, the preparasitic juveniles were highly variable both at the same site and between sites. A. catadecaudata n. sp. collected at Hernani were readily divided into two forms based on the bimodal nature of the relationship between body length (L) and position of node (N): form one, short (2.6 mm) with relatively short body anterior to node (13%); form two, long (3.0 mm) with a relatively long body anterior to the node (17%). The relationship between body length and position of node of the two forms (12 and 17 vs 15%) with little variation; length in relation to egg size (130 and 140 vs 120 and 163 μm); from A. sinuosa in the greater length (2.3-3.3 vs 1.6 mm), position of the node (12-17 vs 17-21%) and the greater length of the stichosome in relation to body anterior to node (35 vs 26%) and from A. unka and A. changshaensis in greater length (2.3-3.3 vs 0.6 and 1.4-1.6 mm respectively) and A. cobbi in the shorter body length (2.3-3.3 vs 4-5.3 mm).

The host of A. sinuosa in Europe is Cicadellidae (Kaiser, 1977). No Cicadellidae were dissected during the course of this study. No parasitism of acridids (P. vittatum and B. lobipennis) was recorded at the Black Mountain site where A. sp. aff. sinuosa predominated and conversely no A. sp. aff. sinuosa was found at Hernani where parasitism of acridids was common. It is not known if parasitism of acridids by A. catadecaudata n. sp. at the Hernani site was caused by form one or two or both but it
Fig. 6. The relationship between female egg diameter and length of infective and position of node. A, B: Agamermis catadecaudata n. sp. population from Hernani; C, D: Mixed population of A. catadecaudata n. sp. (●) and A. sp. aff. sinuosa (▲) from Black Mountain.

appears the host range of A. sp. aff. sinuosa is different to that of A. catadecaudata n. sp.

A. catadecaudata n. sp. was also present at Black Mountain, but had a very low incidence. Given the abundance of acridid hosts, the low incidence of adults in soil samples and apparent absence of parasitism in acridids is unexplained.

A bimodal frequency distribution in both egg size and infective length has been recorded for A. decaudata in North America and both forms were accepted as being of the same species (Christie, 1936). Similarly, and in the absence of evidence of reproductive isolation, the two forms of A. catadecaudata n. sp. are considered to represent a single species.
Discussion

The hosts of the described species vary considerably: *A. decadauada* is recorded from grasshoppers (Orthoptera : Acrididae), *A. sinuosa* is apparently specific to cicadellids (Kaiser, 1977), *A. unka* and *A. chansaensis* to the brown rice planthopper *Nilaparvata lugens* Stål and whitebacked planthopper *Sogatella furcifera* (Horvath) (Hemiptera : Delphacidae) (Bao *et al.*, 1992; Choo & Kaya, 1993) and *A. caatadecuada* n. sp. to a range of orthopteran insects. The host of *A. cobi* is unknown.

*A. decadauada* and *A. caatadecuada* n. sp. share many features including the same extreme sexual dimorphism, bimodal distribution of egg diameter, infective length and position of node and the same host range (Orthoptera) and are obviously very closely related. *A. unka*, *A. chansaensis* and *A. sinuosa* do not exhibit sexual dimorphism to the same extent as *A. decadauada* and *A. caatadecuada* n. sp.

Cobb *et al.* (1923) and Christie (1936) state there is a positive relationship between female length and egg diameter in *A. decadauada*. In *A. caatadecuada* n. sp. there is no significant relationship between egg diameter and female length [\( P \text{ (egg diam.)} = 0.2 \); correlation coefficient < 0.1]. There is a strong positive relationship between egg diameter and length of the infective (correlation coefficient > 0.4) (Fig. 6 A). The data are evenly distributed (unimodal with low SE) which is again at variance with the bimodal distribution displayed by *A. decadauada*. Poinar (1979) suggested the difference in length of infectives probably reflected differences in the availability of nutrients during egg development.

The fact that the relationship LIN is both negative and of similar slope within the two forms but is positive between forms, possibly indicates incipient differentiation into sibling species. The differentiation into sibling species is not as advanced as that apparent in *A. decadauada* where in addition to infective length, egg diameter and female length also have a bimodal distribution.

The failure to record a decaudate parasitic stage during the survey of parasites of acridids throughout the tablelands of New South Wales contrasts with the high incidence of *A. caatadecuada* n. sp. in acridids at Hernani. This indicates differences in host susceptibility to infection between Hernani and the remainder of the State. No eggs or infectives of *A. sp. aff. sinuosa* have been recorded from the Hernani area, indicating there may be some spatial separation of the two species. Mixed populations were recorded at Springmount (Black Mountain) with *A. sp. aff. sinuosa* predominating, whereas only *A. sp. aff. sinuosa* has been recorded in the central and southern tablelands. There also appears to be a regional variation in the ability of *A. caatadecuada* n. sp. to infect acridids for, despite its occurrence in districts other than Hernani, it has only been recorded in acridids in the Hernani area. This may be a consequence of unsatisfied environmental conditions during host infection in other districts, at least as these conditions relate to the infection of acridids. Perhaps, significantly, Hernani has the highest annual rainfall of any district in New South Wales.

Acknowledgments

The authors would like to thank Dr A. Campbell, NSW Agriculture, Armidale for providing the material from Hernani on which the description is based, Ms H. M. Holmes, formerly NSW Agriculture, Rydalmere, for assistance with processing samples and Dr A. Clift, NSW Agriculture, Rydalmere, for regression analysis of morphometric data. The data reported in this paper were obtained during studies of the population dynamics of *P. gutaus* supported by grants from the Tablelands Wingless Grasshopper Committee and Australian Meat Research Council (DAN 19 S).

References


