

Two new species of *Schistonchus* (Tylenchida : Aphelenchoididae) associated with *Ficus macrophylla* from Australia

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Summary – Two new species of the genus *Schistonchus* are described from inflorescences of *Ficus macrophylla* in Australia : *S. macrophylla* n. sp. from Adelaide and *S. altermacrophylla* n. sp. from Sydney. *S. macrophylla* n. sp. is characterised by the tail without a mucron and the excretory pore at the level of the median bulb in both sexes, spicule shape in the males, and a long post-vulval sac in females. *S. altermacrophylla* n. sp. is characterised by having the excretory pore very close to head region. The diagnosis of the genus is emended. Both new species develop concomitantly with the wasp *Pleistodontes froggatti*. *S. macrophylla* n. sp. was carried between inflorescences in the abdomen of the wasp. *S. macrophylla* n. sp. was also recovered from three other species of *Ficus*, all endemic to Australia.

Résumé – Deux nouvelles espèces de *Schistonchus* (Tylenchida : Aphelenchoididae) associées à *Ficus macrophylla* en Australie – Description est donnée de deux nouvelles espèces du genre *Schistonchus* originaires des inflorescences de *Ficus macrophylla* en Australie : *S. macrophylla* n. sp. d'Adelaide et *S. altermacrophylla* n. sp. de Sydney. *S. macrophylla* n. sp. est caractérisée par la queue sans mucron et le pore excréteur au niveau du bulbe médian chez les deux sexes, la forme des spicules chez le mâle et le long sac postvulvaire chez la femelle. *S. altermacrophylla* n. sp. est caractérisé par la position du pore excréteur très proche de la région céphalique. La diagnose du genre est modifiée. Les deux nouvelles espèces se développent concomitamment avec la guêpe *Pleistodontes froggatti*; *S. macrophylla* n. sp. est transporté entre les inflorescences dans l'abdomen de la guêpe. *S. macrophylla* a été également trouvé dans trois autres espèces de *Ficus*, toutes endémiques en Australie.

Key-words : Aphelenchoididae, biology, *Ficus*, inflorescence, Nematoda, *Pleistodontes froggatti*, *Schistonchus*, taxonomy.

The inflorescences (fruits) of various *Ficus* spp., dependent on invading agaonid wasps for pollination, are parasitized by a range of nematodes. Martin *et al.* (1973) found that more than twenty species, from Aphelenchoidea, Cyliandrocorporidae and Diplogasteridae, inhabited the fruit of six species of *Ficus* indigenous to Zimbabwe. *Schistonchus hispida* Kumari & Reddy, 1984 and *S. racemosa* Reddy & Rao, 1986 were described from India.

Speciation and adaptive radiation in *Parasitodiplogaster* from *Ficus* fruits in Panama was discussed by Poinar and Herre (1991). Vovlas *et al.* (1992) examined the biology of *S. caprifici* Gasperrini, 1864 in Italy. This paper describes the morphology and biology of *Schistonchus macrophylla* n. sp. and the morphology of *S. altermacrophylla* n. sp. (Tylenchida : Aphelenchoididae) associated with agaonid wasps found in fruit of the Moreton Bay fig, *F. macrophylla* Desf., from Australia.

Materials and methods

Nematodes for study by light and scanning electron microscopy were collected from fig fruits which were broken open and placed in tap water. Emerging nematodes were collected, then relaxed and fixed in hot FA 4:1. Wasps were dissected in 0.85 % NaCl, and ne-

matodes from these were relaxed and fixed as above. They were prepared for mounting on slides by a process of slow evaporation. Nematodes were transferred from fixative to a solution of 99 ml 30 % ethanol and 1 ml glycerol in glass blocks and placed in a dessicator containing 96 % ethanol for 2 days. For the following 14 days these blocks were kept in an incubator at 40 °C. During the first week of this, one or two drops of a solution of 95 ml 95 % ethanol and 5 ml glycerol were added, four times daily. Slow evaporation was continued for the second week. The processed nematodes were mounted in glycerol and examined using interference microscopy. Spicule length was measured as the length of the median line through the spicule (Hooper, 1986). For scanning electron microscopy, fixed nematodes were dehydrated in a series of ethanol solutions namely : 7.5, 15, 20, 30, 50, 75, 90, 100 % (three times). They were dried, using CO₂ in a critical point drier, then mounted on stubs, sputter coated with 30 nm of gold and viewed at 20 kV.

Monthly collections of fig inflorescences from a mature specimen of *F. macrophylla* growing in the Waite Arboretum, Adelaide, were made during 1993. Fruits from various species of figs growing in the Adelaide Botanic Garden were collected in March, 1994. The fig inflorescences were broken open in tap water, and any

nematodes which emerged in 24 h were collected. The degree of development of male and female florets within the figs was noted. Occasional collections of wasps, emerging from fruit and/or on the tree, were made and these were dissected to look for nematodes.

***Schistonchus macrophylla** n. sp.**

(Figs 1, 2)

MEASUREMENTS

Holotype (female) and *paratypes* (males, females): Table 1.

Juveniles length (μm): J2 ($n = 10$): 290 ± 33 (220-317); J3 ($n = 10$): 460 ± 22 (420-503); J4 ($n = 7$): 500 ± 27 (471-542).

DESCRIPTION

Females: Nematodes ventrally arcuate when heat killed. Greatest width at mid-body. Cuticle finely annulated. Lateral field with three or four lines, obscure under light microscopy except at the mid-body. Head region slightly expanded. Cephalic framework with relatively strong sclerotization. Under light microscopy, lip region somewhat truncate; distinct labial disc, with fused lips, and one cephalic annule. Stylet robust with large spherical knobs, conus 64 % of total stylet length. Prominent stylet musculature appearing to be attached to the shaft at regular intervals, as well as to the knobs. Short procropus with distinct terminal constriction, connected to an ovoid median bulb with valves slightly posterior to centre. Excretory pore 35 to 52 μm behind anterior end, opening in region of median bulb. Oesophageal glands with dorsal and ventral lobes, often indistinct, variable in length, both usually overlapping the intestine. Oesophago-intestinal junction 10 μm behind the bulb. Deirids, hemizonid and phasmids not seen. Ovary monoprodelphic and reflexed; without flexure in some females with slightly prominent lips (possibly young females). Vulval lips usually slightly prominent; anterior vulval lip may overlap the opening. Vagina directed anteriorly; vaginal walls with prominent musculature. Post-vulval sac variable in length, in most specimens about three times as long as maximum body width; no defined spermatheca. Tail conical with rounded tip without mucro.

Males: Nematodes ventrally arcuate when heat killed, more strongly in tail region. Greatest width at mid-body. Cuticle finely annulated. Three lines in the lateral fields, obscure except at mid-body and tail region. Head region, stylet, oesophagus, intestine, excretory pore, and tail shape as for females. Deirids, hemizonid and phasmids not seen. Testis usually reflexed; spicules rose thorn-shaped having a prominent, conical rostrum and broad lamina with a shallow, crescent-shaped groove

close to the ventral edge; small, triangular gubernaculum-like structure present near the spicule tip; spermatozoa flagellate. Three pairs of papillae present; one inconspicuous pair at the rostrum level, an inconspicuous adanal pair, and a third very conspicuous pair ventrally about halfway along the tail. Caudal alae present as a ridge-like thickening of the lateral field between anus and tail tip.

Juveniles: As for females, except the lateral fields containing eight lines extending from the middle of the procropus to the level of the anus.

TYPE HOST AND LOCALITY

Ficus macrophylla Desf. Arboretum, Waite Campus, University of Adelaide, Urrbrae, South Australia ($34^{\circ} 58' \text{S}$, $138^{\circ} 38' \text{E}$). *S. macrophylla* has also been recovered from inflorescences of the following figs growing in Adelaide: *F. baileyana* Domin., *F. macrophylla* Desf., *F. platypoda* (Miq.) Cunn. ex. Miq., and *F. rubiginosa* Desf. ex. Vent. Fruit from *F. racemosa* L. and *F. thoningi* Blume, which are exotic species, but which are also grown in Adelaide, did not contain nematodes.

TYPE SPECIMENS

Holotype (female) deposited in the Queensland Museum, Queensland, Australia (specimen number G20 3476). *Paratypes* (male, female and juvenile) deposited in the Waite Agricultural Research Institute Nematode Collection, Adelaide, South Australia (W.I.N.C. number 802), and (males and females) in the Muséum National d'Histoire Naturelle, Paris, France.

DIAGNOSIS AND RELATIONSHIPS

S. macrophylla n. sp. is characterised by absence of the mucro on the tail tip in all stages, the long post-vulval sac and absence of a defined spermatheca in the female, and rose thorn-shaped spicule with prominent rostrum and with crescent-shaped groove close to ventral edge of the lamina.

Mucro is present on tail tip of males, females and juveniles of *S. racemosa* (Reddy & Rao, 1986), and of males and females of *S. caprifici* (Vovlas *et al.*, 1992) and *S. altermacrophylla* n. sp. Females of all known species in the genus *Schistonchus* have a short post-vulval sac (28 μm long in *S. racemosa* and 9 μm in *S. caprifici*) less than a body width in length, except *S. macrophylla* n. sp. (29-80 μm). The spicule of *S. macrophylla* n. sp. has a broader lamina than *S. racemosa*, and the more prominent rostrum and ventral position of the groove on the lamina distinguishes it from the spicule of *S. altermacrophylla* n. sp.

BIOLOGY

Wasps associated with and containing *S. macrophylla* n. sp. were identified as *Pleistodontes froggatti* Mayr.

* The specific name refers to the type host.

Table 1. Morphometric data of *Schistonchus adults* (all measurements in μm).

Measurements (μm)	<i>S. macrophylla</i> n. sp.			<i>S. altermacrophylla</i> n. sp.		
	Females Paratypes	Holotype	Males Paratypes	Females Paratypes	Holotype	Males Paratypes
n	20		26	10		12
L	500 \pm 47 (445-596)	596	560 \pm 44 (445-618)	500 \pm 49 (411-571)	546	500 \pm 44 (445-570)
Diameter	19 \pm 2 (16-23)	21	19 \pm 2 (16-21)	23 \pm 2 (19-25)	21	18 \pm 2 (15-19)
Stylet	21 \pm 2 (17-28)	28	24 \pm 2 (22-28)	21 \pm 2 (17-26)	23	22 \pm 3 (16-25)
Ant. end-excret. pore	45 \pm 5 (35-52)	56	45 \pm 6 (35-60)	6 \pm 2 (5-9)	9	6 \pm 1 (3-7)
Ant. end-base med. bulb	65 \pm 3 (59-69)	60	61 \pm 3 (51-66)	69 \pm 6 (55-77)	61	65 \pm 7 (60-71)
n (dorsal gland)	20		21	7		8
Ant. end-base dorsal gland	150 \pm 20 (120-182)		120 \pm 20 (96-154)	140 \pm 20 (114-168)		130 \pm 20 (112-163)
n (ventral gland)	10		5	4		5
Ant. end-base ventral gland	100 \pm 9 (81-115)		100 \pm 5 (96-109)	100 \pm 5 (95-104)		90 \pm 11 (70-97)
Ant. end-nerve ring	77 \pm 4 (60-78)	66	72 \pm 4 (60-78)	76 \pm 8 (60-83)	64	72 \pm 8 (60-85)
Post-vulval sac	40 \pm 12 (29-80)	80	— —	14 \pm 3 (8-20)	14	— —
Tail	53 \pm 6 (43-62)	51	40 \pm 4 (34-50)	29 \pm 4 (23-34)	26	34 \pm 2 (28-37)
Spicule	— —		19 \pm 2 (15-24)	— —		21 \pm 2 (18-24)
Testis	— —		400 \pm 59 (275-457)	— —		330 \pm 49 (273-401)
V	66 \pm 1 (63-68)	68	— —	85 \pm 9 (70-95)	72	— —
a	26 \pm 2 (23-31)	28	30 \pm 2 (25-34)	22 \pm 3 (17-29)	26	28 \pm 2 (25-31)
b'	5 \pm 0.9 (3-7)	7	5 \pm 0.8 (4-6)	5 \pm 1.2 (3-8)	8	4 \pm 0.6 (3-5)
c	10 \pm 2 (7-12)	12	14 \pm 1 (11-17)	17 \pm 2 (14-21)	21	15 \pm 1 (13-16)
c'	4 \pm 0.6 (3-5)	4	3 \pm 0.3 (2.5-3.5)	3 \pm 0.3 (2.8-3.8)	3	2 \pm 0.2 (1.7-2.4)

When alate female wasps (n = 74) were dissected, only young inseminated female nematodes were found, always in the haemolymph of the abdomen. Nematodes were not seen in larvae, or in apterous males. It is not known when the nematodes enter the wasp, because no

pupae were found, and it is not known how they leave. Nematode eggs were not seen in wasps. About 25 % of female wasps dissected contained 3.2 (1-8) nematodes, but this varied from 8-55 % in different collections.

About half of the fig inflorescences (n = 102) which

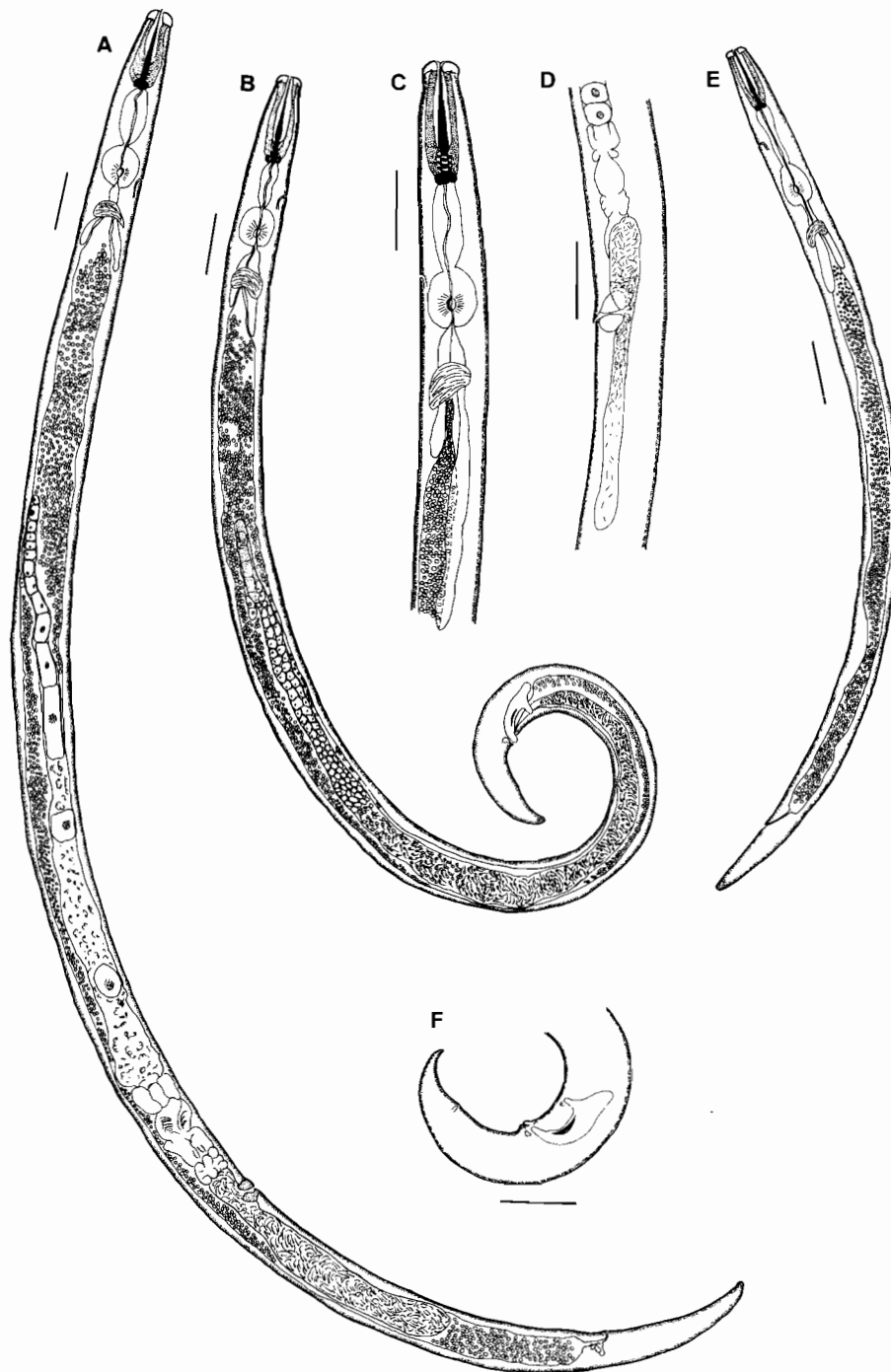


Fig. 1. *Schistonchus macrophylla* n. sp. A: Female; B: Male; C: Oesophageal region of male; D: Vulva and post-vulval sac; E: Juvenile; F: Tail region of male.

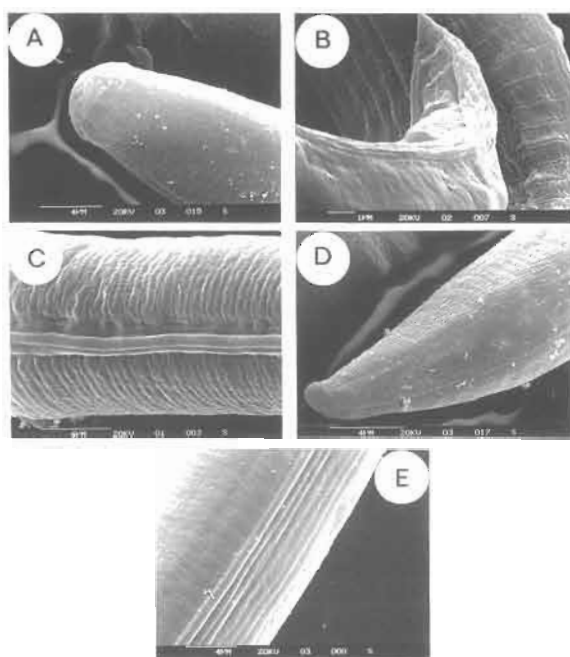


Fig. 2. *Schistonchus macrophylla* n. sp. A : Anterior region of female; B : Posterior region of male; C : Lateral field at midbody of female; D : Lateral field at tail of female; E : Lateral field at midbody of juvenile.

were opened and extracted contained nematodes. Monthly observations on the stage of development of the inflorescences, counts of nematodes extracted, and determination of their stage of development, were made. When a female wasp invaded a young fruit (then soft, hollow, and containing only developing female florets), *Schistonchus* females emerged and began egg-laying. The wasp also laid eggs, and the hatched larvae formed a gall in a female floret and began to grow. At this stage, a few female nematodes, juveniles and eggs could be found in a fig inflorescence, external to plant tissue. With time and further development of the inflorescence, the tissue of which became denser as the florets grew, the nematode population increased, and males were seen. Brown lesions, possibly caused by nematodes feeding on the fig-cells, were found in the fig fruits. By the time that the inflorescence contained both male and female florets, it was very hard and difficult to open, and the numbers of *Schistonchus* observed had increased to several hundred. The sex ratio shifted with this increase, with females outnumbering males by about 2:1. As the inflorescence matured, so did the wasps, and female wasps began to emerge. Such mature figs contained up to 900 nematodes, most of which were adults, having a sex ratio of three females to one male. It seems likely that the female wasps then invaded new young inflorescences, enabling the cycle to continue. Ripe figs did not contain nematodes.

*Schistonchus altermacrophylla** n. sp.

(Fig. 3)

MEASUREMENT

Holotype (female) and *paratypes* (males, females) : Table 1.

Juveniles length (μm)-J2 (n = 3) : 280 ± 30 (245-305); J3 (n = 5) : 350 ± 11 (332-358); J4 (n = 7) : 410 ± 29 (380-460).

DESCRIPTION

Females : Nematodes ventrally arcuate to C-shaped when heat killed. Greatest width at mid-body. Cuticle finely annulated. Three lines in lateral field. Head offset and rounded; basal framework heavily sclerotised. Stylet with fusiform knobs and prominent musculature; conus 71 % of total stylet length. Excretory pore just posterior to head. Procorpus leading to a distinct, ovoid median bulb with valves posterior to centre. Oesophageal gland with two lobes, both overlapping the intestine; dorsal lobe long with two nuclei; ventral lobe shorter. Oesophago-intestinal junction just behind the bulb. Deirids, hemizonid and phasmids not seen. Ovary monoprodelphic and reflexed. Vulva position variable, 70-95 % of total body length; vulval lips slightly protruding. Vagina heavily sclerotised, slightly anteriorly directed. Post-vulval sac short, less than a maximum body width long. Spermatheca ovoid, sac-like. Tail tip narrowly rounded.

Males : Nematodes ventrally arcuate with slightly coiled tail region when heat killed. Greatest width at mid-body. Cuticle, lateral fields, head, stylet, secretory/excretory pore, oesophagus and intestine as in females. Deirids, hemizonid and phasmids not seen. Testis reflexed; spicules rose thorn-shaped with knob-like rostrum and a wide crescent-shaped groove running the length of the lamina. Posterior lip of anus distinctly thickened but no separate; gubernaculum-like structure present; spermatozoa amoeboid. Three pairs of papillae present, one near the rostrum, one adanal and another about halfway between the anus and tail tip. Tail tip mucronate.

Juveniles : As for adults. Tail tip narrowly rounded, not mucronate.

TYPE HOST AND LOCALITY

Ficus macrophylla Desf. Wentworth Park, Sydney, New South Wales (33° 60' S, 151° 12').

TYPE SPECIMENS

Holotype (female) deposited in the Queensland Museum, Queensland, Australia (specimen number G20 3477). *Paratypes* (male, female and juvenile) de-

* Latin *alter* : second (more exactly : one of the two); and *macrophylla*, the host from which the nematode was first recorded.

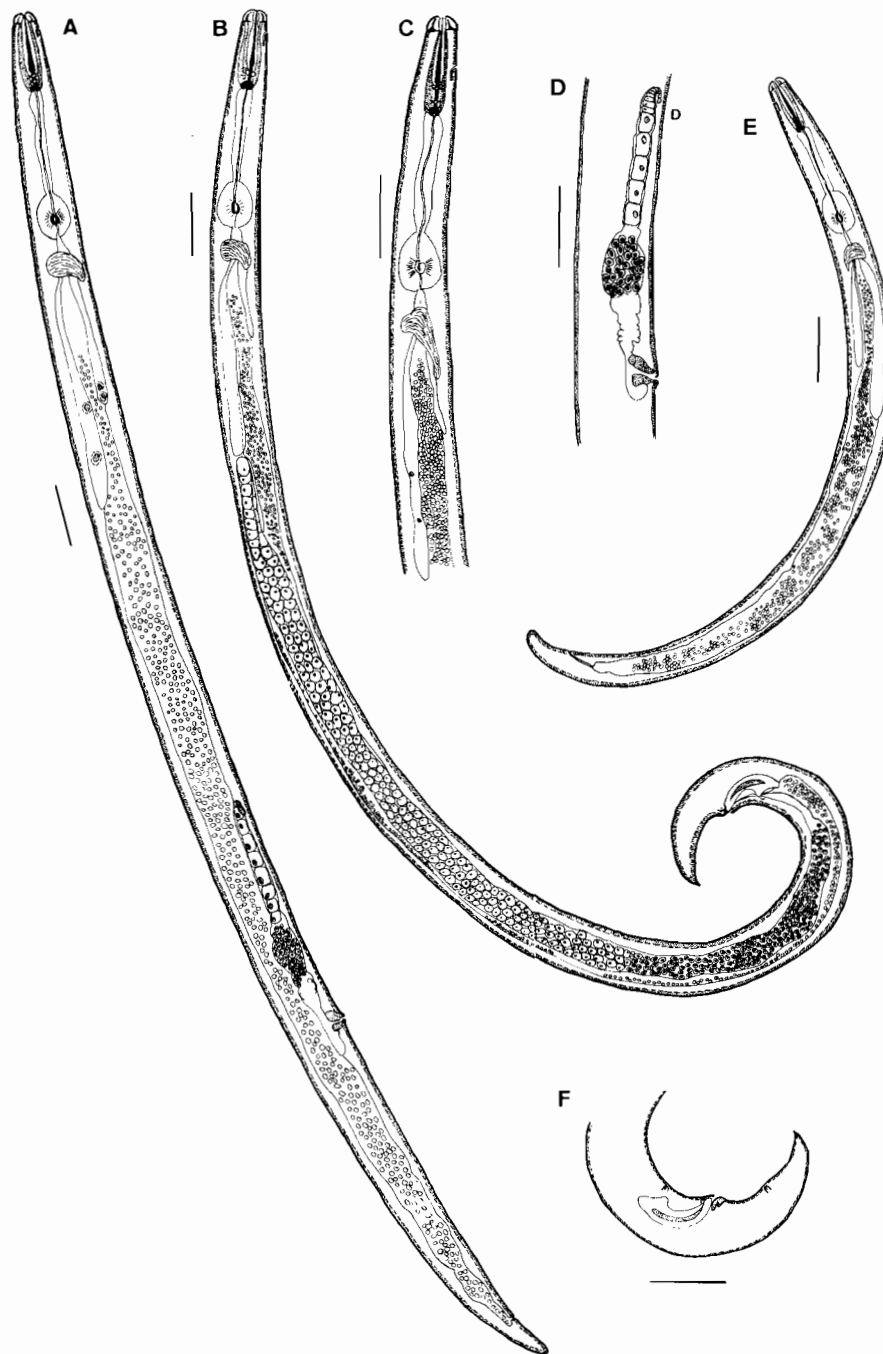


Fig. 3. *Schistonchus altermacrophylla* n. sp. A : Female; B : Male; C : Oesophageal region of male; D : Vulva and post-vulval sac; E : Juvenile; F : Tail region of male.

posited in the Waite Agricultural Research Institute Nematode Collection, Adelaide, South Australia (W.I.N.C. number 803), and also in the Muséum National d'Histoire Naturelle, Paris, France.

DIAGNOSIS AND RELATIONSHIPS

S. altermacrophylla n. sp. is characterised by the opening of the secretory/excretory pore just behind the head

region in all stages, and males without a gubernaculum and with amoeboid sperm.

The anterior position of the opening of the secretory/excretory pore separates *S. altermacrophylla* n. sp. from all other known species of *Schistonchus*, in which it opens at the level or more posteriorly to the median bulb; males of all other described species of the genus have flagellated sperm and a gubernaculum.

DISCUSSION

The scanning electron micrograph of the anterior of adult *S. macrophylla* n. sp. shows only one cephalic annule with a distinct labial disc. Examination, using SEM, of the lateral fields in *S. macrophylla* n. sp. showed variations in structure and line number that are difficult to detect using the light microscope. Illustrations of *S. caprifici* (Vovlas *et al.*, 1992) show a short ventral lobe of the oesophageal glands, opposite the secretory/excretory pore, but this is not mentioned in the description. The ventral lobe appears to be more developed in *S. macrophylla* n. sp. and *S. altermacrophylla* n. sp. The presence of a ventral lobe in the oesophageal glands in the Aphelenchoididae has not been reported before. The structure of the oesophageal glands of *Aphelenchus* exhibits a wide range of variation, even in the progeny of one female (Goodey & Hooper, 1965), but this is the only genus of Aphelenchida in which such variation is known.

This work has revealed information on several characters which requires the emendation of the diagnosis of the genus *Schistonchus*. These include the morphology of the head, presence of a ventral lobe in the oesophageal glands, information on the relative length of the conus (courtesy of Dr. P. Baujard), position of the excretory pore and vulva, and the form of the caudal alae.

Genus *Schistonchus* Cobb, 1927 (Fuchs, 1937) syn. *Aphelenchus* (*Schistonchus*) Cobb, 1927

DIAGNOSIS, emended from Hunt (1993)

Aphelenchoidinae. Medium sized nematodes about 0.6–0.8 mm long. Straight or ventrally arcuate to C-shaped on heat relaxation. Cuticle finely annulated. Cephalic region rounded, more or less offset with six lips, separate (*S. caprifici*) or fused (*S. macrophylla* n. sp.). Labial disc distinct, more or less prominent. Amphid openings near edge of labial disc. Stylet robust, 16–26 µm long, with strong basal knobs. Relative length of conus variable (52 % of total stylet length in *S. caprifici*, 60 % in *S. racemosa*, 64 % in *S. macrophylla* n. sp., and 71 % in *S. altermacrophylla* n. sp.). Procorpus fairly short, cylindrical (except in *S. macrophylla* n. sp., where it is constricted at the posterior end) leading to a strong, ovoid median bulb with post-median valve plates. Dorsal oesophageal gland lobe well developed, ventral lobe present in *S. macrophylla* n. sp. and *S. altermacrophylla*

n. sp. Vulva posteriorly situated at about 63–95 % of the body (position varying from 70–95 % in *S. altermacrophylla*) usually with slightly protuberant lips. Vagina directed anteriorly, sometimes sclerotised. Genital tract monoprodelfic, outstretched or reflexed, with oocytes mostly in one or two rows. Post-uterine sac less than one to more than four body widths long. Tail of medium length, conoid, tapering to either an offset, mucronate or rounded tip. Male tail region more tightly curved than rest of nematode. Spicules rose thorn-shaped with a rostrum and a broadly rounded apex continuing the line of the shaft; tip of the spicule ventrally hooked. Gubernaculum-like structure usually present (absent in *S. altermacrophylla* n. sp.). Spermatozoa flagellate or amoeboid. Three pairs of caudal papillae: one preanal near the rostrum, one adanal and the other nearer the tail tip. Tail short, conoid with either a mucronate tip or smoothly rounded. Cuticle of the lateral field more or less thickened to form caudal alae.

Conclusion

S. macrophylla n. sp. is probably a parasite of fig inflorescences. It was not extracted from leaves or stems of the host fig or soil from underneath the tree, and fungal hyphae were not seen in the fruits. While young inseminated females have been found in female wasps, there was no suggestion that the nematodes were parasitizing the wasps, i.e., there was no development of the nematodes in the wasps. Giblin-Davis *et al.* (1995) reported that mated females of *Schistonchus* spp. were transported in the haemocoel of *Pegoscapus* spp. to syconia of *Ficus* spp. in Florida. *S. macrophylla* n. sp. appears to lie somewhere between *S. racemosa*, carried as second stage juveniles in the abdominal folds of females of the wasp *Ceratosolen* sp. (Reddy & Rao, 1986), and *S. caprifici*, which can develop in and parasitize *Blastophaga psenes* L. (Vovlas *et al.*, 1992). *S. macrophylla* n. sp. and *P. froggatti* seem to have a phoretic relationship, and presumably being carried internally enables the nematode to avoid desiccation.

Nothing is known of the biology and life cycle of *S. altermacrophylla* n. sp. The wasp *P. froggatti* has been found with inflorescences containing these nematodes, but it is not known if they have a phoretic relationship.

Martin *et al.* (1973) found that figs indigenous to Zimbabwe carried nematode and wasp-infested fruit, but that cultivated non-African species were not associated with nematodes or wasps. This seems to be mirrored by the finding reported here, that species of fig indigenous to Australia carried *S. macrophylla* n. sp. but that non-Australian species did not.

Poinar and Herre (1991) described species-specific relationships between various species of *Parasitodiplogaster*, their host wasps, and several species of *Ficus* in Panama. It is possible that the two species of *Schistonchus* described here have evolved as a result of geo-

graphic separation. Nothing is known of the original distribution of the two species, and as yet each has been found only in one geographic area. However, both seem to be associated with the same species of wasp, and *S. macrophylla* n. sp. at least can develop on several species of figs. Forty-two species of figs are found in Australia, usually in the wetter northern and eastern areas (Chew 1989). *F. macrophylla* and *F. rubiginosa* are indigenous in the Sydney area. *F. platypoda* is indigenous to much of the north of Australia, its distribution overlaps that of *F. macrophylla* and *F. rubiginosa*, and it is the only Australian species to grow in the dry inland and in South Australia. *F. baileyana* is indigenous to a limited area in Queensland, which overlaps with *F. platypoda*. All of these species of figs were introduced to Adelaide.

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