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Schistonchus africanus n. sp. (Aphelenchida: Aphelenchoididae) Associated with *Ficus thonningii* (Moraceae) and its Pollinator Wasp *Elisabethiella stuckenbergi* (Chalcidoidea: Agaonidae)

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Abstract: Syconia ("figs") from *Ficus thonningii* and adults of its pollinator wasp *Elisabethiella stuckenbergi* were dissected to elucidate their association with a new species of *Schistonchus* (Aphelenchoididae). *Schistonchus africanus* n. sp. is characterized by a short stylet (13–16 µm long); position of the excretory pore opening in both sexes at a level just behind the stylet knobs; and short post-uterine branch, one body-width long. *Schistonchus africanus* n. sp. parasitizes *F. thonningii* florets and is transported by the winged females of *E. stuckenbergi.* Juveniles, females, and males of the nematode were found in the female and male fig florets and in the abdomen of the vector. Nematode populations extracted from female wasps or fig floret tissues did not differ in their morphology. No association was observed with the wingless males of the pollinator wasp.

Key words: Agaonidae, Aphelenchoididae, *Elisabethiella stuckenbergi, Ficus thonningii,* fig, life history, nematode, *Schistonchus africanus* n. sp., South Africa.

All wasps of the family Agaonidae (Hymenoptera: Chalcidoidea) are associated with fig trees (*Ficus* spp., Moraceae). The pantropical genus *Ficus* is extremely diverse, with approximately 750 species worldwide (Berg, 1989). With a few exceptions (Michaloud et al., 1996), each of fig species has its own species of pollinating fig wasps and an associated assemblage of non-pollinating fig wasps that breed in the fig florets as gallers or parasitoids (Boucek et al., 1981; Compton and Hawkins, 1992; Compton et al., 1994; Compton and van Noort, 1992; Kerdelhué and Rasplus, 1996; West et al., 1996). The afrotropical region has 105 fig tree species (Berg and Wiebes, 1992). The majority of these species are monoecious, with male and female hosts contained in the same infructescence (syconium) (Berg, 1989). One of these monoecious species, *Ficus thonningii* Blume, is a common, widespread species that occurs from South Africa to Ethiopia and Senegal (Berg and Wiebes, 1992). *Ficus thonningii* is often planted as a shade tree. Three species of fig wasps have been recorded as pollinating *F. thonningii* (Boucek et al., 1981), a situation indicative of the taxonomic confusion associated with this host fig. Nonetheless, one of these fig wasps, *Elisabethiella stuckenbergi* Grandi, is a regular pollinator of *F. thonningii* in southern Africa and was the species found in the present study.

The infructescences, or "figs," of several *Ficus* spp. and their associated fig wasps have previously been recorded as hosts of a range of nematode species in Aphelenchoidea, Cylindrocorporidae, and Diplogasteridae (Giblin-Davis et al., 1995; Kumari and Reddy, 1984; Lloyd and Davies, 1997; Martin et al., 1973; Poinar and Herre, 1991; Reddy and Rao, 1986; Vovlas et al., 1992). *Parasitodiplogaster sycophilon* Poinar (Diplogasteridae) has been recorded as a parasite of female *E. stuckenbergi* pollinating *Ficus burkei* Miq. (= *F. thonningii*) in Zimbabwe (Poinar, 1979).

This paper describes the morphology, morphometry, and biology of a new species of *Schistonchus* Cobb, 1927, which is associated with *F. thonningii* florets and *E. stuckenbergi* in South Africa.

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Materials and Methods

Several syconia in phase D (male) as defined by Galil and Eisikowitch (1968) were collected from a single cultivated tree of *F. thonningii* from the garden of the Sun City complex, South Africa, in May 1996 which, even though planted, was still located within the natural geographical range for the species (van Greuning, 1990; von Breitenbach, 1995). Syconia were broken open to collect adult *E. stuckenbergi* among the florets. Staminate and pistillate florets were removed from the infructescences, dissected in tap water, and examined for nematodes. Nematodes collected from flower tissues and wasps were fixed in 4% formaldehyde + 1% propionic acid, processed to dehydrated glycerin, and mounted permanently in anhydrous glycerin (Seinhorst, 1966). Drawings and morphological observations were made on both live and fixed specimens. All measurements were made with a camera lucida and ocular micrometer at ×400 and ×1000, and are herein given in micrometers (µm) as mean and range, along with the standard deviation (SD). Percentages and ratios in Table 1 are defined in Siddiqi (1986).

Systematics

Schistonchus africanus n. sp. (Table 1, Figs. 1, 2)

Holotype (female in glycerin): L = 482; maximum body width = 11.6; anal body width = 6.3; distance from head to valve of median bulb = 59; esophagus length = 145; esophagus overlap of intestine = 65; excretory pore to anterior end = 24; stylet length = 14.5; tail length = 31.7; V% = 70; a = 41.6; b = 6.0; b′ = 3.3; c = 15.2; c′ = 5.0.

Female paratypes in glycerin (n = 20): Measurements and ratios are reported in Table 1.

Description

Female: Female slightly ventrally arcuate when relaxed (Fig. 1), with maximum body width at midbody. Cuticle finely annulated. Lateral field obscure under light microscope. Head region slightly expanded, truncate in profile, with one cephalic annule; cephalic framework showing moderate sclerotization. Stylet delicate, with posteriorly sloping knobs, to which prominent muscu-

TABLE 1. Morphometric data of paratypes of *Schistonchus africanus* n. sp.

	Females (n = 20)			Males (n = 10)		
Morphological characters	Mean	SD	Range	Mean	SD	Range
Measurements in µm						
Body length	481	29.4	429–559	448	46.2	340–538
Maximum body width	11.3	0.8	9.9–13.7	16	1.8	12.5–19.1
Body width at anus	6.7	0.6	5.9–7.7	14.4	1.4	12.5–16.5
Esophagus length (anterior end to valve)	85	5.1	75–98	74	8.3	59–86
Esophagus length (total)	144	12.8	122–170	127	14.2	102–151
Esophagus overlap of intestine	59	13.8	36–83	53	10.6	34–71
Excretory pore from anterior end	18.1	3.4	14.7–26.8	18.0	3.9	12.1–22.1
Stylet length	14.6	0.7	13.2–15.7	14.4	0.7	12.5–15.4
Tail length	33.6	3.7	30.2–47.0	26.6	2.9	21.8–30.4
Spicules (dorsal limb)	—	—	—	21.0	1.7	17.8–23.5
Gubernaculum	—	—	—	5.0	1.0	2.7–5.9
Percentages						
V or T	70	2.0	67–75	48	6.2	37–59
Ratios						
a	42.8	4.3	33.6–52.2	28.7	4.5	21.3–40.2
b	5.6	0.3	5.2–6.1	6.1	0.6	5.0–6.9
b′	3.4	0.4	2.8–4.0	3.5	0.3	3.1–4.0
c	14.5	1.6	9.9–18.5	16.9	2.0	15.0–21.7
c′	5.0	0.6	4.0–6.3	1.9	0.1	1.6–2.1

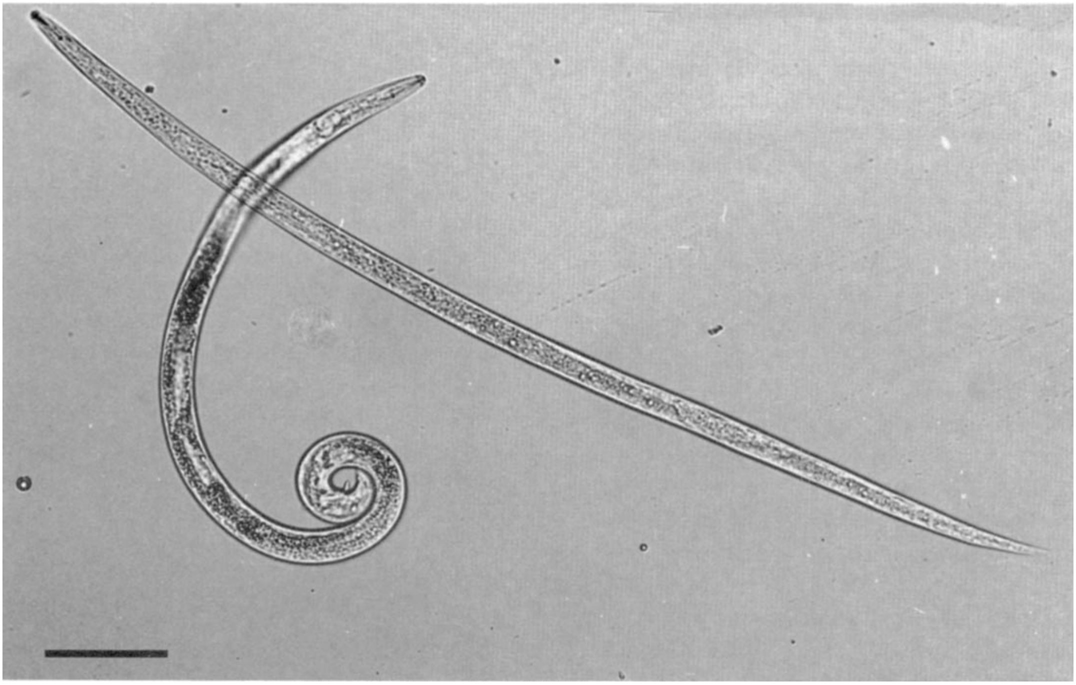

FIG. 1. Photomicrographs of *Schistonchus africanus* n. sp., female and male (coiled). Scale bar = 50 µm.

lature is attached (Fig. 2A). Esophagus with elongated procorpus and ovoid median bulb. Excretory pore opening less than 1/2 stylet length behind stylet knobs (Fig. 2A–C). Hemizonid just below excretory pore. Esophageal glands with subventral and dorsal lobes (Fig. 2C) both overlapping intestine, the dorsal one longer (about 3 times length of ventral lobe). Ovary monodelphic, outstretched (Fig. 2D). Vulva posterior, with a slightly anteriorly directed vagina. Post-uterine sac short, about one body-width long (Fig. 2D). Tail conical with pointed tip (Fig. 2F–H).

Allotype (male in glycerin): L = 452; maximum body width = 18.5; anal body width = 13.9; distance from head to valve of median bulb = 48; esophagus length = 140; esophagus overlap of intestine = 71; excretory pore from anterior end = 20.8; stylet length = 14.2; tail length = 68; testis (from cloaca to top) = 200; spicules (dorsal limb) = 19.8; gubernaculum = 4.6; T% = 44; a = 24.4; b = 6.6; b′ = 3.2; c = 17.1; c′ = 1.9.

Male paratypes in glycerin (n = 10): Measurements and ratios are reported in Table 1.

Description

Body ventrally arcuate when relaxed, more strongly in tail region (Fig. 1). Head region, stylet, esophageal structure, and excretory pore position as in females. Testis usually reflexed. Tail region sharply recurved (Fig. 2I). Spicules paired and ventrally curved, joined by a robust proximal bar, with a prominent dorsal apex and a small ventral rostrum. Gubernaculum triangular in lateral view (Fig. 2I). Three pairs of caudal papillae: one pair preanal near rostrum, one pair adanal, and one pair midway between anus and tail tip. Caudal alae absent. Tail conical with finely rounded tip (Fig. 2I).

Type host and locality

Syconia of a planted *F. thonningii* in the garden of the Sun City complex, near Rustenburg, Northern Province, South Africa, May 1996.

Type designations

Holotype female, allotype male, and additional paratypes deposited in the Nema-

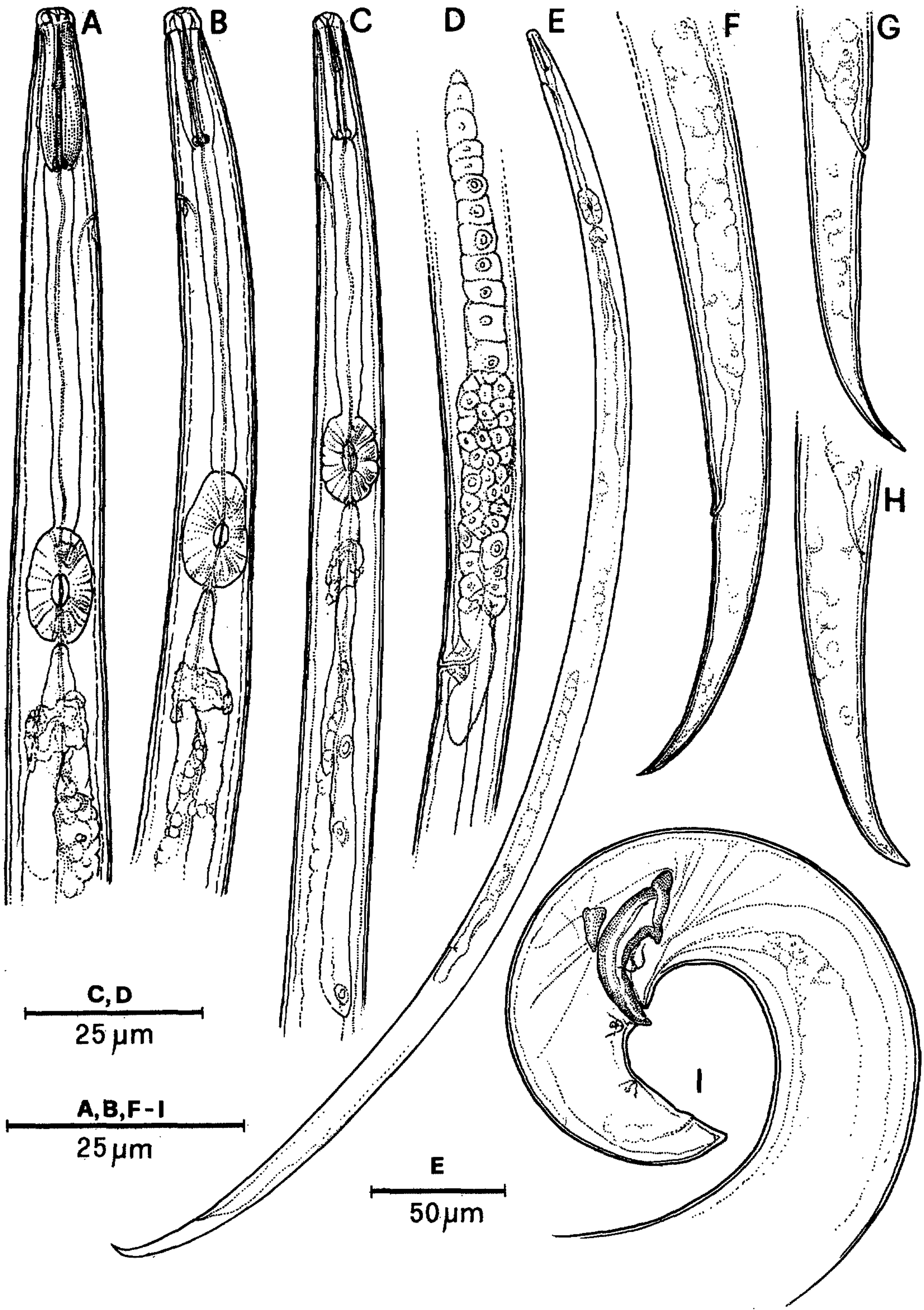

FIG. 2. Drawings of *Schistonchus africanus* n. sp. female (A,C-H), and male (B,I). A) Anterior region of female. B) Anterior region of male. C) Female esophageal region. D) Female vulval region. E) Outline of female body. F-H) Female tails. 1) Male tail.

tode Collection at Istituto di Nematologia Agraria, CNR, Via G. Amendola, 168/5, 70126 Bari, Italy. Other paratype females deposited at the University of California, Davis Nematode Collection, Davis, California; U.S. Department of Agriculture Nematode Collection, Beltsville, Maryland; Entomology and Nematology Department, Rothamsted Experimental Station, Harpenden, England; Museum National d'Histoire Naturelle, Paris, France; Nematode Collection of the Department of Nematology, Landbouwuniversiteit, Wageningen, The Netherlands; National Collection of Nematodes, Plant Protection Research Institute, Pretoria, South Africa.

Diagnosis and relationships

Schistonchus africanus n. sp. is characterized by a stylet shorter (13–16 μm) than that of the other five known species of the genus, the anterior position of the excretory pore, opening just behind the base of the stylet knobs, and the short post-uterine sac, one body-width long.

According to the diagnostic criteria of Lloyd and Davies (1997) on identification of *Schistonchus* spp., *S. africanus* n. sp. should be placed in a group with *S. macrophylla* Lloyd and Davies, 1997 and *S. altermacrophylla* Lloyd and Davies, 1997 on the basis of the anterior position of the excretory pore. *Schistonchus africanus* n. sp. differs from these two species in several respects: *S. africanus* differs from *S. macrophylla* in having a shorter stylet (13–16 μm vs. 17–28 μm), shorter distance of the excretory pore from the anterior end (12–27 μm vs. 35–52 μm), a shorter post-uterine sac (9–19 μm vs. 29–80 μm), and absence of caudal alae in the male vs. a thickened cuticle of the lateral field forming the caudal alae in *S. macrophylla*. *Schistonchus africanus* n. sp. also resembles the other Australian species, *S. altermacrophylla,* with respect to the anterior position of excretory pore, long dorsal lobe of esophagus, and length of the post-uterine branch but differs from it in having a shorter stylet (13–16 μm vs. 17–26 μm), excretory pore situated more posteriorly (12–27 μm vs. 3–7 μm), and presence (vs. absence in *S. altermacrophylla*) of a gubernaculum.

The anterior position of the excretory pore separates *S. africanus* n. sp. from the other three species of the genus, *S. caprifici* (Gasperini, 1864) Fuchs, 1937, *S. hispida* Kumari and Reddy, 1984, and *S. racemosa* Reddy and Rao, 1986, in which it opens level or posterior to the median bulb. The stylet of *S. africanus* is shorter than in these three species (13–16 μm vs. 21–24 μm, 20–25 μm, and 21–24 μm, respectively).

Remarks

Specimens of *S. africanus* n. sp. were collected from florets of the syconia but not from the syconial walls. Florets of both sexes were infected by the nematode, with a density of 150–2,000 nematodes/g of flower tissue (fresh weight). About 45% of *E. stuckenbergi* females were inhabited by juveniles and adults of *S. africanus* n. sp., which were found in the abdomen of the wasp. Nematode densities ranged from 5 to 88 specimens per adult female. The nematode sex ratio in all wasps was about 1 male:5 females. Male wasps did not contain nematodes.

The relationship between the wasp, nematode, and fig is schematically represented in Fig. 3. Once enclosed from their natal gall, the female pollinators actively load pollen from the anthers into special pollen pockets (Boucek et al., 1981). The male florets are present in relatively low densities and randomly dispersed among the female florets. The female pollinators then leave the fig via an opening chewed through the fig wall outside by the males (Boucek et al., 1981). The nematodes enter the female wasp abdomen before she exits her gall and are carried within the abdomen during dispersal of wasps from their natal figs and their subsequent location of receptive (B phase) fig syconia for oviposition and pollination. Once the females have located their receptive figs, they squeeze their way into the fig through the ostiole, a narrow opening at the top of the fig inflorescence. During oviposition, nematodes are released from the wasps and migrate to adjacent florets where they repro-

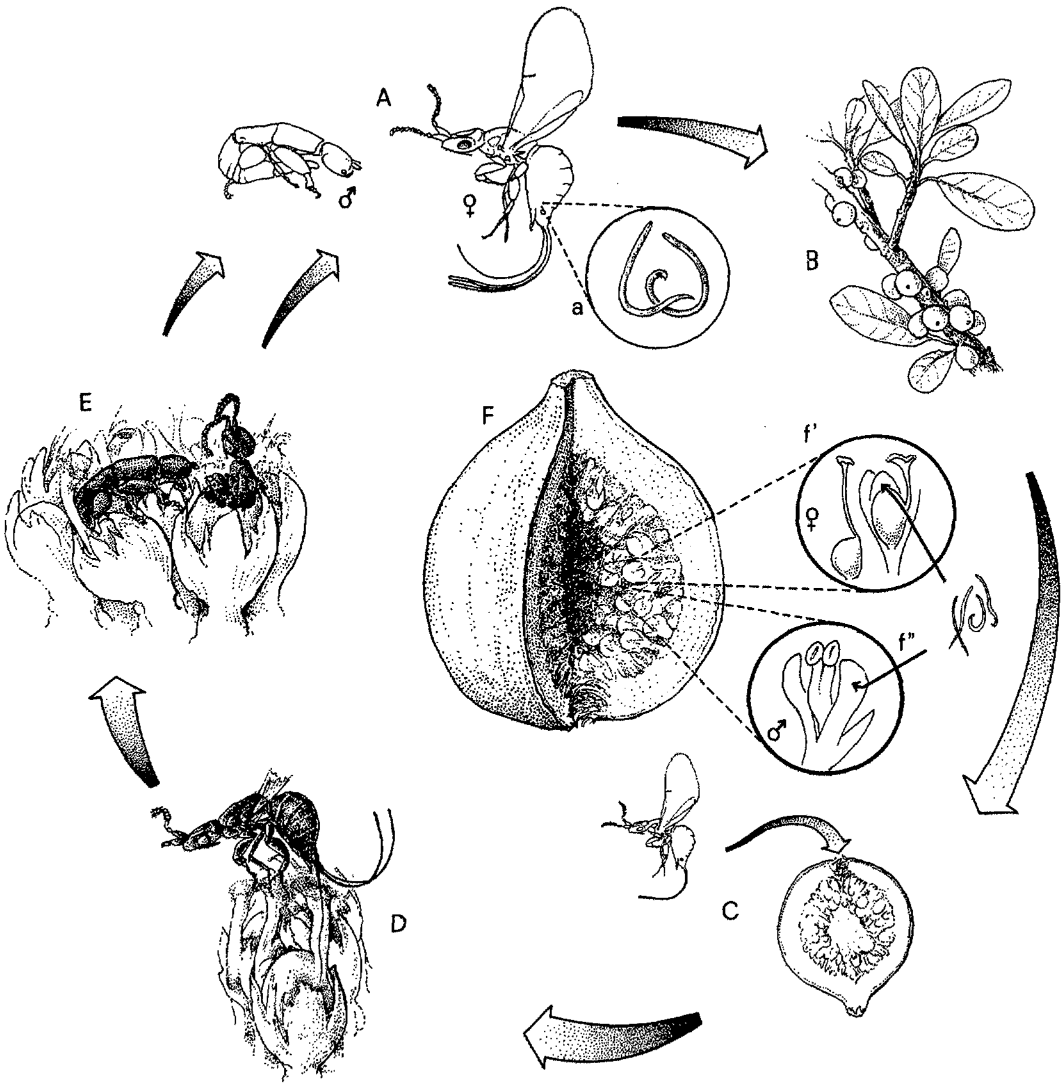

FIG. 3. Relationship between the fig wasp (*Elisabethiella stuckengergi*), the fig nematode *Schistonchus africanus* n. sp., and their host fig tree (*Ficus thonningii*). Illustrations are schematically represented and not in scale. A) Male and female of fig wasp (female redrawn from Boucek et al. [1981]; male redrawn from Berg and Wiebes [1992]). Nematodes are transported from one fig crop to another by the vector wasp. B) General appearance of *Ficus thonningii* with leaves and figs. C) Penetration of female wasp into the fig lumen through the ostiole. D) Oviposition of fig wasp and arrival of nematodes. E) A wingless male (left) and a female (right) of the fig wasp within the flower ovary, emerging partially. F) Syconium with female and male florets infected by *Schistonchus africanus* n. sp.

duce, continuing their life cycle in tandem with that of the fig wasps.

In contrast to the rest of the non-pollinating wasp species that oviposit through the fig wall, there were two additional non-pollinating wasps that entered the fig through the ostiole, *Philocaenus barbarus* Grandi and *Crossogaster odorans* Wiebes. Detected in all syconia examined, their life cycles mirror that of *E. stuckenbergi*, but they play no role in the pollination process. Two parasitoid wasp species, *Sycoryctes hirtus* Wiebes and *S. remus* Wiebes, frequently were found among florets of fig syconia.

The nematodes extracted from female wasps and from fig florets did not differ in their morphology. *Schistonchus africanus* n. sp. is an obligate parasite of fig (*Ficus* *thonningii*) syconia, and its survival and spread through syconia would be impossible without its vector (*Elisabethiella stuckenbergi*). It is adapted for using the female wasp for transportation to new syconia, similarly to the process in other *Schistonchus* spp.: *Schistonchus caprifici—Ficus carica sylvestris—Blastophaga psenes* (Vovlas et al., 1992), *Schistonchus racemosa—Ficus racemosa—Ceratosolen* sp. (Reddy and Rao, 1986), and *Schistonchus sp.—Ficus laevigata—Pegoscapus* sp. (Giblin-Davis et al., 1995).

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