

FIVE NEW SPECIES OF *DELADENUS* (NEOTYLENCHIDAE),
ENTOMOPHAGOUS-MYCETOPHAGOUS NEMATODES
PARASITIC IN SIRICID WOODWASPS

BY

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Five new species of *Deladenus* parasitizing siricid woodwasps from world wide sources are described in detail and their differences from other species of the genus are given. A key to the seven species of *Deladenus* known to parasitize siricids is included. The biology of these nematodes involves two life cycles associated with profound functional dimorphism of adult female nematodes and of spermatozoa. One cycle is parasitic with a sphaerulariid form of female reproducing ovoviviparously within the haemocoel of various siricids and the other is free living involving a neotylenchid form of female that reproduces oviparously while feeding on the symbiotic fungus within coniferous timber. Parasitism by three of the five new species of nematode results in sterilization of their female hosts; another species does not sterilize its only known host, while the other varies in its effect depending on host species.

Nematodes of the woodwasp, *Sirex noctilio* F., a serious pest of *Pinus radiata* D. Don. forests in Australia and New Zealand, were discovered by Zondag (1962) and shown by Bedding (1967, 1972a, 1972b) to have an unusual kind of life history involving profound female and spermatozoan dimorphism associated with free-living mycetophagous and parasitic life cycles; the species concerned and another were described and named *Deladenus siricidicola* Bedding, 1968 and *Deladenus wilsoni* Bedding, 1968.

A world wide search by C.S.I.R.O. (with help from the Commonwealth Institute of Biological Control) for siricids and their parasites has led to the discovery of a further five new species of *Deladenus* in siricids. The present paper is a description of these with observations on their biology and includes a key for the identification of all seven species of *Deladenus* found parasitizing siricids and their parasitoids.

MATERIALS AND METHODS

Nematodes from sixteen species of siricid and eight species of ichneumonid hosts, collected in most European countries, North Africa, Japan, Canada, U.S.A., India, Pakistan and New Zealand were cultured either on the fungus *Amylostereum areolatum* (Fr.) Boidin (which is symbiotically associated with some species of *Sirex*) or on *Amylostereum chailletii* (Pers. ex Fr.) Boidin (associated with many other siricid species).

Morphological examination and extensive interbreeding tests have shown that with one exception (a new genus of Neotylenchidae) all of these nematodes are *D. siricidicola*, *D. wilsoni* or one of the five new species described in this paper. However, the description of each species is based on specimens cultured from nematode larvae from a single host collected as follows :

Deladenus canii ex testes of a male *Sirex cyaneus* F. from *Abies balsamea* Mill. collected in Fundy National Park, New Brunswick, Canada, 1967.

Deladenus imperialis ex testes of a male *Sirex imperialis* Kirby from *Abies pindrow* Spach in Murree, Pakistan, 1968.

Deladenus rudyi ex testes of a male *S. cyaneus* from *Abies cilicilia* Carr. in Bucak, Turkey, 1968.

Deladenus nevexii ex testes of a male *Xeris spectrum* L. from *Abies concolor* Lindl. & Gord. in Glenbrook, Nevada, U.S.A.

Deladenus proximus ex testes of a male *Sirex nigricornis* F. from *Pinus taeda* L. in Sumter National Park, S. Carolina, U.S.A., 1972.

The nematodes were killed by maintaining them at 60° for 2 minutes, fixed in warm TAF (Courtney, Polley & Miller, 1955) and processed to pure glycerine using the method of Seinhorst (1959). Specimens were examined alive, in TAF and in glycerine. The use of a silver deposition technique (Bedding, 1968a) assisted surface and *en face* examination.

DELADENUS CANII N. SP.

(Table I; Fig. 1A, B, Fig. 2A-H)

Very similar to *D. siricidicola* Bedding, 1968 in all forms.

Mycetophagous female. — Cuticle with transverse striae about 1 μ m apart becoming slightly closer in head region; alternate striae very shallow as they approach lateral fields. Deirids and phasmids not observed.

Lateral fields not readily observed without silver deposition; extending from tip of tail for about 98 % of body length varying in different specimens from a fifth to half of body width; anteriorly usually arising as four incisures which branch until full complement of 11-14 is reached about a fifth of way along body length. Incisures branching and merging throughout length, usually reduced to 7-8 at level of vulva; terminating in 5-7.

Four lips present each with a single papilla. Amphid apertures close to entrance of vestibule; these and associated cylindrical pouches conspicuous after silver deposition. Head framework divided into eight sectors (Fig. 2, B, C).

Stylet (9-10 μ m) finely tapering anteriorly with well developed basal knobs; lumen not visible anteriorly, very narrow posteriorly. Corpus of oesophagus cylindrical to fusiform; lumen narrow with only a trace of medium chamber apparent. Isthmus very narrow, joining wider lumen of intestine immediately behind nerve ring; ovoid plug situated in lumen at junction with isthmus. Duct of dorsal oesophageal gland

TABLE I *Measurements of adults (mycetophagus ♀♀, ♂♂ and infective ♀♀) of Deladenus canii n. sp.*

	Mycetophagus females				Males				Infective females			
	Holotype	mean	standard error	range	Allotype	mean	standard error	range	paratypes (n = 12)	mean	standard error	range
L (mm)	1.64	1.89	0.04	1.61- 2.39	1.56	1.46	0.02	1.30- 1.64	1.19	0.04	0.91- 1.37	
a	58.6	53.5	1.02	47.9 -62.0	74.3	66.5	2.04	59.1 -74.0	60.8	1.9	54.2 -69.9	
b	17.4	19.0	0.42	14.8 -22.5	15.8	15.7	0.44	13.8 -19.1	10.3	0.3	8.4 -11.3	
c	41.0	47.9	0.86	41.7 -54.4	33.45	33.1	0.97	30.2 -40.0	36.6	1.16	29.7 -50.6	
V	94.7	95.1	0.10	94.5 -95.8	—	—	—	—	93.9	0.34	92.4 -94.7	
G ₁ or T	81.6	86.4	0.71	80.1 -89.8	81.86	86.3	0.82	81.1 -90.0	43.4	1.86	39.5 -54.6	
Stylet length (μm)	10	9.5	0.13	8.5 -10	9	9	0.12	8-10	21	0.46	19-24	
Oesophageal length (μm)	95	105	1.95	86-123	99	93	1.63	86-103	116	2.77	104-129	
Excretory pore to ant. end (μm)	94	103	1.80	81-116	90	82	2.26	63-92	83	2.95	73-111	
Hemizonid to ant. end (μm)	141	145	1.94	108-176	135	126	2.95	116-140	125	3.11	110-143	
Excretory pore in front of hemizonid (μm)	47	52	2.15	29-63	45	44	1.73	29-53	41	2.14	24-54	
Dorsal gland duct from ant. end/oesophageal length	—	—	—	—	—	—	—	—	—	—	—	
Sub-ventral gland duct from ant. end/oesophageal length	54	61	1.60	50-66	60.6	—	—	—	68.3	1.11	63.6 -77.7	
Vulva - post. end (μm)	87	92	1.49	80-105	—	—	—	—	72	1.76	63-81	
Tail length (μm)	40	39.9	0.61	33-64	44	44	0.37	41-48	33	0.51	31-36	
Spicule length (μm)	—	—	—	—	17	17.7	0.36	16-10	—	—	—	

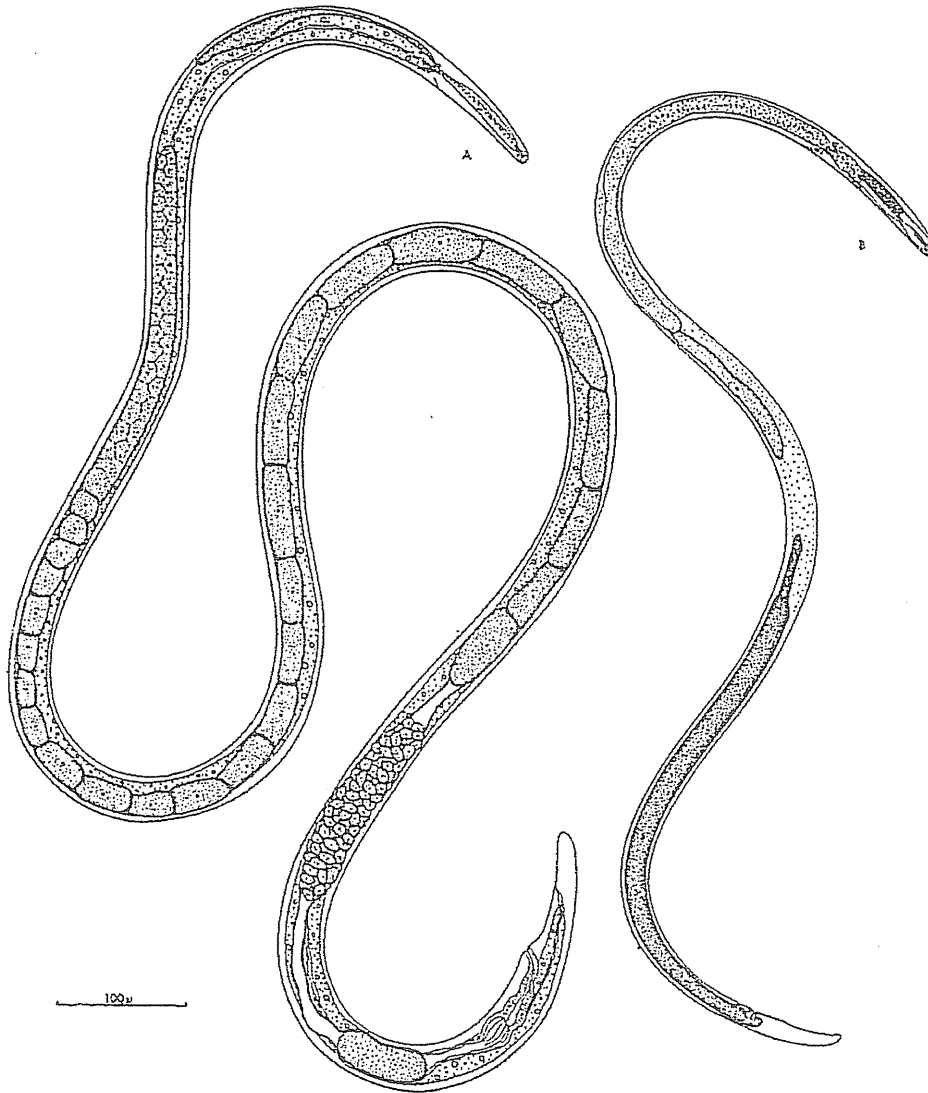


Fig. 1. *Deladenus canii* n. sp. : A, mycetophagous female; B, infective female.

opening close to base of stylet. Dorsal oesophageal gland (often obscured by food reserves) greatly enlarged posterior to oesophagus and lying adjacent to intestine in uninucleate lobe of twice the length of the oesophagus; lobe often with long narrow neck anteriorly and expanded posteriorly. Only trace of subventral glands apparent; fine ducts opening into hollow chamber about $3/5$ of way along oesophagus from anterior end.

Excretory pore with well cuticularized, terminally cylindrical tube; usually just in front of nerve ring; one and a half to two body widths in front of hemizonid.

Vulva a broad transverse slit with protuberant lips; vagina well cuticularized; no post-vulval uterine sac; long gonoduct packed with large, amoeboid spermatozoa ($10-12\ \mu\text{m}$) and usually containing one or two undeveloped eggs, although very old females may accumulate 20-40, some hatching within parent after death. Prodelphic ovary outstretched, with two rows of oocytes anteriorly and one row posteriorly.

Male. — Similar to mycetophagous female. Lateral incisures not branching and merging along length as much as in mycetophagous female. Lateral field fanning out towards edge of bursa, from one third to one half body width; bursa striated, enveloping tail and extending in front of spicules. Testes outstretched. Spicules ($16-19\ \mu\text{m}$) and gubernaculum tylenchoid; spicules appearing Y-shaped ventrally with well defined thickened lateral borders surrounding inner membranous area. Spermatozoa of two types, usually only one type in a single individual; one type as described for the mycetophagous female and other (found in infective females) much smaller ($1-2\ \mu\text{m}$) spherical amoeboid and composed mainly of nucleus.

Infective female. — Cuticle with transverse striae about $1.2\ \mu\text{m}$ apart becoming closer in head region.

Lateral fields extending from tip of tail for about 97 % of body length; varying in different specimens from a quarter to a third body width. 8-13 incisures for most of body length, not repeatedly branching and merging as in mycetophagous female.

Lips appear fused. Amphid apertures opening close together on either side of entrance of vestibule which is slit-like, running dorso-ventrally (Fig. 2, G); amphid pouches larger than those of mycetophagous female. Cephalic framework divided into eight sectors as in mycetophagous female.

Stylet ($19-24\ \mu\text{m}$) very different from that of mycetophagous female and male: stout, with wide lumen; lacking conspicuous knobs; not tapered anteriorly but dorsally extended further than ventrally.

Corpus of oesophagus approximately cylindrical; slightly constricted near stylet base; lumen wide anterior to ducts of sub-ventral glands; broadening slightly at entry of ducts then becoming very fine. Isthmus short and only slightly narrower than corpus. Duct of dorsal gland about a stylet length behind stylet base; dorsal oesophageal gland finely granular, probably confined within oesophagus. Complicated sub-ventral glands with numerous ducts radiating from each side of small chamber; not extending anterior to ducts; extending posteriorly almost down to ovary; three lobes distinguishable laterally, posterior two each with a single nucleus. Sub-ventral gland duct usually a little less than half way between nerve ring and dorsal gland duct.

Little trace of intestine apparent, but lumen although not visible initially is sometimes discernible after penetration of and feeding within host; rectum narrow and straight.

Nerve ring about one and a half body widths behind sub-ventral gland ducts. Excretory pore varying in position from just in front of to just behind sub-ventral gland ducts.

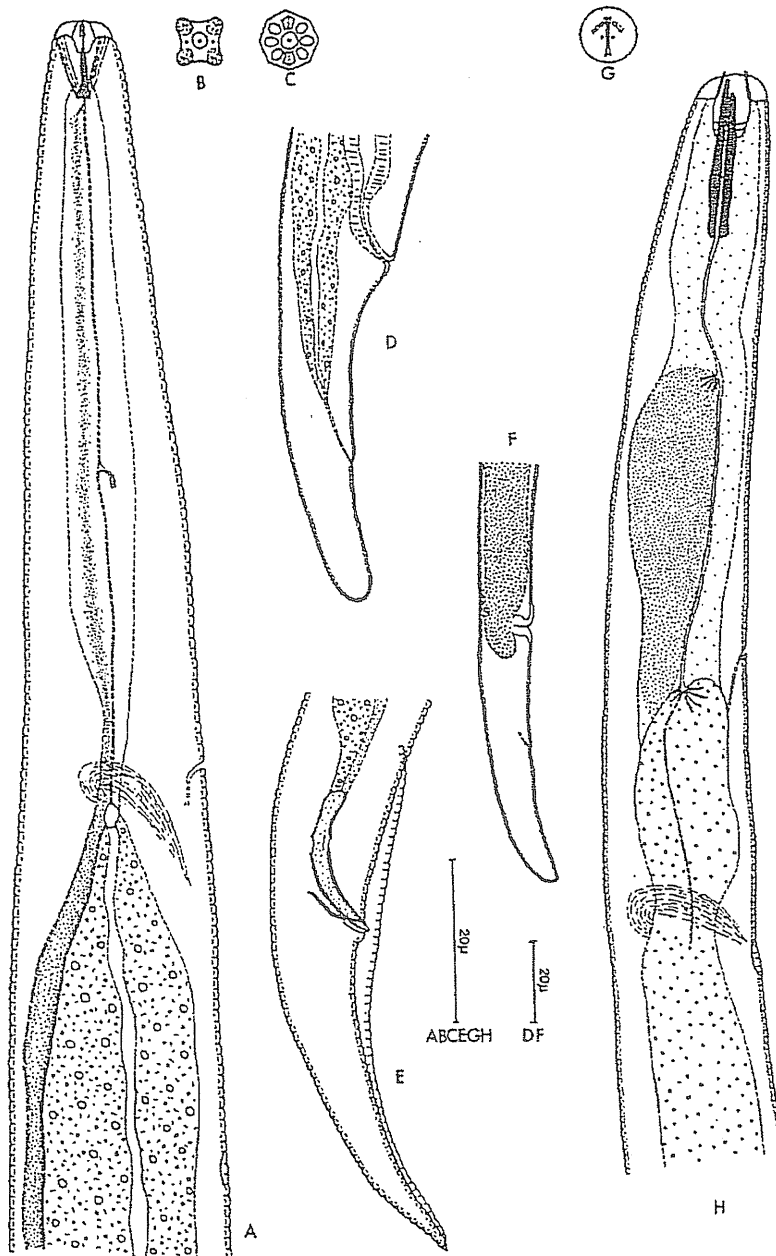


Fig. 2. *Deladenus canii* n. sp.: A, anterior end of mycetophagous female — lateral; B, en face view of lip region of mycetophagous female; C, cephalic framework of mycetophagous female; D, posterior end of mycetophagous female — lateral; E, posterior end of male — lateral; F, posterior end of infective female — lateral; G en face view of infective female; H, anterior end of infective female — lateral.

Vulva appearing in ventral view as a narrow transverse slit on a small circular, heavily cuticularized surround; lips barely protuberant; vagina heavily cuticularized; small post-vulval uterine sac. Ovary prodelphic, undeveloped; thin walled oviduct normally packed with small spermatozoa (1-2 μ m) occupying about half body length.

Mature parasitic female. — Very large (3.5-15 mm long, 0.1-0.5 mm wide), cylindrical; rounded tail; often slightly greenish. Stylet, retracted into head for about its own length; oesophagus and glands degenerate; thick hypodermis, nematode a reproductive tube filled with developing eggs and larvae; position of vulva just discernible.

Holotype on slide T-231 t and *allotype* on slide T-232 t of U.S.D.A. Nematode Collection (Beltsville, Maryland, U.S.A.).

Differential diagnosis. — (Based on mycetophagous forms unless otherwise stated).

Other species	<i>D. canii</i>
<i>D. arboricolus</i> (Cobb, 1922), J. B. Goodey & Franklin in T. Goodey, 1956	Much longer; duct to dorsal gland near stylet base; larger c & V.
<i>D. aridus</i> Andr��ssy, 1957	Much longer; greater values for c & V; different vaginal and tail shape; excretory pore anterior to hemizonid.
<i>D. durus</i> (Cobb, 1922)	11-14 incisures; longer stylet, no fine mucron on male tail.
<i>D. norimbergensis</i> Ruhm, 1956	Stylet longer; isthmus of oesophagus much narrower; vulva heavily cuticularized; post-vulval region more tapered.
<i>D. obesus</i> Thorne, 1941	Amphid apertures less widely spaced; no post-rectal sac; differently shaped vulva and tail.
<i>D. saccatus</i> Andr��ssy, 1952	Much longer; greater values for c & V; no post-vulval sac; excretory pore anterior to hemizonid; differently shaped vulva and tail.
<i>D. siricidicola</i> Bedding, 1968	Dorsal gland extends along the gut for twice oesophageal length and has long narrow neck. Slightly shorter mean stylet length. Mean distance between excretory pore and hemizonid greater. Greater mean G in infective female.
<i>D. wilsoni</i> Bedding, 1968	Much greater distance between excretory pore and hemizonid.

Biology. — Similar to that of *D. siricidicola* (Bedding, 1967, 1972a; 1972b).

D. canii has been found parasitizing only North American *Sirex cyaneus*. Female *S. cyaneus* drill into dead or dying coniferous timber to oviposit and inject mucus and arthrospores of the symbiotic fungus *Amylostereum chailletii*. The larvae bore through the wood feeding on the growing fungus and adult insects emerge one to three years after oviposition.

Juveniles of *D. canii* released ovoviviparously by parent nematodes into the haemocoel at the late pupal stage of their host migrate to its reproductive organs. In a female host, most juvenile nematodes penetrate the eggs all of which become inviable and may each contain 50-200 juveniles; some juveniles also lie free in the ovaries and others enter the ooidial glands. In male hosts, many thousands of juveniles

pack the testes which appear hypertrophied, often fused and devoid of spermatozoa. The vesiculae seminales are, however, full of active spermatozoa and, as with parasitism by *D. siricidicola*, successful copulation will doubtless occur and there will be no transference of nematodes from parasitized males to unparasitized females. Since nematodes within males die soon after their host, entry into male insects is a "dead end" for the nematodes.

Parasitized female *S. cyaneus* deposit eggs containing juvenile nematodes and arthrospores into timber; the nematodes migrate out of the eggs and feed on the fungus as it grows. On culture plates of fungus, juveniles mature to neotylenchid type adults within five days at 22°; large amoeboid spermatozoa are transferred during copulation and females commence oviposition within a day laying 300-800 eggs within two to three weeks. Eggs hatch after 3 to 4 days at 22° and larvae feed on young uncontaminated fungus and mature into neotylenchid type adults. This cycle can continue indefinitely.

Unlike *D. siricidicola* which forms infectives readily on old culture plates, *D. canii* produces these only occasionally in such circumstances, and old plates are populated almost exclusively by juvenile stages. Details of infective production of all species of *Deladenus* parasitizing siricids will be published shortly, but as with *D. siricidicola* whether a larva of *D. canii* becomes a mycetophagous or an infective female depends upon environmental influences.

After copulation and transference of micro-spermatozoa, infective female nematodes penetrate host larvae, grow many hundred-fold in volume and commence ovarian development at the onset of host pupation. Several thousand juveniles are produced by each parent nematode during host pupation and most of these escape into the host haemocoel before the adult insect emerges from the wood.

DELADENUS IMPERIALIS N. SP.

(Table II; Fig. 3, A-E)

Very similar to *D. canii* in all forms except as stated below.

Mycetophagous female. — Stylet 8-10 μ m. Corpus of oesophagus cylindrical tapering gradually to isthmus. Dorsal oesophageal gland lying adjacent to intestine, about same length as oesophagus; lobe occupying third to half body width, tapering posteriorly. Excretory pore little less than half way from nerve ring and anterior end; three to four body widths in front of hemizonid. Post-vulval region narrow, straight and tapering.

Male. — Spicules (13-19 μ m) with only weak posterior proximal border.

Mature parasitic female. — 5-18 mm long, 0.2-0.5 mm wide; cylindrical; rounded tail; distinct blue-green colouration.

Holotype on slide 1974 : 31 and allotype on slide 1974 : 32 of British Museum Collection.

Differential diagnosis. — Most similar to *D. siricidicola* and *D. canii*; separated

TABLE II *Measurements of adults (mycetophagous ♀♀, ♂♂ and infective ♀♀) of Deladenus imperialis n. sp.*

	Mycetophagous females				Males				Infective females			
	paratypes (n = 30)				paratypes (n = 25)				paratypes (n = 25)			
	Holotype	mean	standard error	range	Allotype	mean	standard error	range	mean	standard error	range	
L (mm)	1.53	1.66	0.05	1.18-2.13	1.17	1.42	0.03	1.11-1.75	1.16	0.016	1.01-1.39	
a	56.6	50.2	1.11	40.4-62.5	73.1	62.1	1.58	50.4-78.2	62.1	1.04	52.5-73.5	
b	16.6	17.9	0.54	12.5-23.2	13.1	15.0	0.47	11.7-19.2	9.7	0.11	8.9-11.0	
c	40.2	42.8	2.00	31.1-66.5	30.8	34	0.91	26.8-43.9	34.8	0.58	29.4-39.6	
V	94.8	94.9	0.11	93.5-95.9	—	—	—	—	94.1	0.10	92.1-95.2	
G ₁ or T	78.2	80.1	1.84	65.7-89.1	77.6	84	1.05	75.0-90.0	38.1	0.99	31.5-46.2	
Stylet length (μm)	8	9	0.15	8-10	8.5	8.9	0.08	8-10	21.5	0.23	20-24	
Oesophageal length (μm)	92	92.2	1.30	75-110	89	94.8	1.51	87-117	118.6	1.16	111-130	
Excretory pore to ant. end (μm)	46	56.3	1.15	46-71	51	52.0	0.95	44-62	50.1	0.95	41-58	
Hemizonid to ant. end (μm)	126	128.2	3.57	111-137	115	118.7	1.91	99-135	131.3	1.44	121-148	
Excretory pore in front of hemizonid (μm)	80	70.3	1.97	51-95	64	64.0	1.47	47-78	80.0	2.13	55-96	
Dorsal gland duct from ant. end/	—	—	—	—	—	—	—	—	—	—	—	
oesophageal length	—	—	—	—	—	—	—	—	30.3	0.47	26.9-36.0	
Sub-ventral gland duct from ant. end/	—	—	—	—	—	—	—	—	—	—	—	
oesophageal length	—	—	—	—	—	—	—	—	65	0.73	58-71	
Vulva - post. end (μm)	79	84	1.3	71-99	—	—	—	—	68	0.95	—	
Tail length (μm)	38	39	1.3	32-51	38	42.2	0.68	36-49	33	0.65	30-41	
Spicule length (μm)	—	—	—	—	16	15.9	0.37	13-19	—	—	—	

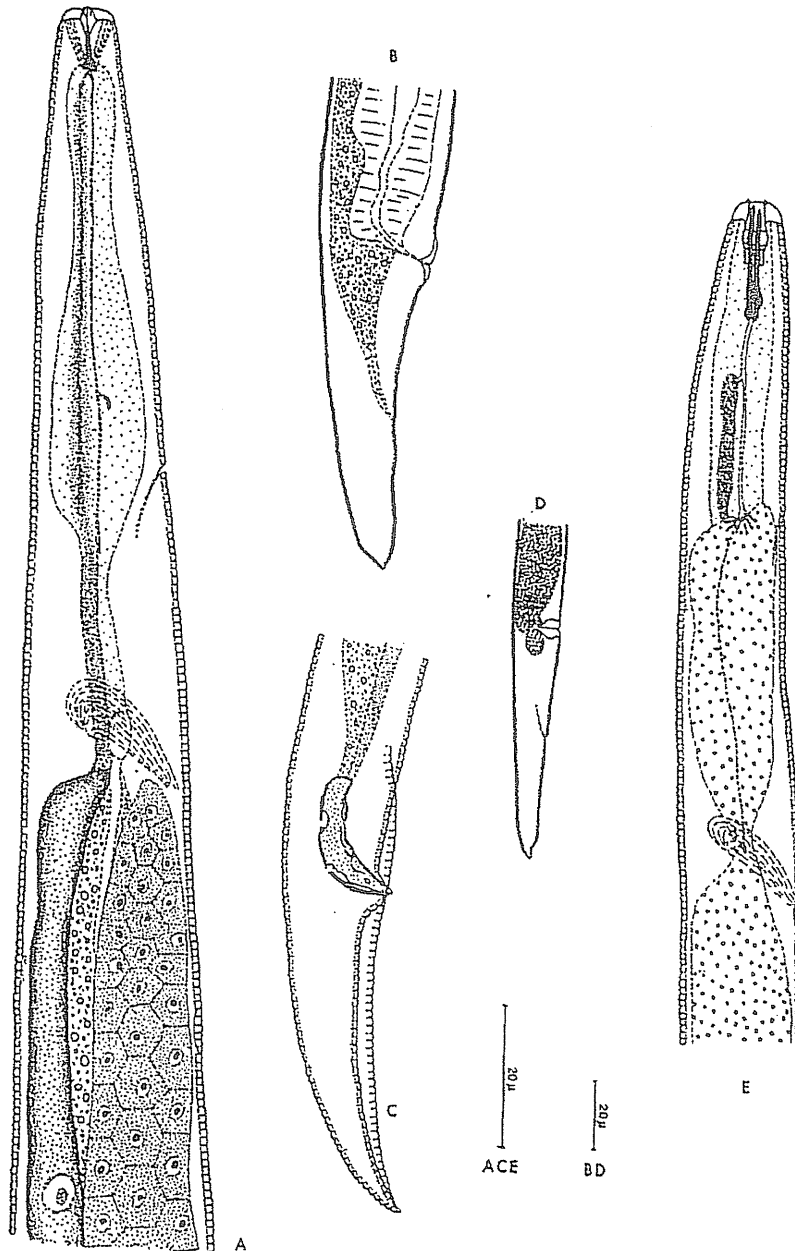


Fig. 3. *Deladenus imperialis* n. sp. : A, anterior end of mycetophagous female — lateral; B, posterior end of mycetophagous female — lateral; C, posterior end of male — lateral; D, posterior end of infective female — lateral; E, anterior end of infective female — lateral.

from these species by the greater mean distance between its hemizonid and excretory pore and from *D. canii* by the oesophageal gland which has no long narrow neck and is only half as long as in *D. canii*. Different from other species of *Deladenus* in same characters as *D. canii*.

Biology. — Similar to *D. canii* but juvenile nematodes do not enter the eggs of their usual host, *S. imperialis*, and are packed within the oviducts so that during oviposition viable eggs surrounded by nematodes are inserted into the wood together with the symbiotic fungus, *A. chaillatii* on which both nematodes and *Sirex* larvae feed. Such behaviour enables parasitism to continue even if oviposition within a tree is by a single female. Infective females and associated males are very rarely formed on culture plates.

DELADENUS RUDYI N. SP.

(Table III, Fig. 4, A-E)

Similar to *D. canii* in all forms except as stated below.

Mycetophagous female. — Stylet 8-9 μ m. Corpus of oesophagus basically cylindrical but constricted somewhat after anterior third; tapering to narrow isthmus. Dorsal oesophageal gland usually short and squat, only about half length of oesophagus; occupying at least half body width. Excretory pore a little less than half way from nerve ring to anterior end. Post-vulval region shorter than in *D. canii*.

Male. — Tail truncated and shorter than *D. canii*; gubernaculum usually strongly posteriorly reflexed. (This character not found in some strains from other sources). Spicules (15-19 μ m) with only weak posterior proximal border.

Infective female. — Stylet (14-21 μ m) shorter, oesophagus shorter and gonad longer than *D. canii*.

Mature parasitic female. — 5-15 mm long, 0.2-0.5 mm wide, cylindrical; often bright green coloration with distinct beading of exterior.

Holotype on slide 1974 : 29 and allotype on slide 1974 : 30 of British Museum Collection.

Differential diagnosis. — Most similar to *D. imperialis*; separated from this species by the squat oesophageal gland in mycetophagous forms; truncated male tail, slightly greater mean length of spicules, smaller c in all forms, longer G in the infective. Different from other species in same characters as *D. imperialis*.

Biology. — Similar to *D. canii*. Host range — *S. cyaneus*, *Urocerus gigas* L., *U. augur* (Klug), *U. japonicus* (Smith), *U. antennatus* (Marlatt), *X. spectrum* L. Infective stages very rarely formed on culture plates.

TABLE III Measurements of adults (*mycetophagous* ♀♀, ♂♂ and *infective* ♀♀) of *Deladenus rudyi* n. sp.

	Mycetophagous females paratypes (n = 18)				Males paratypes (n = 20)				Infective females paratypes (n = 12)			
	Holotype	mean	standard error	range	Allotype	mean	standard error	range	mean	standard error	range	
L (mm)	1.87	1.71	0.04	1.46-1.98	1.37	1.5	0.03	1.25-1.72	1.05	0.04	0.88-1.25	
a	49.2	49.4	0.99	43.6-56.7	72.1	67.3	1.36	55.4-84.0	59.9	0.97	54.2-61.1	
b	19.7	17.8	0.60	15.5-21.1	14.1	14.9	0.43	11.8-19.4	10.3	0.25	8.7-11.3	
c	51.9	53.2	1.67	41.7-60.0	41.5	41	0.98	32.1-49.1	36.4	1.31	30.6-43.3	
V	93.8	95.4	0.11	94.6-96.1	—	—	—	—	94.2	0.09	93.7-94.7	
G ₁ or T	84.7	81.5	1.22	68.9-91.7	84.7	77.6	3.57	63.0-89.7	49.3	1.97	39.1-56.6	
Stylet length (μm)	8	8.3	0.11	8-9	8	8.7	0.10	8-9	17.8	0.56	14-21	
Oesophageal length (μm)	95	96	1.64	79-104	97	106	2.96	82-130	101	1.85	92-111	
Excretory pore to ant. end (μm)	63	54	1.18	46-60	62	53.3	1.55	35-65	49	1.51	41-60	
Hemizonid to ant. end (μm)	129	120	2.86	105-145	130	118	1.92	103-129	120	2.32	108-130	
Excretory pore in front of hemizonid (μm)	66	66.1	2.77	56-97	68	65.1	1.25	57-74	73.2	1.19	67-79	
Dorsal gland duct from ant. end/ oesophageal length	—	—	—	—	—	—	—	—	31.0	1.25	25.0-37.0	
Sub-ventral gland duct from ant. end/ oesophageal length	51.6	56	2.97	48.4-61	—	—	—	—	67.6	1.22	62.0-75.0	
Vulva - post. end (μm)	79	78	1.62	63-90	—	—	—	—	60	1.60	51-71	
Tail length (μm)	36	32	0.81	27-36	33	37	0.58	32-41	30	0.98	24-32	
Spicule length (μm)	—	—	—	—	17	16.8	0.33	15-19	—	—	—	

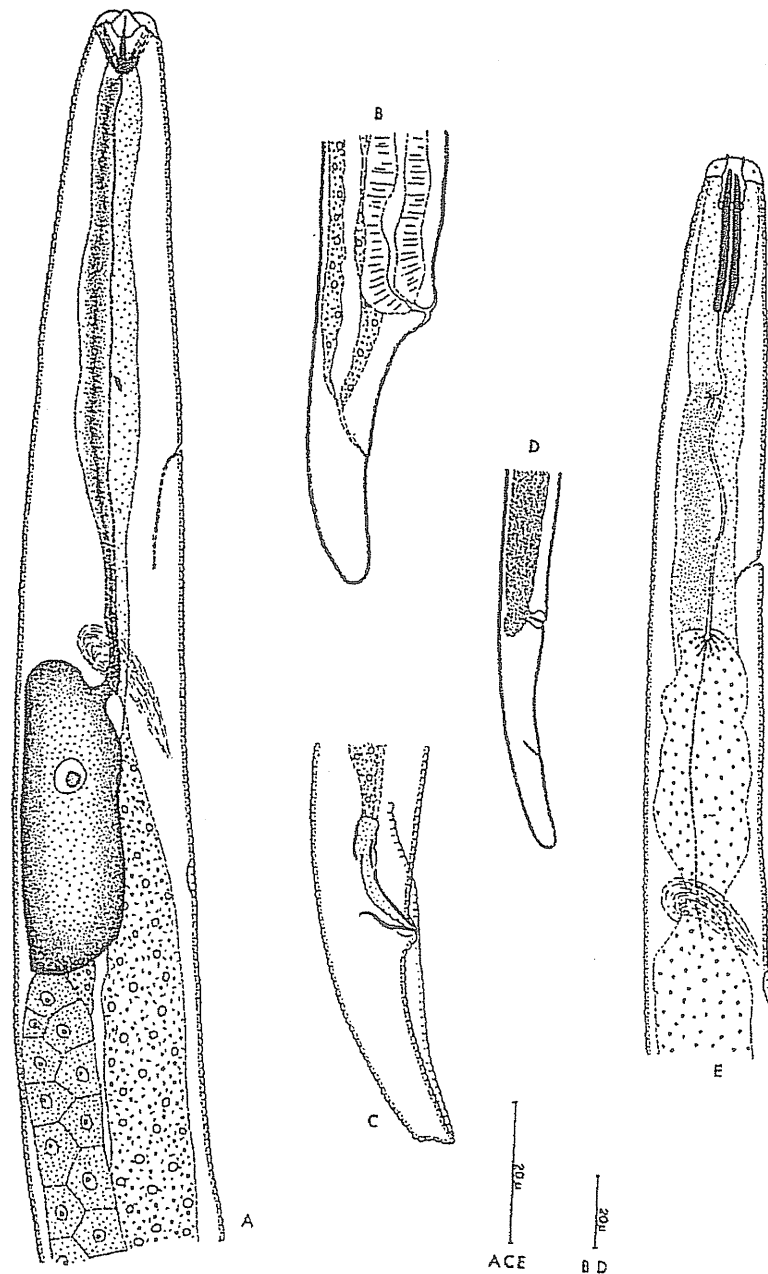


Fig. 4. *Deladenus rudyi* n. sp.: A, anterior end of mycetophagous female — lateral; B, posterior end of mycetophagous female — lateral; C, posterior end of male — lateral; D, posterior end of infective female — lateral; E, anterior end of infective female — lateral.

DELADENUS NEVEKII N. SP.

(Table IV; Fig. 5, A-E)

Similar to *D. canii* in all forms except as stated below.

Mycetophagous female. — Corpus of oesophagus somewhat constricted after anterior third, then broadens greatly posteriorly before tapering sharply posteriorly to join long narrow isthmus. Duct of dorsal oesophageal gland opening very close to base of stylet. Lobe of dorsal oesophageal gland not much longer than oesophagus. Excretory pore funnel shaped, opening well anterior to nerve ring. Ovary with three rows of oocytes anteriorly. Post-vulval region only slightly curved ventrally; tip of tail pointed.

Male. — Spicules (16-22 μ m) broad with border interrupted and membranous area unevenly sclerotized.

Infective female. — Stylet (16-19 μ m) shorter than in *D. canii* with slight knobs at base; dorsal gland duct nearer to stylet base than other species and sub-ventral gland ducts more than two thirds way from nerve ring to stylet base. Tail pointed.

Mature parasitic female. — 6-12 mm long, 0.2-0.5 mm wide; cylindrical; very pale green to white in colour.

Holotype on slide T-233 t and *allotype* on slide T-234 t of U.S.D.A. Nematode Collection.

Differential diagnosis. — Most similar to *D. imperialis*; separated from this species by oesophageal shape of mycetophagous forms, pointed tail of mycetophagous and infective females, longer unevenly sclerotized spicules in the male and larger G, closer proximity of the dorsal and sub-ventral gland ducts in the infective female. Different from other species in same characters as *D. canii*.

Biology. — Similar to *D. canii*. Host range — *S. cyaneus*, *S. longicauda* Middlekauff, *U. albicornis* (F.), *U. californicus* Norton, *X. spectrum* L. and *X. morrisoni* (Cresson). When *S. cyaneus* is the host insect, because most juvenile nematodes are released by parent nematodes after emergence of host from pupation, they do not enter the eggs, and testes in freshly emerged insects may contain only a few hundred juveniles. When *Xeris* species are hosts, juveniles enter all eggs but they enter only 25 to 75 % of the eggs of *Urocetus californicus* Norton. When parasitizing *Xeris* species which carry no symbiotic fungus, the nematodes will only become established in timber already infected with *A. chailletii* from other siricid species. Infective stages are rarely formed on culture plates.

TABLE IV *Measurements of adults (mycetophagous ♀♀, ♂♂ and infective ♀♀) of Deladenus peveyii n. sp.*

	Mycetophagous females				Males				Infective females			
	Holotype	mean	standard error	range	Allotype	mean	standard error	range	mean	standard error	range	
L (mm)	1.64	1.69	0.04	1.42-1.98	1.35	1.52	0.06	1.03-1.83	1.08	0.025	0.89-1.22	
a	38.1	36.9	1.37	31.5-47.3	60.3	53.4	1.35	47.2-61.8	55.0	1.6	43.8-61.6	
b	17.8	15.7	0.26	14.2-17.5	12.1	14.3	0.39	11.8-16.5	9.3	0.12	8.6-9.8	
c	43.1	40.8	0.82	38.0-45.0	33.7	34.0	1.23	28.7-42.5	32.0	0.59	27.8-34.9	
V	95.2	94.5	0.28	93.7-95.2	—	—	—	—	93.4	0.21	92.7-93.7	
G ₁ or T	71.6	84.7	1.35	71.3-89.6	87.6	86.1	0.74	81.2-90.1	50.1	1.3	41.5-56.1	
Stylet length (μm)	9.5	9.1	0.10	9-10	9	9.4	0.17	8-10.3	17	1.8	16-19	
Oesophageal length (μm)	92	108.2	1.78	97-119	111	106	2.51	87-119	116.8	2.47	103-127	
Excretory pore to ant. end (μm)	58	64.8	1.45	55-71	70	60.4	2.39	44-75	60.2	3.18	54-70	
Hemizonid to ant. end (μm)	127	—	—	119-160	134	137	4.38	103-158	131.2	2.36	111-138	
Excretory pore in front of hemizonid (μm)	69	75	2.36	64-87	64	77	2.32	59-90	68.5	2.34	54-82	
Dorsal gland duct from ant. end/oesophageal length	—	—	—	—	—	—	—	—	23.6	0.55	19.8-26.1	
Sub-ventral gland duct from ant. end/oesophageal length	—	54.9	1.15	49.1-59.0	—	—	—	—	59.4	0.63	56.7-61.7	
Vulva - post. end (μm)	79	93.2	1.74	81-102	—	—	—	—	71.4	1.41	65-80	
Tail length (μm)	38	41.1	0.88	36-47	40	44.8	1.78	33-55	33.8	0.67	30-38	
Spicule length (μm)	—	—	—	—	18	18.7	0.45	16-22	—	—	—	

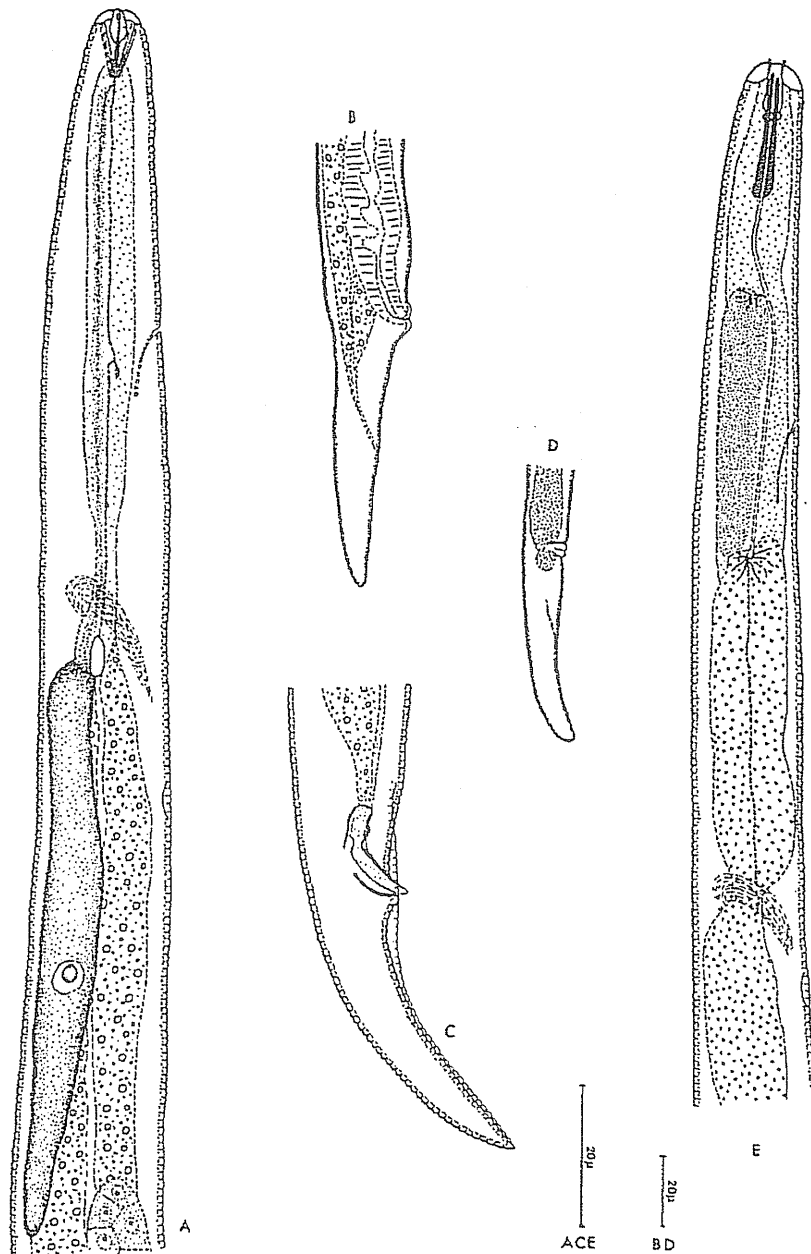


Fig. 5. *Deladenus nevexii* n. sp. : A, anterior end of mycetophagous female — lateral; B, posterior end of mycetophagous female — lateral; C, posterior end of male — lateral; D, posterior end of infective female — lateral; E, anterior end of infective female — lateral.

DELADENUS PROXIMUS N. SP.

(Table V; Fig. 6, A-E)

Similar to *D. canii* in all forms except as stated below.

Mycetophagous female. — Stylet (11-12 μ m) with reduced basal knobs. Excretory pore well posterior to nerve ring and close (1-11 μ m) to hemizonid.

Male. — Spicules (24-28 μ m) and gubernaculum longer than *D. canii*.

Infective female. — Stylet (22-31 μ m) longer and stouter than in other species and with distinct basal knobs. Dorsal gland duct more posterior than in other species. Excretory pore and hemizonid close together and in same region as nerve ring. G much smaller than in other species.

Mature parasitic female. — 5-18 mm long, 0.2-0.5 mm wide; green colouration.

Holotype on slide T-235 t and allotype on slide T-236 t of U.S.D.A. Nematode Collection.

Differential diagnosis. — Most similar to *D. wilsoni*; separated from this species by larger and differently shaped spicules in the male and by the much larger knobbed stylet and much smaller G of the infective female. Readily separable in all stages from *D. siricidicola*, *D. canii*, *D. imperialis*, *D. rudyi* and *D. nevexii* by the close proximity of its hemizonid and excretory pore. Different from other species in same characters as *D. canii*.

Biology. — Similar to *D. canii*. Enters the eggs of its hosts, *S. nigricornis* and *S. abbottii* Kirby. Readily forms infective females on culture plates.

KEY TO THE FREE LIVING STAGES OF SPECIES OF DELADENUS
PARASITIC IN SIRICIDS

Separation of *Deladenus* species based on parasitic or juvenile forms is not feasible. Prior to classification it is necessary to culture juveniles on the symbiotic fungus of their host. Examination of at least five individuals of all forms is desirable for accurate classification because of considerable variation between specimens of the same species.

1. Hemizonid and excretory pore of all forms less than 15 μ m apart 2
 Hemizonid and excretory pore of all forms more than 20 μ m apart 3
2. Spicules 19-23 μ m long; stylet of infective ♀ without conspicuous knobs, G of infective greater than 40 (\bar{x} = 54) *D. wilsoni*
 Spicules 24-28 μ m long; stylet of infective ♀ with conspicuous knobs, G of infective less than 40 (\bar{x} = 28) *D. proximus*

TABLE V Measurements of adults (*mycetophagous* ♀♀, ♂♂ and *infective* ♀♀) of *Deladenus proximus* n. sp.

	Mycetophagous females					Males					Infective females				
	paratypes (n = 12)					paratypes (n = 12)					paratypes (n = 12)				
	Holotype	mean	standard error	range	Allotype	mean	standard error	range	mean	standard error	range	mean	standard error	range	
L (mm)	1.80	2.03	0.04	1.76-2.2	1.37	1.52	0.02	1.34-1.59	1.28	0.02	1.17-1.37				
a	60.0	47.6	1.17	40-53.7	68.5	56	1.18	48-62	58	0.91	53-62				
b	18.5	19.1	0.42	16.3-21.3	14.4	15.5	0.21	13.6-17.5	10.2	0.19	9.5-11.6				
c	48.6	53	2.20	44-60	31.8	32	0.69	27-35	39	1.43	34-42				
V	95.4	95.6	0.08	95.1-95.9	—	—	—	—	94.6	0.09	94.2-95.3				
G ₁ or T	83.1	88.9	1.17	84.8-94.8	83.8	90.3	0.68	87.3-93.9	28.3	1.26	20.9-34.3				
Stylet length (μm)	11	11.4	0.15	11-12	11	11	—	11	26.4	0.53	22-31				
Oesophageal length (μm)	97	107	1.97	89-116	95	98	1.64	89-107	125	1.73	116-135				
Excretory pore to ant. end (μm)	127	140	3.09	127-159	123	126	2.59	111-142	127	2.33	111-142				
Heminozoid to ant. end (μm)	135	145	2.99	132-162	124	129	2.56	114-143	130	1.73	118-142				
Excretory pore in front of hemizonid (μm)	8	8.52	0.85	1-11	1	2.1	0.63	0-7	3.2	0.85	0-8				
Dorsal gland duct from ant. end/oesophageal length	—	—	—	—	—	—	—	—	39.6	1.04	31.7-44.8				
Sub-ventral gland duct from ant. end/oesophageal length	—	56.5	1.66	49.5-67.1	—	—	—	—	68.3	1.26	62.2-74.8				
Vulva - post. end (μm)	82	89	1.42	79-95	—	—	—	—	67	0.98	63-73				
Tail length (μm)	37	39	1.38	31-47	43	48	0.73	44-52	32	0.81	30-35				
Spicule length (μm)	—	—	—	—	24	25	0.41	24-38	—	—	—				

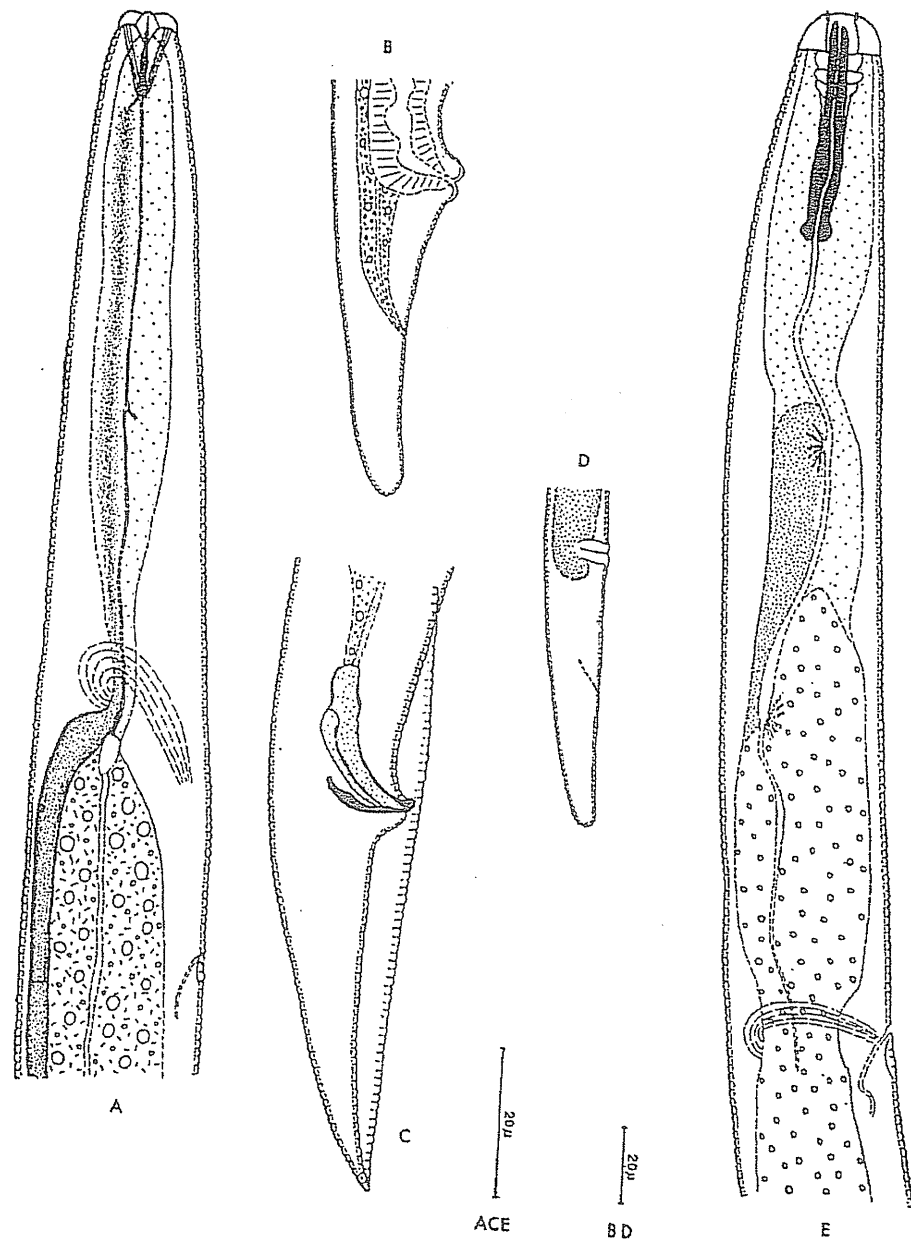


Fig. 6. *Deladenus proximus* n. sp.: A, anterior end of mycetophagous female — lateral; B, posterior end of mycetophagous female — lateral; C, posterior end of male — lateral; D, posterior end of infective female — lateral; E, anterior end of infective female — lateral.

3. Hemizonid and excretory pore in males and infectives ♀♀ 22-54 μm apart 4
 Hemizonid and excretory pore in males and infectives ♀♀ 47-96 μm apart 5
4. Oesophageal gland without long neck usually about same length as oesophagus.
 Mean distance between hemizonid and excretory pore in mycetophagous females 41 μm *D. siricidicola*
 Oesophageal gland usually with long neck and about twice length of oesophagus. Mean distance
 between hemizonid and excretory pore in mycetophagous females 52 μm *D. canii*
5. Mycetophagous and infective female tails acutely pointed.
 Oesophagus of mycetophagous female broadens posteriorly.
 Ratio of dorsal gland duct from anterior end/length of oesophagus of infective ♀ : 20-26 % *D. nevexii*
 Mycetophagous and infective female tails not acutely pointed.
 Oesophagus of mycetophagous females roughly cylindrical.
 Ratio of dorsal gland duct from anterior end/length of oesophagus of infective ♀ : 25-37 % 6.....
6. Dorsal gland of mycetophagous females and male usually shorter than oesophagus and squat.
 Male tail truncated, gubernaculum usually reflexed posteriorly. Infective ♀ stylet 14-21 μm long *D. rudyi*
 Dorsal gland of mycetophagous female and male usually as long as oesophagus and tapering
 posteriorly. Male tail tapering, gubernaculum not reflexed posteriorly. Infective ♀ stylet 20-24 μm
 long *D. imperialis*

DISCUSSION

The evolution of at least seven species of *Deladenus* parasitic in siricids alone is not surprising; some 24 species of host insect from numerous world-wide sources are involved and these infect a variety of coniferous tree species and have at least two associated species of symbiotic fungi. However, the very similar life histories of these species reflect a similarity in the biology of their hosts, the most important aspects of which are the long developmental period (at least a year) and the presence of a symbiotic fungus, providing time and a food supply for free-living generations. The entry or non-entry of juvenile nematodes into the eggs of their hosts is directly connected with the time at which the parent nematode releases juveniles, and is probably indirectly connected, for evolutionary reasons, with whether the host species is mainly solitary or gregarious in its attack on trees. This aspect of the biology is of course of fundamental importance when considering biological control of the host insect species.

Morphologically there is great variability between specimens of a single species from a single source, and these differences are sometimes almost as great as between two specimens of different species. This greatly increases the difficulties of separating species on morphological examination alone particularly since the commonly used de Man ratios are almost useless for separating species of this genus, at least; although

they are devised to allow comparison of animals of widely differing lengths, they none the less vary very considerably with length in *Deladenus* species (Bedding, unpublished) as well as in other genera (Geraert, 1968). Actual measurements are often a much more reliable guide to specific differences. In practice it has been found (R. J. Akhurst, unpublished) that detailed cross-breeding experiments are often a more satisfactory means of species separation in this genus. Thus *D. canii* which is very difficult to separate from *D. siricidicola* by morphological examination is readily separable by cross-breeding experiments and strains of *D. rudyi*, some of which are morphologically readily distinguishable, interbreed readily.

Despite the profound functional dimorphism of mycetophagous and infective females it is of interest to note that a seemingly minor detail such as the proximity of excretory pore and hemizonid is characteristic of both mycetophagous and infective females of a given species and possession of a pointed tail is characteristic of both mycetophagous and infective females of *D. nevexii* yet is not found in the other species described.

The finding of another five species of *Deladenus* adds to the armoury of nematodes that can be considered for release against *S. noctilio* in Australia and New Zealand. The ability of these nematodes to pass through an indefinite number of free-living generations without intervention of an insect host greatly facilitates the laboratory maintenance of different strains and species from many sources and also allows for the mass culture of nematodes for field releases (Bedding & Akhurst 1974).

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ZUSAMMENFASSUNG

Fünf neue entomophag-mycetophage Nematodenarten der Gattung Deladenus (Neotylenchidae), Parasiten von Holzwespen (Siricidae)

Fünf neue Arten von *Deladenus*, Parasiten von Holzwespen (Siricidae) aus verschiedenen Gebieten der Erde, werden ausführlich beschrieben und die Unterschiede zu anderen Arten der Gattung aufgeführt. Ein Bestimmungsschlüssel zu den sieben Arten, von denen bekannt ist, daß sie Siriciden parasitieren, ist beigelegt. Die Biologie dieser Nematoden schließt zwei Lebenszyklen ein, verbunden mit einem starken funktionellen Dimorphismus der erwachsenen Weibchen und der Spermien. Der eine Zyklus ist parasitisch mit einem spaerulariiden Weibchen, das in der Leibeshöhle verschiedener Siriciden lebt und sich ovovivipar vermehrt. Die andere Generation ist freilebend und hat eine neotylenchide Weibchenform mit oviparer Vermehrung. Sie ernährt sich von symbiontischen Pilzen der Wespen im Nadelholz. Der Parasitismus hat bei drei der neuen Arten eine Sterilisierung des weiblichen Wirtes zur Folge. Die vierte Art sterilisiert ihren einzigen bisher bekannten Wirt nicht, und bei der fünften neuen Art hängt die Wirkung von der Artzugehörigkeit des Wirtes ab.

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