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DELADENUS WILSONI N. SP. AND *D. SIRICIDICOLA* N. SP.
(NEOTYLENCHIDAE), ENTOMOPHAGOUS-MYCETOPHAGOUS
NEMATODES PARASITIC IN SIRICID WOODWASPS

BY

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Deladenus wilsoni n. sp. and *D. siricidicola* n. sp. are described in detail and their differences from other species of the genus are given. Both species have strongly dimorphic females; one form, which feeds and reproduces in coniferous timber on the symbiotic fungus of siricid woodwasps is typical of the genus *Deladenus* (Neotylenchidae), and the other, which penetrates the insect larva and reproduces in the insect haemocoel, is typical of the family Allantonematidae. The morphological differences between the two forms throw doubt on the phylogenetic validity of several characters used in nematode taxonomy, particularly in this group.

Nematode parasites of Siricidae were discovered by Zondag (1962) in *Sirex noctilio* F. in New Zealand. They were found in 1964-65 by F. Wilson and J. P. Spradbery (personal communication) in four other siricid species and in the cynipid parasite *Ibalia leucospoides* (Hocken.) from various European countries, and in 1965 by Hocking (1967) in two species of *Rhyssa* (ichneumonid parasites of siricids) introduced into Tasmania from Europe and India.

The life-history of these nematodes, which involves a striking female dimorphism associated with free-living and parasitic cycles, was briefly described by Bedding (1967), who stated that at least two new species of *Deladenus* Thorne were involved, but the infective females and mature parasitic females were not like neotylenchids and alone would be placed in the Allantonematidae. The present paper describes the two species found. A detailed account of the biology of the species will be published shortly.

MATERIAL AND METHODS

Nematodes from various siricid and ichneumonid hosts collected in many European countries and from *Sirex noctilio* collected in New Zealand were cultured on the fungus *Amylostereum chailletii* (Fr.) Boidin (which is symbiotically associated with siricids), and morphological examination and interfertility tests showed that all of these nematodes belong to one or other of the present two species. However, the description of each species is based on specimens cultured from larvae from a single parent nematode, collected as follows:

Deladenus wilsoni ex haemocoel of a male *Rhyssa persuasoria* L. (Ichneumonidae) from *Abies alba* Mill. collected in Hodruša Valley, Banská Stianica, Czechoslovakia.

Deladenus siricidicola ex testis of a male *Sirex juvencus* L. (Siricidae) from *Picea abies* (L.) collected in Varbely, Sopron, Hungary.

The nematodes were killed by maintaining them at 60°C for 2 minutes, fixed in 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, 1968) assisted surface and *en face* examination.

DELADENUS WILSONI N. SP.

(Table I; Fig. 1 A, B, Fig. 2 A-I, Figs. 3-7)

Mycetophagous female. — Cuticle with transverse striae about 1 μ 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 visible without silver deposition; extending from tip of tail for about 98% of body length (25-40 striations from anterior end): varying in different specimens from tenth to a third of body width; anteriorly usually arising as three incisures which branch until full complement of 10-13 is reached at about a fifth of way along body length. Incisures branching and merging throughout length and in some specimens even forming whorls; usually reduced to 7-9 at level of vulva; terminating in 5-7 (Figs. 3 & 4).

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.

Stylet (10-11 μ) finely tapering anteriorly with well developed basal knobs; lumen not visible anteriorly, very narrow posteriorly. Corpus of oesophagus fusiform; lumen narrow with only a trace of median-chamber apparent in most specimens. Isthmus very narrow, joining wide lumen of intestine immediately behind nerve ring. Duct of dorsal oesophageal gland opening close to base of stylet. Dorsal oesophageal gland (almost completely obscured by food reserves in many specimens) greatly enlarged posterior to oesophagus and lying adjacent to intestine in uninucleate lobe of length similar to oesophagus. Only trace of sub-ventral glands apparent; fine ducts opening into hollow chamber about half way along oesophagus.

Intestinal lumen wide (up to a fifth body width) and not greatly convoluted; cells of intestine very opaque.

Excretory pore with well cuticularized, terminally funnel-shaped tube; coincident with or just in front of hemizonid and always well behind nerve ring; excretory cell large, situated from a tenth to a sixth of body length from anterior end.

Vulva a broad transverse slit with protuberant lips; vagina well cuticularized;

TABLE I
 Measurements of adults (*Mycetophagous* ♀♀, ♂♂ and *Infective* ♀♀) of
Deladenus wilsoni n. sp.

	Mycetophagous females			Males			Infective females		
	Holotype	paratypes (n = 50)	Allotype	paratypes (n = 50)	paratypes (n = 50)	paratypes (n = 50)	paratypes (n = 50)	paratypes (n = 50)	paratypes (n = 50)
	mean	standard error	range	mean	standard error	range	mean	standard error	range
L (mm)	1.72	.051	1.49-2.7	1.75	.026	1.29-2.02	1.16	.018	0.88-1.74
a	61.4	.89	34.6-62.6	64.1	1.22	40-79.2	63.8	.98	48.9-81.2
b	18.1	.32	15.5-26.5	19.5	.3	13.6-22.4	11.8	.15	9.8-15.1
c	49.1	.81	46.6-66.9	42.2	.6	31.1-54.4	36.2 (f)	.57	28.3-45.8
V	95.3	.051	94.6-96.2	—	—	—	93.7	.08	91.9-94.7
G ₁ or T	82.2	.92	54-95.1	84.1	1.28	66.4-94.3	54	.94	41.3-70.5
L/Excretory pore from fore-end	15.6	.25	12.7-19.6	15.4	.17	11.7-16.4	10.4 (a)	.16	8.3-15.4
L/Hemizonid from fore-end	14.6	.24	12-18.8	14.7	.14	11.7-16.3	10.1 (a)	.17	8.2-15.4
Excretory pore in front of hemizonid (μ)	8	.49	0-11	6	.53	0-10	2.6 (f)	.41	—
Stylet length (μ)	10	—	10-11	10	—	10-11	19	.41	14-30
Tail/anal body width	2.5	.045	1.6-2.6	2.4	.037	1.8-3.1	2.7 (g)	.051	1.6-3.7
L/Sub-ventral gland opening from fore-end	—	—	—	—	—	—	18.3 (h)	.34	14.2-21.7
(a) 44 ♀♀			(c) 21 ♀♀			(f) 42 ♀♀			
(b) 40 ♀♀ or ♂♂			(d) 47 ♂♂			(g) 33 ♀♀			
			(e) 38 ♂♂			(h) 29 ♀♀			

no post-vulval uterine sac; long oviduct packed with large, amoeboid spermatozoa (10-12 μ) and usually containing one or two undeveloped eggs, although very old females may accumulate two or three dozen, some hatching within parent

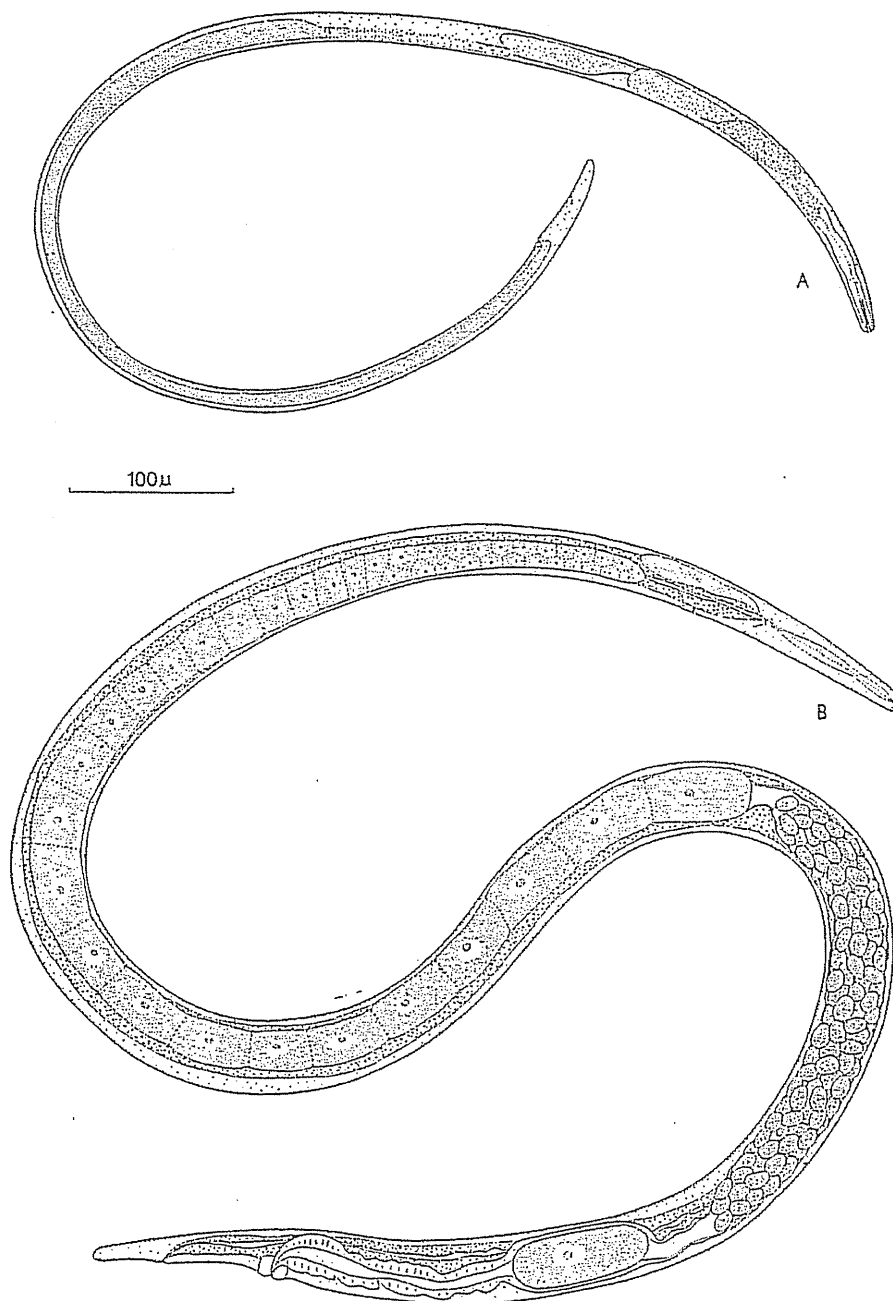


Fig. 1. *Deladenus wilsoni* n. sp.: A, infective female; B, mycetophagous female.

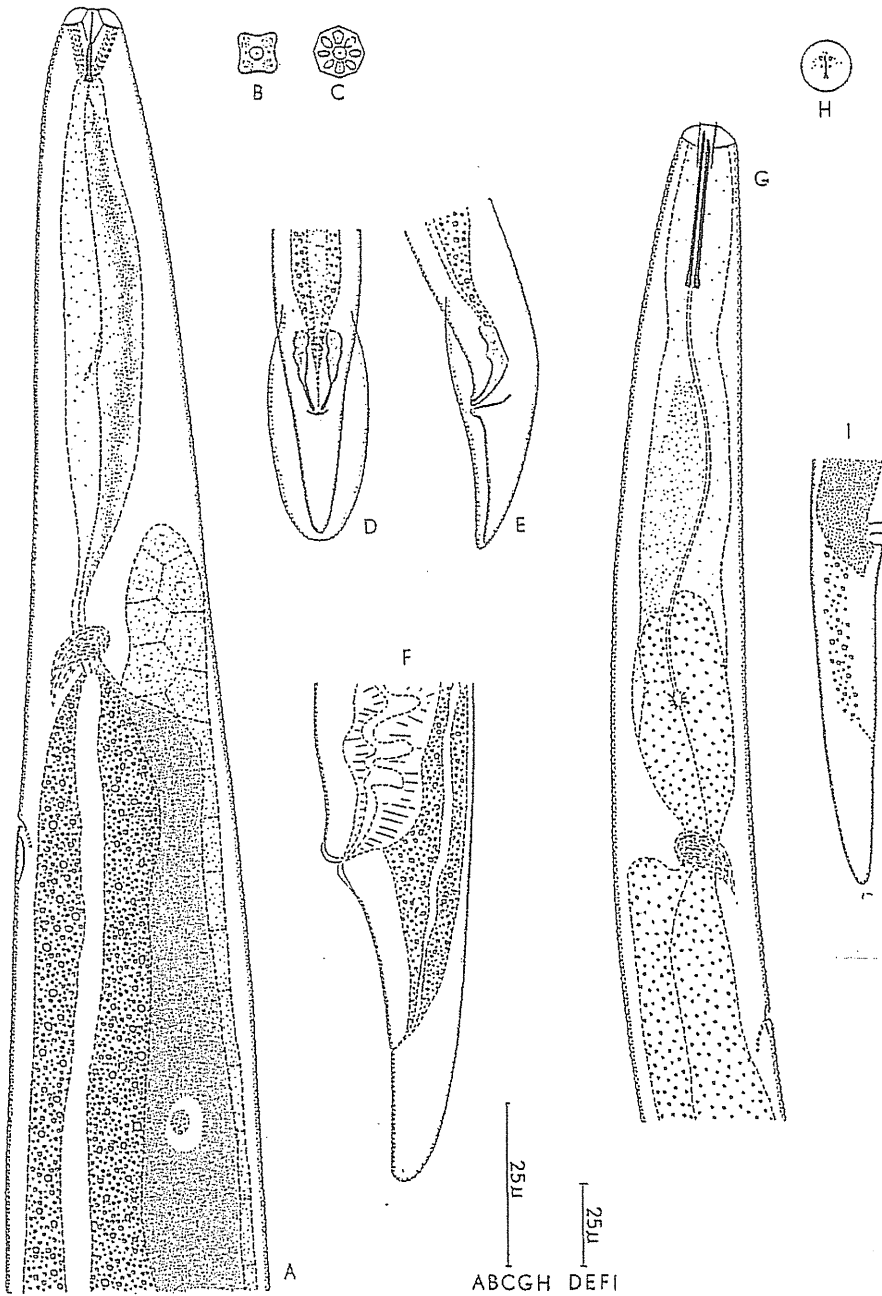


Fig. 2. *Deladenus wilsoni* n. sp.: A, anterior end of mycetophagous female — lateral; B, en face view of lip region of mycetophagous female; C, cephalic framework of mycetophagous female; D, posterior end of male — ventral; E, posterior end of male — lateral; F, posterior end of mycetophagous female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

after death. Prodelphic ovary usually 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 a seventh to a third of body width; bursa striated, enveloping tail and extending in front of spicules (Fig. 5). Testis outstretched. Spicules (19-23 μ) 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 above for the mycetophagous female and other (found in infective females) much smaller (1-2 μ) spherical and composed mainly of nucleus.

Infective female. — Cuticle with transverse striae about 1.2 μ 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 fifth to a third of body width; anteriorly usually arising as 3 incisures with 4 incisures for a distance of 3-5 body widths behind the nerve ring giving way to 8-13 for most of remaining body length; 3-5 incisures on tail. Incisures not repeatedly branching and merging as in mycetophagous females.

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

Stylet (14-30 μ) very different from that of mycetophagous female and male: stout, with a wide lumen; lacking conspicuous knobs; not tapered anteriorly but dorsally extended further than ventrally.

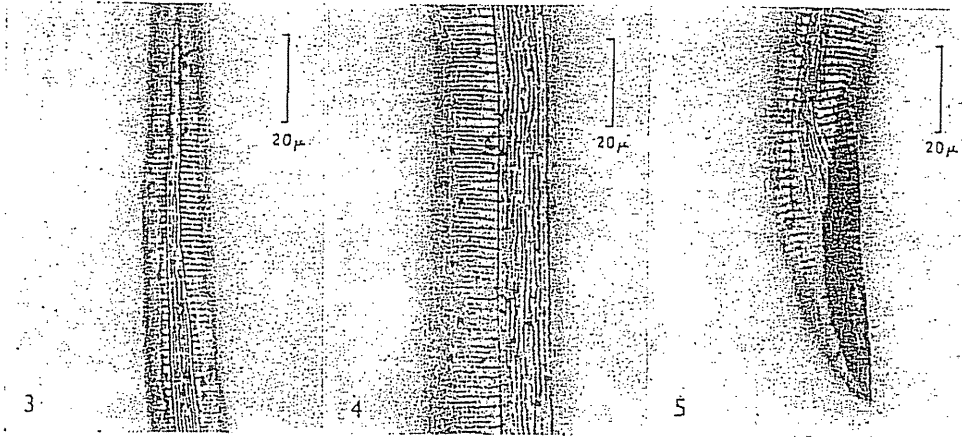
Corpus of oesophagus approximately cylindrical; slightly constricted near stylet base; lumen very wide anterior to ducts of sub-ventral glands; broadening slightly at entry of ducts then becoming very fine. Isthmus short and broad. Outlet of dorsal gland little less than a stylet length behind stylet base; dorsal oesophageal gland finely granular, confined within oesophagus. Complicated sub-ventral glands with numerous ducts radiating from each side of oesophageal lumen; extending anteriorly about a body width in front of ducts and posteriorly down to ovary; three lobes distinguishable laterally, posterior two each with a single nucleus and filled with coarse globules anteriorly, usually only finely granulated posteriorly.

Only trace of intestine apparent is in the posterior region; no lumen; rectum narrow and straight.

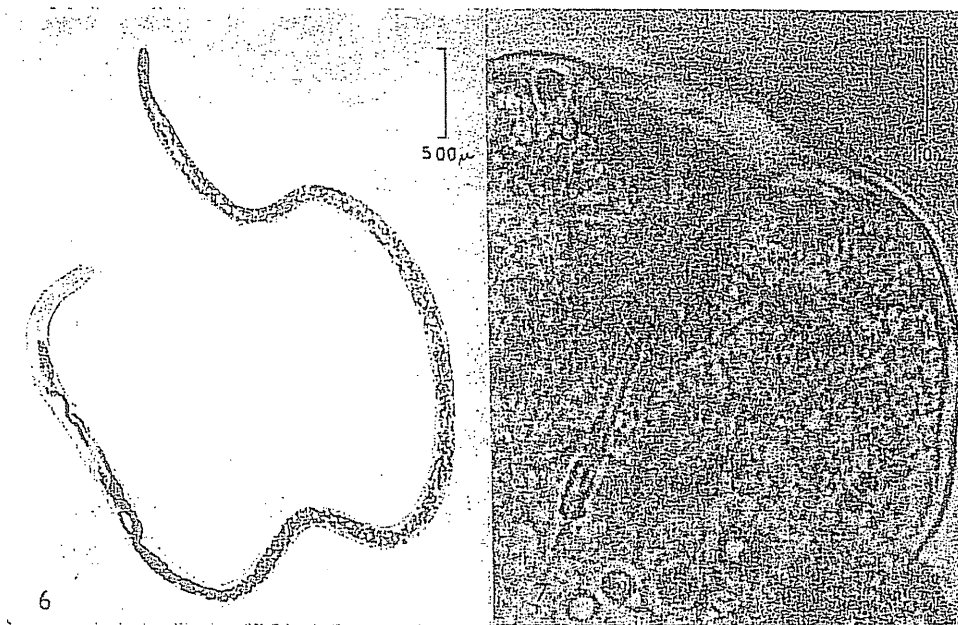
Nerve ring about a body width behind sub-ventral gland ducts. Excretory pore coincident with or close to hemizonid and well behind nerve ring.

Vulva appearing in ventral view as a narrow transverse slit on a small circular, heavily cuticularized surround; lips barely protuberant; vagina heavily cuticu-

R. A. BEDDING: *Deladenus wilsoni* n. sp. and *D. siricidicola* n. sp.



Figs. 3-5. Photomicrographs showing lateral field of *Deladenus wilsoni* n. sp. after silver deposition. 3 — anterior end of mycetophagus female. 4 — mid region of mycetophagus female. 5 — posterior end of male.



Figs. 6 & 7. *Deladenus wilsoni* n. sp. 6 — mature parasitic female. 7 — anterior end of mature parasitic female showing retraction of stylet.

larized; small post-vulval uterine sac. Ovary prodelphic, undeveloped; thin walled oviduct normally packed with small spermatozoa (1-2 μ) occupying about half body length. (At an earlier research stage (Bedding, 1967) it had been thought that the parasitic life cycle was parthenogenetic.)

Mature parasitic female. — Very large (3.25-25 mm long, 0.1-0.5 mm wide), cylindrical; rounded or tapering tail; often greenish in colour; occasionally distinctly beaded externally (depending on host); crudely striated, striations 3-15 μ apart. 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.

Larvae. — From 0.25 mm long; stylet (10-11 μ) identical with that of mycetophagous female and male; hemizonid and excretory pore coincident or close; no distinction observed between larvae destined to be different types of female.

Differential diagnosis. — (Infective or parasitic females, which have not been described for other species, not included).

Other Species	<i>D. wilsoni</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) Thorne, 1941	10-13 incisures; longer stylet; wide intestinal lumen; no fine mucron on male tail.
<i>D. norimbergensis</i> R�hm, 1956	Stylet longer; isthmus of oesophagus much narrower; gut lumen wider; vagina heavily cuticularized; post vaginal region more tapered.
<i>D. obesus</i> Thorne, 1941	Amphid apertures less widely spaced; trace of hollow chamber in corpus of oesophagus; no post-rectal sac; differently shaped vagina and tail.
<i>D. saccatus</i> Andr�ssy, 1952	Much longer; greater values for c & V; differently shaped vagina and tail; no post-vulval sac; excretory pore anterior to hemizonid.

Type slides. — Holotype ♀: slide no. 1968/23. Allotype ♂: slide no. 1968/24. Paratypes: 5 mycetophagous ♀♀, slide no. 1968/25. 5 ♂♂, slide no. 1968/27. 5 infective ♀♀, slide no. 1968/26, all at the Department of Zoology, British Museum (Natural History), London, S.W. 7. Corresponding fifteen paratypes also at each of the following institutions: Nematology Department, Rothamsted Experimental Station, Harpenden (slide nos. 67/3/1, 67/3/2 and 67/3/3), The Australian Museum, Sydney (slide nos. W4166-8), and The Entomology Division, D.S.I.R., New Zealand (slide nos. 1-3, *Deladenus wilsoni*).

DELADENUS SIRICIDICOLA N. SP.

(Table II; Fig. 8 A-J)

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

Mycetophagous female. — Lateral fields varying from a fifth to a half of body

TABLE II
*Measurements of adults (Mycetophagous ♀♀, ♂♂ and Infective ♀♀) of
 Deladenus siridicola n. sp.*

	Mycetophagous females			Males			Infective females		
	Holotype	paratypes (n = 50)	Allotype	paratypes (n = 50)	paratypes (n = 50)	paratypes (n = 50)	paratypes (n = 50)	paratypes (n = 50)	paratypes (n = 50)
	mean	standard error	range	mean	standard error	range	mean	standard error	range
L (mm)	1.94	.039	1.50-2.71	1.48	.021	1.15-1.92	1.22	.027	0.80-1.60
a	53.9	.97	33-69.1	59.2	.99	43.2-77.5	61.2	1.41	44-109.1
b	19.6	.39	15.2-26.6	15.7	.24	12.1-22.4	10.9	.13	9.3-13.7
c	45.1	.74	32.6-58.9	34.4	.33	26.1-37	35.1	.53	27-43.8
V	95.2	.087	93.2-96.2	—	—	—	94.1	.059	92.8-95
G ₁ or T	89.8	1.06	60.7-92.2	85.3	.56	76.3-91.9	36.7	.78	27.6-52
L/Excretory pore from fore-end	17.5	.35	13.6-24	16.8	.22	13.7-20.7	12.6	.17	10.5-15.7
L/Hemizonid from fore-end	13.3	.23	10-17.1	13.2	.13	9.7-13.8	9.3 (b)	.12	7.9-11.8
Excretory pore in front of hemizonid (μ)	34	1.23	24-58	24	.8	22-46	33 (b)	.85	22-45
Stylet length (μ)	10	—	10-11	10	—	10-11	21	.23	19-25
Tail/anal body width	2.7	.03	1.9-2.9	3.3	.055	2.3-4.2	3.2 (c)	.067	1.7-4.2
L/Sub-ventral gland opening from fore-end	—	—	—	—	—	—	16.5	.2	13.4-20

(a) 42 ♀♀
 (d) 45 ♀♀
 (e) 46 ♂♂

(a) 44 ♀♀ or ♂♂
 (b) 48 ♀♀ or ♂♂

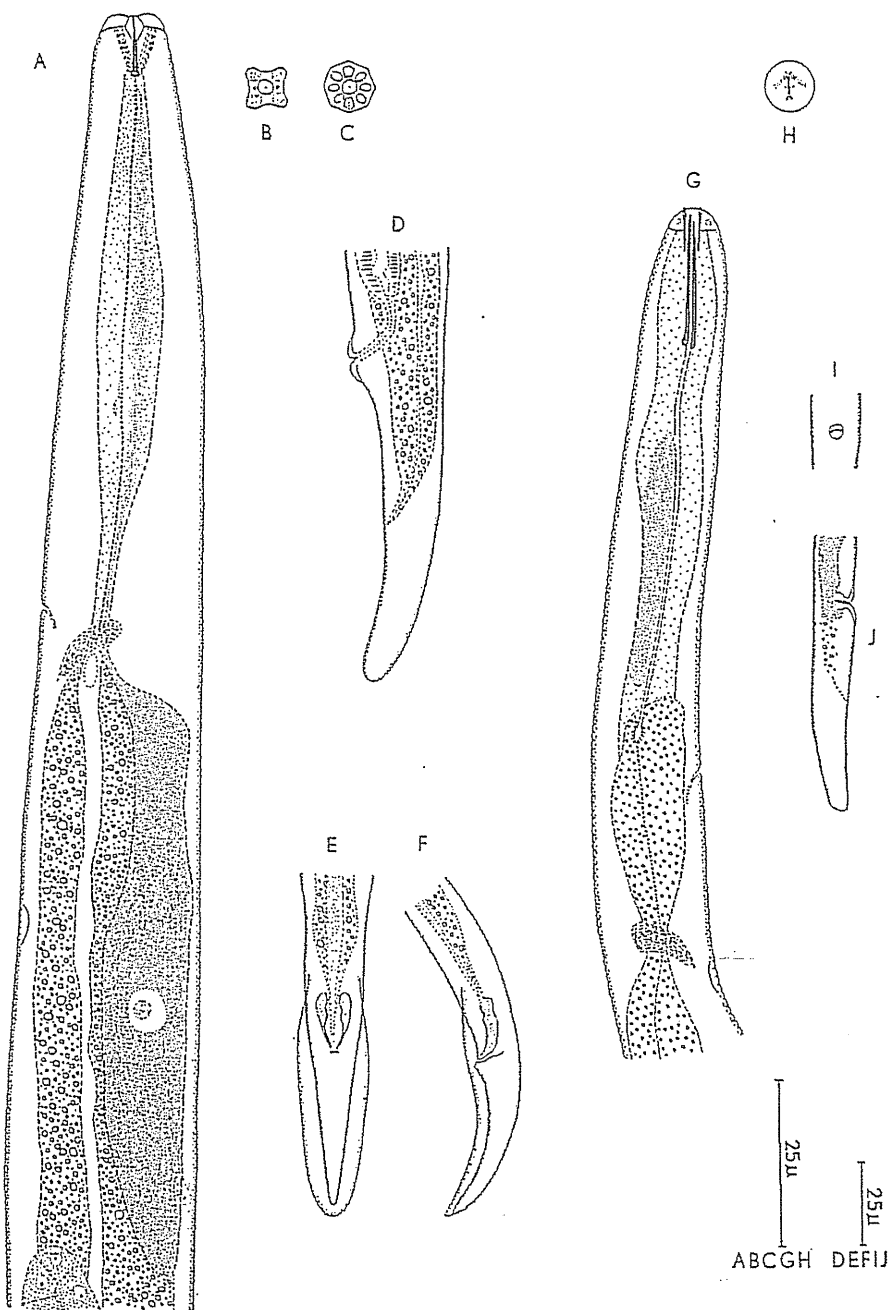


Fig. 8. *Deladenus siricidicola* n. sp.: A, anterior end of mycetophagous female — lateral; B, en face view of lip region of mycetophagous female; C, cephalic framework of mycetophagous female; D, cephalic framework of mycetophagous female — lateral; E, posterior end of male — ventral; F, posterior end of male — lateral; G, anterior end of infective female — lateral; H, en face view of infective female; I, vulva of infective female — ventral; J, posterior end of infective female — lateral.

width; anteriorly usually arising as four incisures which branch until full complement of 12-15 is reached at about a fifth of way along body length.

Ovoid plug sometimes visible in intestine at junction with oesophagus.

Excretory pore $1\frac{1}{2}$ -2 body-widths in front of hemizonid; varying in position just in front of or behind nerve ring.

Male. — Lateral fields usually from a third to a half body width, c usually much less than in *D. wilsoni*.

Infective female. — Sub-ventral gland not extending much in front of gland ducts. Usually much shorter ovary than in *D. wilsoni*.

Excretory pore and hemizonid far apart, as in mycetophagous female and male.

Mature parasitic female. — Indistinguishable from *D. wilsoni* when obtained from same host species.

Larvae. — Hemizonid and excretory pore well separated.

Differential diagnosis. — Most similar to *D. wilsoni*; easily separated from this species (even in the larval forms) by the much greater distance between its hemizonid and excretory pore. Different from other species of *Deladenus* in same characters as *D. wilsoni*.

Type slides. — Holotype ♀: slide no. 1968/18. Allotype ♂: slide no. 1968/19. Paratypes: 5 mycetophagous ♀♀, slide no. 1968/20. 5 ♂♂, slide no. 1968/21. 5 infective ♀♀, slide no. 1968/22, all at The Department of Zoology, British Museum (Natural History). Corresponding fifteen paratypes also at each of the following institutions: Nematology Department, Rothamsted Experimental Station, (slide nos. 67/4/1, 67/4/2, 67/4/3); The Australian Museum, (slide nos. W4169-71) and The Entomology Division, D.S.I.R., New Zealand (slide nos. 1-3, *Deladenus siricidicola*).

DISCUSSION

There can be little doubt that if the infective or parasitic forms of either of these species had not been experimentally derived from the mycetophagous females, they would have been placed in the Allantonematidae. In fact, Dale (1967) states that W. C. Clark who examined the nematodes from *Sirex noctilio* in New Zealand, considered that they belonged to the genus *Parasitylenchus* Micoletzky of this family.

Although there are no differences between the Allantonematidae and Neotylenchidae that do not occur between the two forms of *Deladenus wilsoni* and *D. siricidicola*, these nematodes are placed in the genus *Deladenus* (Neotylenchidae) because: (a) the mycetophagous female and the male fit perfectly into this genus; (b) there is no allantonematid genus suitable for the infective female; and (c) it is probable that the mycetophagous female is the more primitive form.

Rühm (1956) synonymized the genus *Sphaerulariopsis* Wachek (Allantonematidae) with *Stictylus* Thorne (Neotylenchidae) because of similarity in morphology (particularly of the stylets), and although Nickle (1963) rejected this synonymy on the basis of differences in the ovaries of the two genera, the present

work shows that this is not a reliable criterion. Many other neotylenchid species have been found either in insect frass or in insect galls, and it seems likely that some, at least, of these have allantonematid forms parasitic on insects.

Apart from ovarian dimorphism, *Deladenus wilsoni* and *D. siricidicola* show extreme dimorphism of the stylet, lip region, oesophagus, oesophageal glands, intestine, spermatozoa and vulva, most of which characters have assumed general taxonomic importance. These considerable differences constitute major adaptations of morphology to function, and indicate that such characters may have little phylogenetic importance because they vary so considerably within a single species.

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ZUSAMMENFASSUNG

Deladenus wilsoni n. sp. und *D. siricidicola* n. sp. (Neotylenchidae), zwei entomophag-nyctophag Nematoden, die in Holzwespen (Siricidae) parasitieren

Deladenus wilsoni n. sp. und *D. siricidicola* n. sp. werden ausführlich beschrieben und Merkmale, die diese von anderen Arten unterscheiden, werden mitgeteilt. Die Weibchen beider Arten zeigen einen ausgeprägten Dimorphismus. Die eine Form, die sich in Nadelholz von dem symbiontischen Pilz von Holzwespen (Siricidae) ernährt und vermehrt, ist typisch für die Gattung *Deladenus* (Neotylenchidae). Die andere, die in die Insektenlarve eindringt und sich im Haemocoel des Insekts vermehrt, ist typisch für die Familie Allantonematidae. Die morphologischen Unterschiede zwischen den beiden Formen machen die phylogenetische Gültigkeit mehrerer Merkmale, die in der Nematodentaxonomie und besonders in dieser Gruppe gebraucht werden, zweifelhaft.

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