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Description of *Bursaphelenchus abruptus* n. sp. (Nemata: Aphelenchoididae), an Associate of a Digger Bee[1]

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Abstract: Bursaphelenchus abruptus n. sp., an associate of the digger bee, *Anthophora abrupta* (Hymenoptera: Anthophoridae), is described and illustrated. *Bursaphelenchus abruptus* n. sp. can be differentiated from other species of *Bursaphelenchus* by the absence of head annules, stylet length, length of the postuterine sac, shape of female tail, spicule morphology, and male caudal papillae arrangement. Two plant-pathogenic fungi, *Monilinia fructicola* and *Botrytis cinerea,* and a *Monilia* sp. isolated from an adult bee from Prince Georges County, Maryland, were good hosts for *B. abruptus* n. sp. Dauer juveniles (JIII) of *B. abruptus* n. sp. were isolated from the reproductive tracts of *A. abrupta* from Montgomery County, Alabama, for measurements and comparison with J2–JIII intermolts from a 4-week-old monoxenic culture on *Monilia* sp. Gonad lengths in dauer juveniles isolated from *A. abrupta* were highly variable (49 ± 23 μm SD; range 21–93 μm; n = 29) compared with J2–JIII intermolts from culture (28 ± 7 μm SD; range = 16–42 μm; n = 16), suggesting that postembryonic gonad development may continue while dauers are in the bee host. Adult males and females of *B. abruptus* n. sp. were examined with scanning electron microscopy (SEM) for ultrastructural comparisons with other members of the genus *Bursaphelenchus.*

Key words: Anthophora abrupta, Aphelenchoididae, bee, *Bursaphelenchus abruptus* n. sp., *B. fraudulentus, B. kolymensis, B. mucronatus, B. xylophilus,* Dufour's gland, morphology, mycophagy, nematode, scanning electron microscopy, taxonomy.

A new species of *Bursaphelenchus,* morphologically similar to the pinewood nematodes, *Bursaphelenchus xylophilus* (Steiner & Buhrer) and *B. mucronatus* Mamiya & Enda, was recovered as dauer juveniles in the reproductive tracts of adult male and female digger bees, *Anthophora abrupta* Say, from two locations in Maryland and one location in Alabama (6). This nematode is described herein as *Bursaphelenchus abruptus* n. sp.

The bee host, *A. abrupta,* is a solitary and univoltine species that nests gregariously in the soil and is distributed in the eastern United States from New York to Florida and west to Kansas (12). Each nest is composed of about seven urn-shaped cells, which are constructed of soil and provisioned by females with pollen, nectar, and secreted acylglycerides from the Dufour's glands (12,13). Dauer juveniles of *B. abruptus* n. sp. were recovered in the lateral oviducts, Dufour's glands, and poison sacs of 3–82% of the female bees dissected in a recent survey and are apparently transferred from one bee generation to the next during cell construction or oviposition (6). Once inside the newly provisioned cell, *B. abruptus* n. sp. molts from the dauer stage to the propagative phase and feeds on contaminant or possibly insect pathogenic fungi (6).

In addition to the taxonomic description of *B. abruptus* n. sp. using light microscopy (LM) and scanning electron microscopy (SEM) for morphological observations, this paper reports information on the ability of *B. abruptus* n. sp. to feed and reproduce on one fungus isolated from an adult bee and two plant-pathogenic fungi.

MATERIALS AND METHODS

Dauer juveniles of *B. abruptus* n. sp. were isolated from the reproductive tract of an adult female of *A. abrupta* from Prince Georges County, Maryland, on 8 June 1986 and inoculated onto a culture of *Mo-*

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nilinia fructicola (Wint.) Honey on 5% (v/v) glycerol supplemented potato dextrose agar (GPDA). After several weeks in culture, nematodes were collected in a Baermann funnel for 4–5 hours and surface-disinfected in a centrifuge tube with 0.1% Merthiolate (w/v) (sodium ethylmercurithiosalicylate) for 10 minutes, aseptically concentrated on a sterile 20-μm nitex filter, and allowed to migrate through an antibiotic–antimycotic mixture in low temperature gelling agarose as described by Giblin and Platzer (3). Nematodes were collected in sterile water from the agar surface, quantified, and pipetted aseptically into 7-day-old cultures of *M. fructicola* on GPDA. Monxenic cultures of *B. abruptus* n. sp. were maintained at 25 C and used for all subsequent studies unless otherwise stated.

Adults of *B. abruptus* n. sp. were collected from 14-day-old cultures on *M. fructicola* and heat-killed for measurements in temporary water mounts. All nematodes were drawn and measured with the aid of a camera lucida and a stage micrometer. Type specimens were from 21-day-old cultures, fixed in TAF (triethanolamine–formaldehyde) for 24 hours, and processed slowly into glycerol before measurement (15). Male spicule terminology used in this description has been previously described (17). Spicule length is the distance between the condylus and the posteriormost point of the cucullus measured in a straight line, and spicule width is the length of the capitulum.

Dauer juveniles of *B. abruptus* n. sp. were collected from a heavily infested female (n = 365 dauers) from Montgomery County, Alabama, on 18 May 1988, heat-killed, fixed in formalin-glycerol, and slowly dehydrated into glycerol with cotton blue stain (15). Measurements of these nematodes were made from temporary mounts in glycerol. *Bursaphelenchus abruptus* n. sp. in the J2–JIII intermolt (molt completed but J2 cuticle retained) were observed in a 28-day-old culture on *Monilia* sp. These nematodes were washed from the plate, heat-killed, fixed in formalin–acetic acid (FAA), and stained in 1% acetic orcein for 24 hours for visualization of gonad primordia (15). These measurements were made in temporary mounts in acetic orcein.

For SEM observations, adult males and females of *B. abruptus* n. sp. were collected from culture on a Baermann funnel, heat-killed, placed in 3% glutaraldehyde in 0.1 M phosphate buffer (pH 7.2) for several days, and postfixed in 2% OsO_4 overnight. Specimens were dehydrated into 100% ethanol, critical point dried using carbon dioxide, mounted on stubs, sputter-coated with 20 nm of gold–palladium, and observed with a JEOL 35C SEM at 15 kV. Cephalic and lip region terminology used in this description is as proposed by Giblin-Davis et al. (5).

A *Monilia* sp. was isolated into pure culture on GPDA and identified by Dr. T. Matsumoto (California Department of Food and Agriculture) from the cuticle of an adult male of *A. abrupta* collected on 8 June 1986 from Prince Georges County, Maryland. Pure cultures of *Monilia* sp., *M. fructicola,* and *Botrytis cinerea* Pers. were subcultured onto 12 GPDA plates each and grown for 7 days at 25 C before inoculation with 26 ± 11 SD *B. abruptus* n. sp. in 100 μl of sterile water. Nematode inoculum was collected and disinfested as described above. Two plates each of GPDA and nutrient agar (NA) were inoculated and included as contamination checks. Three culture plates for each fungus were harvested overnight on the Baermann funnel at 3 and 6 weeks after inoculation and a measured aliquot of the nematodes counted on a dissecting scope.

Systematics

Bursaphelenchus abruptus n. sp.
(Figs. 1–6)

Measurements were made of the holotype male and allotype female in glycerol, and of the other specimens in temporary water mounts in Tables 1–2.

Male (n = 20): Body cylindrical, tapered

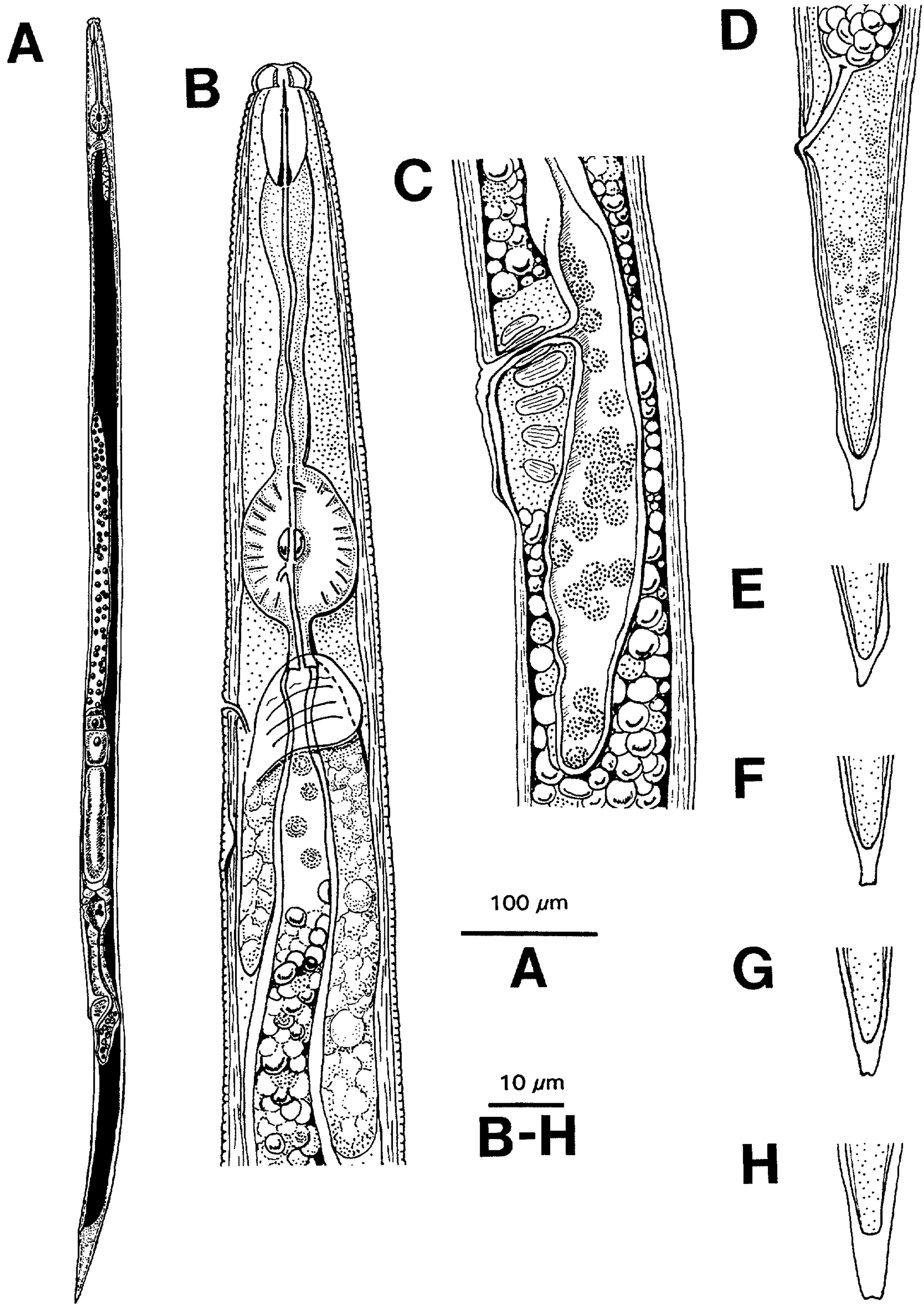

FIG. 1. Adult females of *Bursaphelenchus abruptus* n. sp. in lateral view. A) Whole nematode. B) Anterior body portion. C) Vulva and postuterine sac. D) Tail. E–H) Variations in tail terminus.

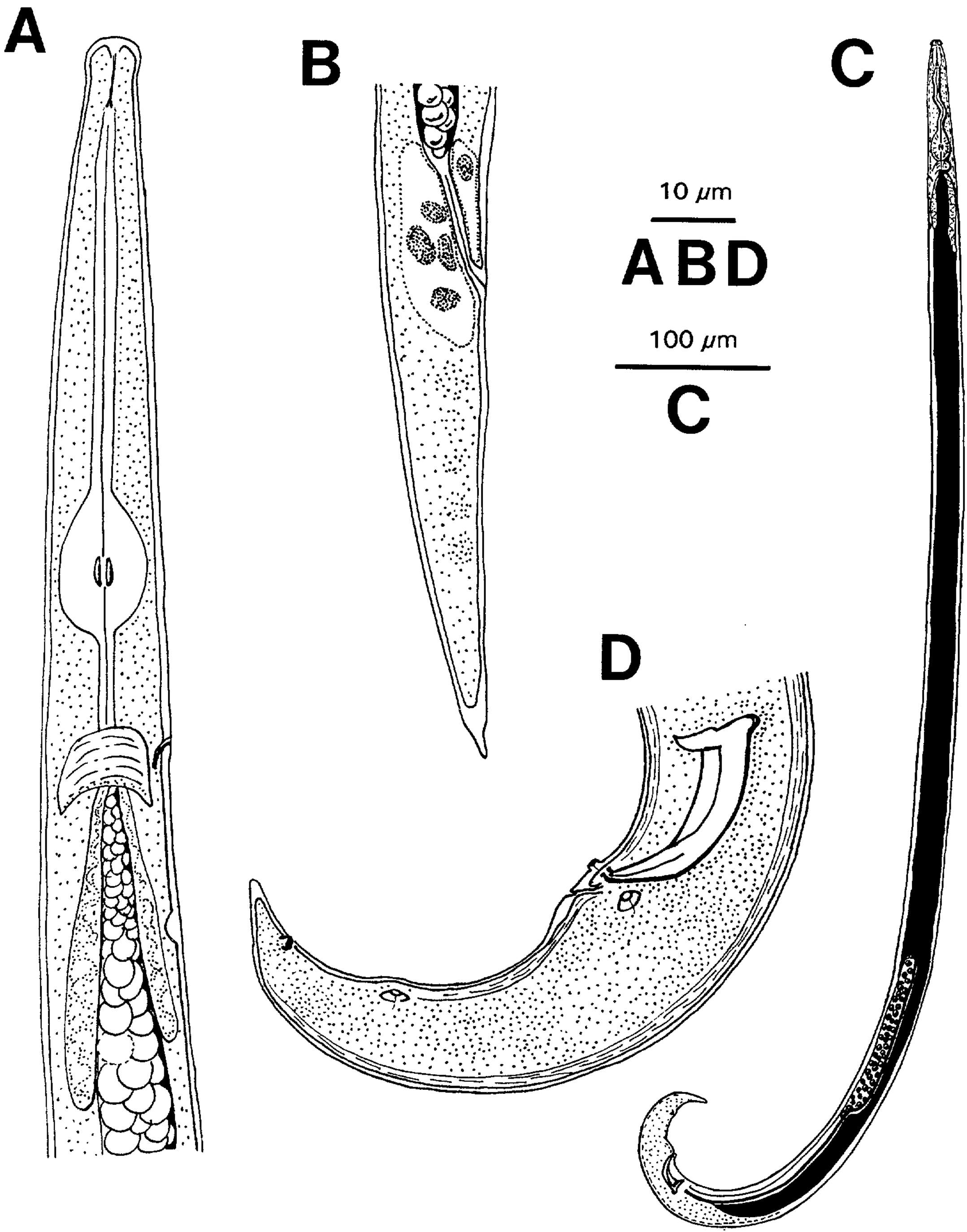

FIG. 2. *Bursaphelenchus abruptus* n. sp. male in lateral view. A) Dauer juvenile anterior region. B) Dauer juvenile tail. C) Whole adult. D) Adult tail.

at both ends, J-shaped when heat killed (Fig. 2C). The anterior regions (exterior and interior) of adult males and females were the same and are described in detail for the male only. Cuticle with fine annulation, annules about 1 μm wide at midbody (Fig. 3C). Lateral field with four incisures, beginning just above level of meta-

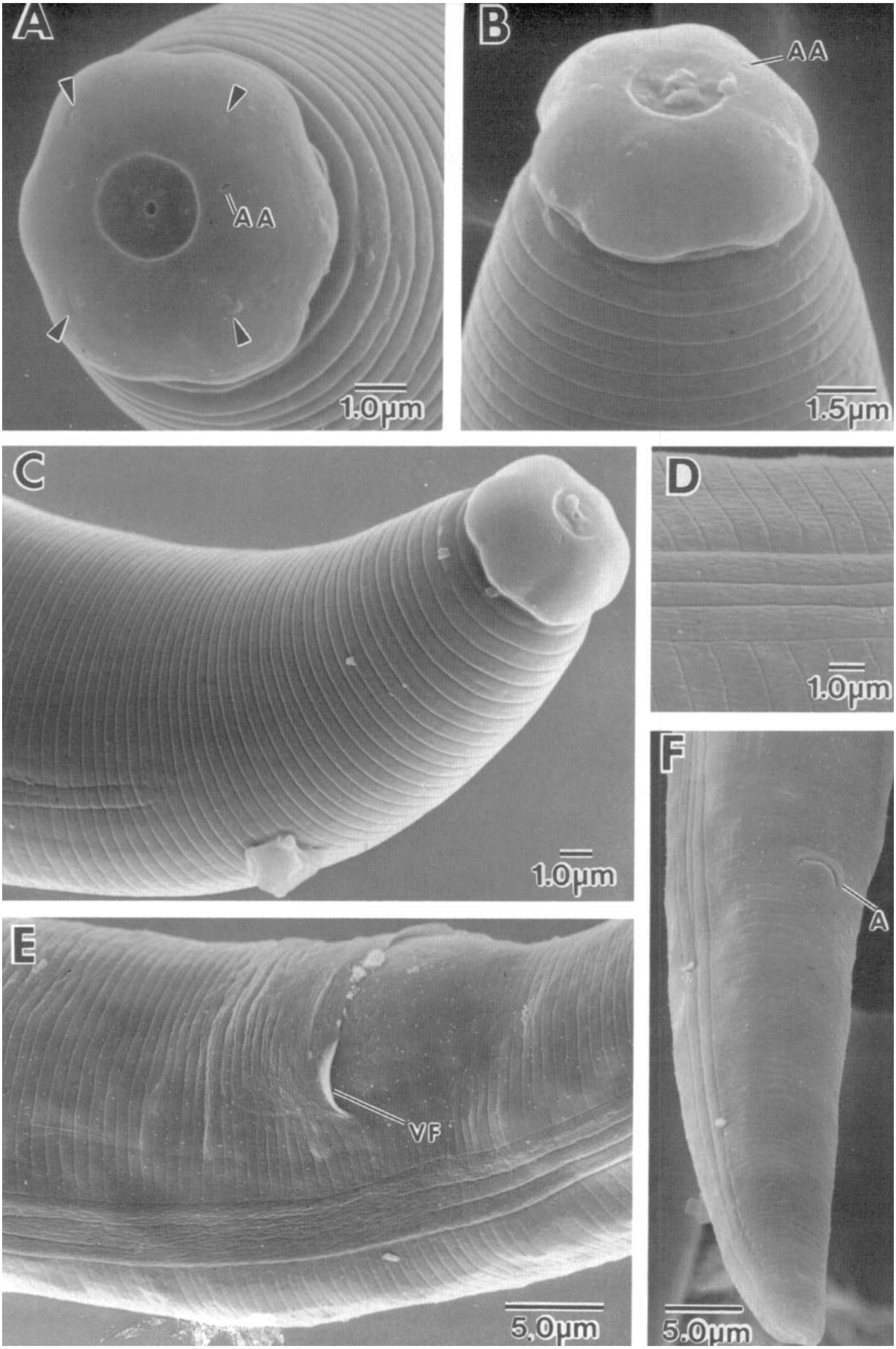

FIG. 3. Scanning electron micrographs of adult females of *Bursaphelenchus abruptus* n. sp. A) En face view, AA = amphidial aperture, arrows = cephalic papillae. B) Head, nearly ventral view. C) Cephalic region, lateral view. D) Lateral field. E) Vulval flap (VF) and lateral field. F) Tail, subventral view, A = anus.

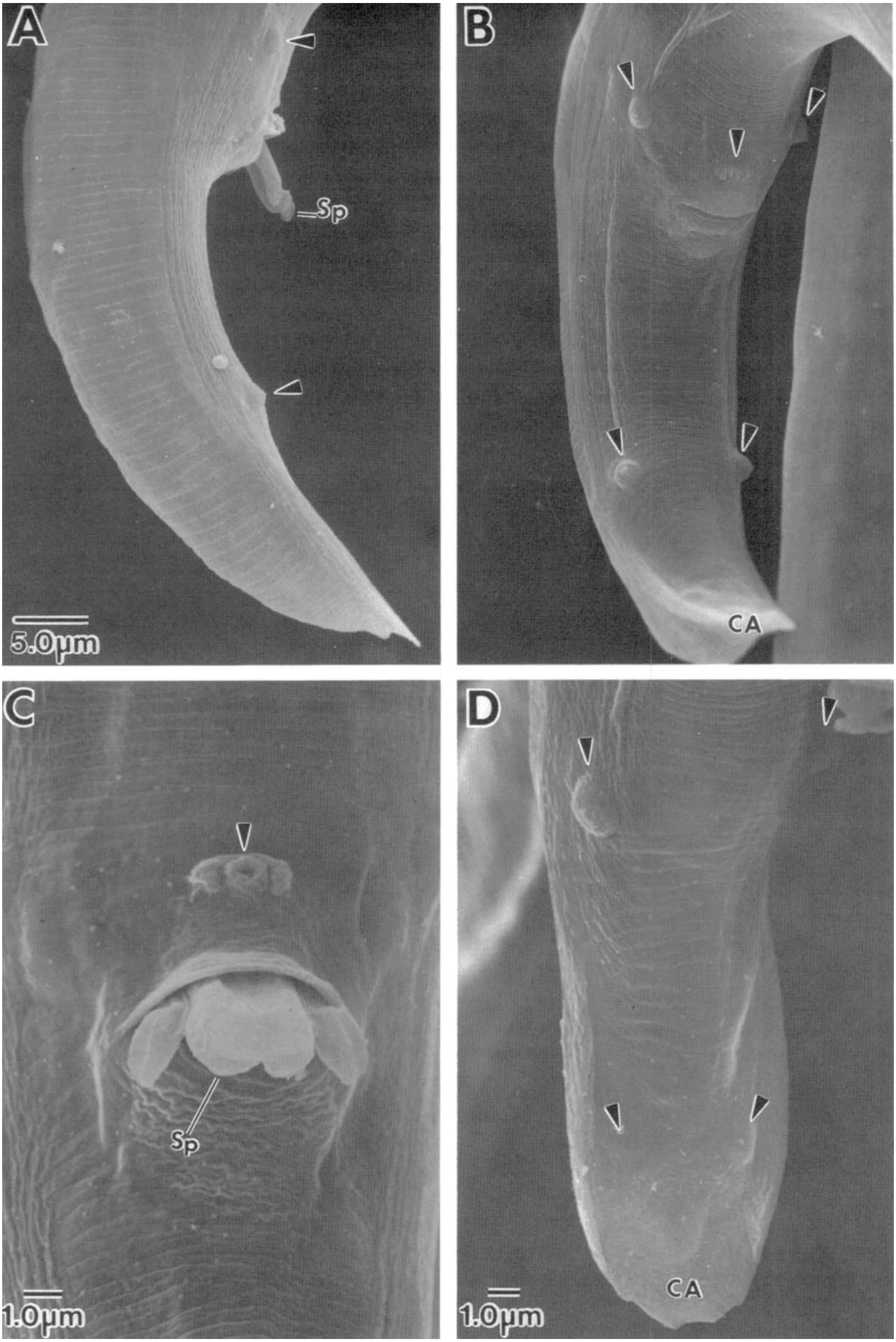

FIG. 4. Scanning electron micrographs of adult males of *Bursaphelenchus abruptus* n. sp. A) Tail with spicule (Sp) protracted, lateral view, arrows = caudal papillae. B) Tail, ventral view, CA = caudal alae. C) Single preanal papilla and protracted cucullus of spicules, ventral view. D) Tail terminus, nearly ventral view.

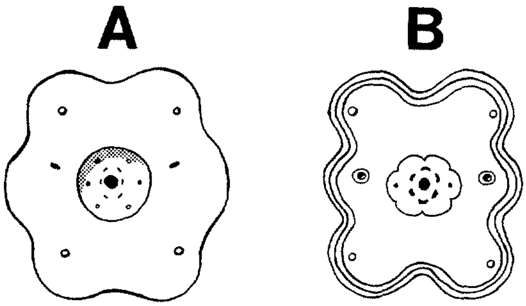

FIG. 5. Diagrammatic representations of the en face pattern of *Bursaphelenchus* spp. females from scanning electron micrographs. A) *B. abruptus* n. sp. B) *B. xylophilus*, drawn from SEM observations in references 11 and 16.

corpus, extending posteriorly to level of ventral preanal papilla; less distinct from ventral preanal papilla to bursal flap = caudal alae (Fig. 4B). Head offset from body (Figs. 1A,B,2C,3A–C). En face pattern (SEM) consisting of a clearly defined circular oral aperture (ca. 0.02 μm) surrounded by a circular and sunken depression about 2 μm in diameter (Figs. 3A,B,5A). Labial sensillae frequently obscured; a composite of several SEM en face patterns suggests a full complement of six inner labial sensillae adjacent to the stoma and six peripheral sensillae just inside the sunken depression (Figs. 3A,5A). Sunken depression surrounded by six cephalic sectors (Figs. 3A,5A). Pore-like amphid openings dorso-medially located on lateral cephalic sectors and a slightly elevated cephalic papilla clearly resolved on each subdorsal and subventral cephalic sector (Figs. 3A,5A). Transverse striae not visible on head with SEM (Figs. 3A,B,5A). Stylet two part; cone short, one third or less total stylet length, shaft with basal thickenings

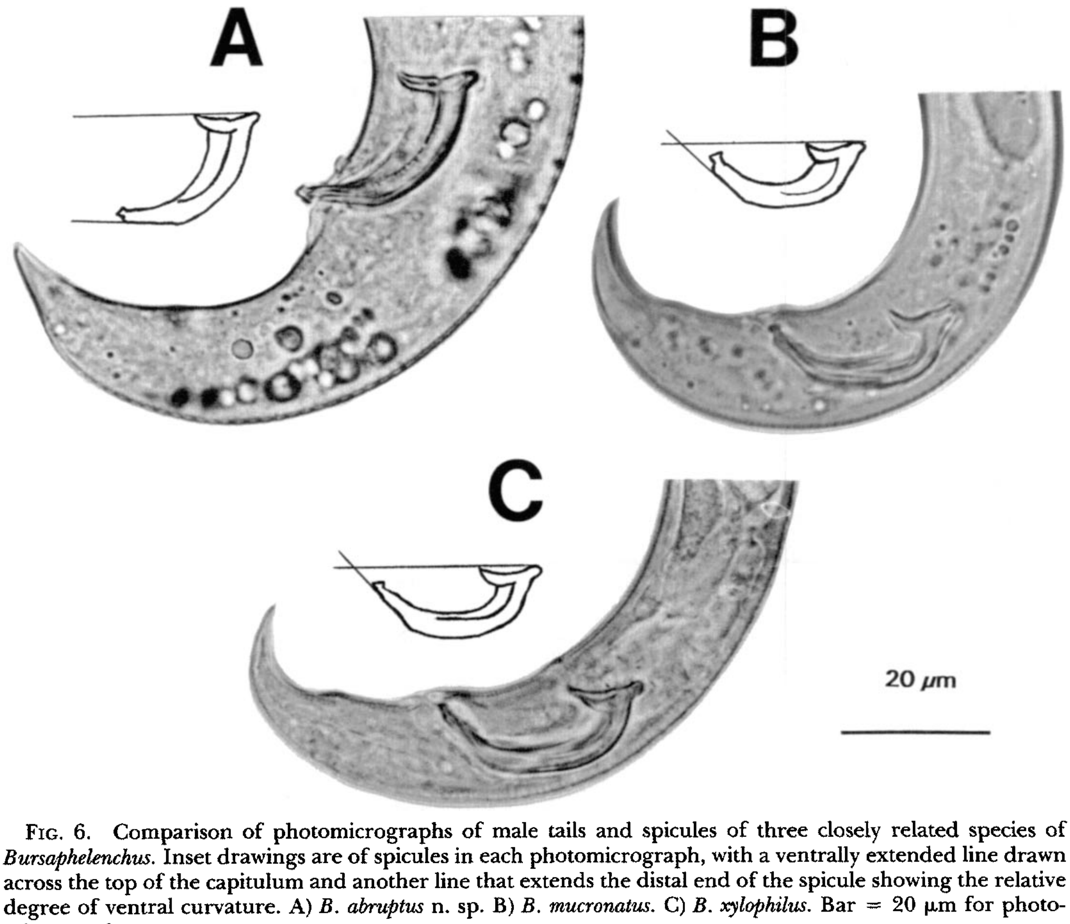

FIG. 6. Comparison of photomicrographs of male tails and spicules of three closely related species of *Bursaphelenchus*. Inset drawings are of spicules in each photomicrograph, with a ventrally extended line drawn across the top of the capitulum and another line that extends the distal end of the spicule showing the relative degree of ventral curvature. A) *B. abruptus* n. sp. B) *B. mucronatus*. C) *B. xylophilus*. Bar = 20 μm for photomicrographs.

TABLE 1. Morphometrics of male holotype in glycerol and 20 male specimens of *Bursaphelenchus abruptus* n. sp. in temporary water mounts.

Measure	Holotype	*n*	Mean	SD	Range
			Measurements in μm		
Length	979	20	915	50.9	833–1014
Width	26	20	31	2.5	26–38
Stylet length	16	20	16	0.7	15–17
Esophagus length	89	20	91	2.5	85–95
Spicule length	29	20	27	1.4	23–30
Spicule width	10	20	10	0.7	9–11
Anal body width	23	20	26	1.6	23–28
Tail length	62	20	60	3.5	55–67
			Ratios and percentages		
a	38	20	30	3.2	22–35
b	11	20	10	0.5	9–11
c	16	20	15	1.0	13–17

(Fig. 1B). Procorpus about two and one half stylet lengths long, ending in well-developed metacorpus (Fig. 1B). Dorsal esophageal gland orifice opens into lumen of metacorpus about one metacorpal valve length above metacorpal valve (Fig. 1B). Esophagointestinal junction about one metacorpus valve length behind metacorpus. Postcorpus glandular. Excretory pore behind metacorpus, at level of nerve ring, hemizonid about one stylet length behind excretory pore (Fig. 1B). Gonad outstretched (Fig. 2C). Tail arcuate, about two anal body widths long; terminus claw-like from lateral view (Figs. 2C,D). Bursal flap (= caudal alae) envelopes tail terminus, flap usually elliptically shaped from ventral view (Fig. 4D). Spicules paired, arcuate, rostrum sharply pointed, distal end with cucullus (Figs. 2D,6A), spicule median length/capitulum length ratio is about 2.7 (range = 2.4–3.0; *n* = 20). Seven preanal and postanal papillae present; one preanal papilla (P1) in ventral midline about 4 μm above cloaca (Figs. 2D,4B,D), one pair subventral preanal papillae (P2) at or about 1 μm above level of P1 (Figs. 2D,4A,B), one pair of postanal papillae (P3) at 50–55% of tail length from cloaca (Figs. 2D,4B,D), one ventral pair of papillae (P4) about 5 μm from tail terminus, obscure in most specimens (Figs. 2D,4D).

Female (n = 23): Body ventrally arcuate or straight when killed by heat treatment

TABLE 2. Morphometrics of female allotype in glycerol and 23 female specimens of *Bursaphelenchus abruptus* n. sp. in temporary water mounts.

Measure	Allotype	*n*	Mean	SD	Range
			Measurements in μm		
Length	1170	23	1120	136.2	900–1394
Width (at vulva)	47	23	37	6.8	27–52
Stylet length	17	23	17	0.8	16–19
Esophagus length	92	19	94	11.7	83–127
Postuterine sac	52	23	57	11.0	30–75
Vulval–anus distance	203	22	205	32.2	160–282
Anal body width	18	22	17	2.6	13–23
Tail length	61	22	57	5.4	46–65
			Ratios and percentages		
a	25	23	31	3.7	24–40
b	13	19	12	1.5	7–14
c	19	22	20	1.7	16–22
V	77	23	77	10.3	75–79

TABLE 3. Morphometrics of J2–JIII and JIII stages of *Bursaphelenchus abruptus* n. sp.

	J2–JIII from culture†				JIII from bee‡			
Measure	*n*	Mean	SD	Range	*n*	Mean	SD	Range
				Measurements in μm				
Length	16	747	63.2	626–889	29	687	68.0	529–811
Width	16	25	3.2	18–31	29	18	1.9	14–23
Esophagus length	16	64	3.2	59–71	29	69	3.9	61–78
Gonad length	16	28	6.9	16–42	29	49	22.9	21–93
Anal body width	15	16	1.3	13–18	29	11	1.1	9–14
Tail length	15	48	4.3	40–55	29	51	4.2	42–58
				Ratios and percentages				
a	16	30	3.5	24–37	29	39	2.8	33–43
b	16	12	0.7	11–13	29	10	0.7	9–11
c	15	16	1.3	13–19	29	13	0.9	11–15

† Measured in temporary mounts in 1% acetic orcein.
‡ Measured in temporary mounts in glycerol.

(Fig. 1A). Lateral field with four incisures as in males except from 5 μm above to 5 μm below vulva, where they were indistinct (stretch marks) (Fig. 3E). Lateral field extends to tail terminus; decreases to three incisures posterior to level of anus (Fig. 3F). Ovary single, outstretched anteriorly, oocytes in single file except at anterior half of ovary. Eggs two to three times longer than wide, 81 ± 8 μm long, 31 ± 2 μm wide (n = 20). Vulva with prominent annulated cuticular flap; covering and extending 5–7 μm posterior to vulval opening, 10–15 μm wide (Figs. 1C,3E). Exposed area 5 μm posterior to vulval flap often swollen and not annulated (Fig. 3E). Postuterine sac about 1.5 vulva body diameters (mean = 1.6, range = 0.6–2.1; n = 23), 11–36% (mean = 28%; n = 22) of vulval–anus distance, often filled with sperm (Fig. 1A,C). Anus a dome-shaped slit in ventral view (Fig. 3F). Tail uniformly tapered with round, digitate, or squared terminus (Fig. 1D–H), 3.3 times longer than anal body width (range = 2.3–4.6; n = 22).

Dauer juvenile (designated JIII versus J3 for propagative third-stage juvenile) (n = 29): High, dome-shaped head, lips not defined. Stylet and esophagus indistinct (Fig. 2A). Body filled with granular material. Lateral field with four incisures. Gonad variable in length (Table 3) and development (7–34 total nuclei). Tail conoid, terminus mucronate or pointed (Fig. 2B). JIII males differ from JIII females by possessing spicule promordia (Fig. 2B).

Diagnosis

Bursaphelenchus abruptus n. sp. is a member of the *B. xylophilus* group (1) and is distinguished from all other described species of *Bursaphelenchus* by the unique morphology of the spicules in males and the absence of annulation on the head of both sexes.

Relationships

Bursaphelenchus abruptus n. sp. is closest to *B. xylophilus*, *B. fraudulentus* (Rühm), *B. mucronatus*, and *B. kolymensis* Korentchenko in spicule morphology in the male, presence of a cucullus on the distal ends of spicules and sharply pointed rostrum, and the presence of a vulval flap in females. Males of *B. abruptus* n. sp. can be differentiated from all of these species by the degree of ventral curvature of the spicules. In *B. abruptus* n. sp., a line drawn through the anteriormost points of the condylus and rostrum and projecting ventrally will not intersect a line that ventrally extends the dorsal distal fourth of the lamina within two spicule median lengths of the cucullus (Figs. 2D,6A). Conversely, lines drawn as described above for spicules of *B. xylophilus* (Fig. 6C), *B. fraudulentus*, *B. mu-*

cronatus (Fig. 6B), and *B. kolymensis* will intersect within at least one spicule length.

Male *B. abruptus* n. sp. possess two pairs of subventral postanal papillae, of which one pair is about 3–5 μm above the origin of the bursal flap and one pair is in between the origin of the bursal flap and the tail terminus. In *B. xylophilus,* there are two pairs of adjacent subventral postanal papillae at the origin of the bursal flap that can be discerned by SEM but appear as a single pair with light microscopy (11,16). In *B. mucronatus,* there are also two pairs of adjacent subventral postanal papillae at the origin of the bursal flap that can be discerned by light microscopy (Giblin-Davis, unpubl. obs.) but were originally described as a single pair (9). In *B. fraudulentus* and *B. kolymensis,* only one pair of postanal papillae has been reported, which occurs at the origin of the bursal flap (7,14).

A single ventral preanal papilla has been reported for *B. xylophilus* (11,16) and occurs in *B. mucronatus* (Giblin-Davis, unpubl. obs.) and *B. abruptus* n. sp., but has not been reported for *B. fraudulentus* or *B. kolymensis.*

The absence of head annules and lip sectors, and the presence of a circular oral depression in *B. abruptus* n. sp. contrasts with what has been observed by SEM for *B. xylophilus* (11,16) (Fig. 5A,B). Stylet length in females of *B. fraudulentus, B. kolymensis,* and *B. xylophilus* is reportedly less than 15 μm and between 14–16 μm for *B. mucronatus* (17), which is shorter than the stylet length of females of *B. abruptus* (16–19 μm) (Table 2). In males, there is some overlap in measurements of stylet length for *B. fraudulentus, B. kolymensis, B. mucronatus* (17), and *B. abruptus* but not between *B. xylophilus* (13–14 μm) and *B. abruptus* (15–17 μm) (Table 1).

In *B. abruptus* n. sp., the execretory pore is located at the level of the nerve ring as in *B. xylophilus* and *B. mucronatus,* whereas in *B. kolymensis,* the execretory pore is located at the level of the juncture of the procorpus and metacorpus. Position of the excretory pore has not been reported for *B. fraudulentus.* Females of *B. xylophilus* (11,16) and *B. mucronatus* (Giblin-Davis, unpubl. obs.) possess one pair of papillae posterior to the vulval flap opening, whereas *B. fraudulentus, B. abruptus* n. sp., and *B. kolymensis* do not. *Bursaphelenchus abruptus* n. sp. females have a short postuterine sac (0.6–2.0 times body width at the vulva and extending 11–36% of the vulval–anal distance), as does *B. kolymensis* (3.8 times body width at vulva and extends 32% of vulval–anal distance [7]), whereas *B. xylophilus* and *B. mucronatus* females have long postuterine branches (seven times body width at vulva and extend 75% of vulval–anal distance [9,10]). The postuterine sac of *B. fraudulentus* has not been described. Female tails are uniformly conoid in *B. abruptus* n. sp. and *B. kolymensis* versus rounded in most populations of *B. xylophilus,* and mucronate in *B. mucronatus* and *B. fraudulentus.*

Biological characteristics

The biology of *B. abruptus* n. sp. is different from that of *B. xylophilus, B. mucronatus, B. fraudulentus,* and *B. kolymensis* in that *B. abruptus* n. sp. propagates in subterranean bee brood cells on fungi and is carried in the reproductive tracts of a bee. The other species in this group propagate in the sapwood of trees, e.g., gymnosperms (*B. xylophilus, B. mucronatus,* and *B. kolymensis*) or angiosperms (*B. fraudulentus*) and are associated or suspected to be associated with wood-boring longhorn beetles (Cerambycidae). These *Bursaphelenchus* species are either facultative plant and fungal parasites or mycophagous only.

The connection of *B. abruptus* with the soil environment and its morphological similarities to *B. xylophilus, B. mucronatus, B. fraudulentus,* and *B. kolymensis* from arboreal niches suggest that it may be related to the ancestor(s) of the form that became associated with trees and longhorn beetles. It is equally as likely that *B. abruptus* is a species that has evolved more recently from an arboreal form reintroduced into the soil when *Bursaphelenchus*-infested trees died and rotted on the ground near nesting aggregations of *A. abruptus*, or possibly the nematodes were acquired by wood-nesting *Anthophora* (*Clisodon*) and introduced into the soil environment, where they became associated with soil dwelling *Anthophora*. Also, the morphological similarities may be due to convergence. The association between *B. abruptus* and *A. abrupta* may be relatively recent in origin because the dauer juveniles lack organ specificity during their infestation of a bee host and because there are two types of humoral host defense reactions that have been observed in the poison sacs of the host (6).

Type host and locality

Holotype male and allotype female from 21-day-old culture on *M. fructicola*. The culture was started from dauer juveniles of *B. abruptus* n. sp. isolated from the reproductive tract of an adult female of *A. abrupta* caught with a collecting net in Prince Georges County, Maryland, on 8 June 1986.

Type designations

Holotype male and allotype female and additional material deposited at the University of California-Riverside Nematode Collection. Paratypes (males and females same data as holotype) deposited at the University of California, Davis; USDA Nematode Collection, Beltsville, Maryland; and the Nematology Department, Rothamsted Experiment Station, Harpenden, England.

Etymology

This species name is derived from the name of the bee host species with which this nematode is associated.

Discussion

The tested fungi were suitable hosts for *B. abruptus* n. sp. and population levels per plate were similar to levels reported for *B. seani* on *M. fructicola* and *B. cinerea* (2). However, there were many individual plate colonization failures due to the low inoculation density, especially with *Monilia* sp. Check plates remained clean of contaminants throughout the experiment. After 3 weeks, the mean yields per plate were as follows: 73,207 ± 31,631 SD (range = 40,160–103,200) for *Monilia* sp., 46,982 ± 30,729 SD (range = 17,933–79,152) for *M. fructicola,* and 13,854 ± 17,654 (range 3–33,733) for *B. cinerea*. After 6 weeks, the mean yields per plate were as follows: no plates with nematodes for *Monilia* sp., 69,333 ± 39,795 SD (range = 39,680–114,560) for *M. fructicola,* and 37,986 ± 31,723 (range 9,306–72,060) for *B. cinerea*. Generation times were not carefully quantified for *B. abruptus* n. sp., but appear similar to *B. seani* and *B. xylophilus* (4–5 days from J2 to J2 at 25 C) (4,8). All three species of fungi were severely damaged by the feeding of *B. abruptus* n. sp. by 3 weeks postinoculation in successful cultures. These preliminary results confirm that *B. abruptus* n. sp. is mycophagous with a potentially wide host range and that *M. fructicola* is a good choice for a laboratory host. The nematodes may benefit their bee host by destroying potentially pathogenic fungi in brood cells.

Gonad lengths and the number of gonad nuclei in male and female dauer juveniles (JIII) isolated from *A. abrupta* were highly variable and showed a greater range than those of J2–JIII intermolts of both sexes from culture (Table 3), suggesting that postembryonic gonad development continues while dauers are in the bee host. This contrasts with observations for other species of *Bursaphelenchus* (e.g., *B. seani* and *B. kevini*), where postembryonic gonad development is suspended at the J2–JIII intermolt until development to the propagative J4 commences (1,4). A report that there are two dauer juvenile stages (JIII and JIV) for *Bursaphelenchus* sp. (= *B. abruptus* n. sp.) (6) was not substantiated by the present study. No JIII–JIV molt was observed for nematodes isolated from bees, and the maximum gonad development for any single dauer juvenile was less than for JIII–J4 intermolts observed in fungal cultures.

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