

Speciation and adaptive radiation in the fig wasp nematode, *Parasitodiplogaster* (Diplogasteridae : Rhabditida) in Panama

George O. POINAR, Jr. and Edward A. HERRE

Department of Entomological Sciences, University of California, Berkeley, CA 94720, USA
and Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panama.

SUMMARY

The following species of the hereby redefined genus *Parasitodiplogaster* are described from fruits of *Ficus* spp. in Panama : *P. citrinema* n. sp. from *F. citrifolia* P. Miller, *P. duganema* n. sp. from *F. dugandii* Standl., *P. maxinema* n. sp. from *F. maxima* P. Miller, *P. nymphanema* n. sp. from *F. nymphaeifolia* L., *P. obtusinema* n. sp. from *F. obtusifolia* HBK, *P. paranema* n. sp. from *F. paraensis* (Miq.) Miq., *P. pertanema* n. sp. from *F. pertusa* L. f., *P. popenema* n. sp. from *F. popenoei* Standl., *P. trigonema* n. sp. from *F. trigonata* L. and *P. yoponema* n. sp. from *F. yoponensis* Desv. All of the above species, which are presumed to have evolved from a free-living diplogasterid stem species, represent allopatric species which are carried by specific fig wasp species to specific fig fruit species. The diverse morphological characters (especially those of the alimentary tract) exhibited among these ten new species of fig wasp nematodes represent examples of selective adaptation to physical and nutritional conditions found in the fruits (sycones) of the different fig species.

RÉSUMÉ

Spéciation et divergence adaptative chez le nématode de la guêpe du figuier Parasitodiplogaster (Rhabditida : Diplogasteridae) au Panama

Le genre *Parasitodiplogaster* est redéfini et les espèces nouvelles suivantes, provenant de fruits de *Ficus* spp. au Panama, sont décrites : *P. citrinema* n. sp. sur *F. citrifolia* P. Miller, *P. duganema* n. sp. sur *F. dugandii* Standl., *P. maxinema* n. sp. sur *F. maxima*, P. Miller, *P. nymphanema* n. sp. sur *F. nymphaeifolia* L., *P. obtusinema* n. sp. sur *F. obtusifolia* HBK, *P. paranema* n. sp. sur *F. paraensis* (Miq.) Miq., *P. pertanema* n. sp. sur *F. pertusa* L. f., *P. popenema* n. sp. sur *F. popenoei* Standl., *P. trigonema* n. sp. sur *F. trigonata* L. et *P. yoponema* n. sp. sur *F. yoponensis* Desv. Présumées avoir évolué à partir d'un rameau de Diplogastérides libres, elles forment un groupe d'espèces allopatriques, transportées par des guêpes spécifiques sur des fruits de figuiers spécifiques. Les variations des caractères morphologiques présentes chez ces dix espèces (en particulier ceux liés au tractus digestif) représentent un exemple d'adaptation sélective aux conditions physiques et alimentaires des fruits (des sycones) des différentes espèces de figuier.

The genus *Parasitodiplogaster* Poinar, 1979, was described as a parasite of the fig wasp *Elisabethiella stuckenbergi* Grandi (Agaonidae : Hymenoptera) from the fruits of *Ficus burkei* (Miq.) Miq. in Rhodesia.

Several years ago, one of us (EAH) discovered nematodes in the fruits of different *Ficus* species in Panama. These nematodes all belong to the genus *Parasitodiplogaster*, which is the first record of this group in the New World. The present study redefines the genus *Parasitodiplogaster* and describes ten new species from Panamanian fig fruits.

Materials and methods

Fig fruits were collected from wild trees of *Ficus citrifolia* P. Miller, *F. dugandii* Standl., *F. maxima* P. Miller, *F. nymphaeifolia* L., *F. obtusifolia* HBK, *F.*

paraensis (Miq.) Miq., *F. pertusa* L. f., *F. popenoei* Standl., *F. trigonata* L. and *F. yoponensis* Desv. by EAH in the vicinity of the Panama Canal, Republic of Panama. The figs were placed in 70 % alcohol and sent to GOP, Jr. for determination. The preserved fruits were cut open and adult nematodes were removed from the cavity and processed to glycerin for taxonomic studies. In some cases, juvenile nematodes were also removed from adult fig wasps found inside the fruits.

The anterior pharynx was measured from the tip of the head to the line separating the anterior and posterior pharynx; the posterior pharynx was measured from the line separating the anterior and posterior pharynx to the base of the posterior pharynx. Specific names of the nematodes are based on the specific names of the *Ficus* spp. in which the nematodes occurred. In illustrations of the pharyngeal region of the various *Parasitodiplogaster* species, the pattern of vertical lines represents strong musculature, broken vertical lines represents weak

musculature and fine wavy lines represents glandular tissue.

Parasitodiplogaster Poinar, 1979

DIAGNOSIS (emended)

Diplogasteridae (Micoletzky, 1922) Steiner, 1929. Adults variable in size, ranging from 0.5 to 4.0 mm in length; cuticle smooth or with faint annulations, often swollen around vulva; six lips partly or completely fused; amphids pore-like, on lateral lips; stoma variable, from reduced to distinct; glottoid apparatus inconspicuous or lacking; pharynx composed of an anterior portion containing faint to distinct crescent valve plates near the base and a basal portion sometimes terminating in faint crescent valve plates; ovaries paired, tips usually reflexed; four vaginal glands (variable in size) surrounding vagina; testis single, tip outstretched or reflexed; spicules paired, separate, gubernaculum present, bursa absent; pre-and post-cloacal genital papillae present; found in fig fruits (*Ficus* spp.) and fig wasps (Agaonidae : Hymenoptera).

Parasitodiplogaster citrinema n. sp. (Figs 1B, 3C)

MEASUREMENTS

Adults : See Tables 1 and 2.

DESCRIPTION

Females : Medium to large nematodes with a well-developed stoma and very muscular anterior pharynx with inconspicuous valve plates at base; base of anterior pharynx distinctly wider than proceeding posterior pharynx; posterior pharynx short, also muscular; base of posterior pharynx with valve area; pharyngeal-intestinal valve well-developed; excretory pore opposite posterior pharynx; intestinal lumen distinct, wide, filled with viscous material and containing both bacterial rods and cocci; vaginal glands large, cuticle expanded in region of vulva, especially on ventral side; tail bearing a fine mucron at tip.

Males : General features same as described under females; testis outstretched; spicules short and wide;

Table 1

Morphometric data for females of *Parasitodiplogaster* species.

Species	L (μ m)	Body width (μ m)	Stoma width (μ m)	Stoma L (μ m)	L. ant. pharynx (μ m)	L. post. pharynx (μ m)	Post. pharynx Ant. pharynx	Ant. end to E. P. (μ m)	Ant. end to N. R. (μ m)	V	L tail (μ m)	Width tail (μ m)	L egg (μ m)	Width egg (μ m)
<i>citrinema</i> n. sp. (N = 3)	1 950 1 800-2 040	98 45-120	5	7 5-8	141 138-144	79 75-81	.56 .52-.59	216	177 174-180	50 45-53	91 88-93	30	60 57-63	32 30-36
<i>duganema</i> n. sp. (N = 4)	2 080 1 728-2 208	96 79-108	2	5 4-6	101 98-105	87 79-92	.86 .81-.90	173 165-184	141 130-152	53 49-54	97 89-108	36 31-41	58 57-59	39 35-41
<i>maxinema</i> n. sp. (N = 3)	1 789 1 500-2 280	47 45-51	2.5 2-3	5 4-6	159 150-168	69 60-75	.43 .40-.47	175 165-180	168 159-180	48 46-51	126 102-150	28 24-30	54 48-60	32 24-39
<i>nymphanema</i> n. sp. (N = 10)	2 136 1 560-2 880	96 75-129	3	4 3-5	116 78-135	72 60-84	.61 .56-.69	197 135-273	137 96-159	50 44-63	132 75-183	35 24-48		
<i>obtusinema</i> n. sp. (N = 2)	2 745 2 550-2 940	133 105-162	3.5 3-4	4.5 4-5	102 99-105	79 78-81	.78 .74-.82	256 237-276	150 141-159	51 50-52	168	48 45-51	124 120-129	81 72-90
<i>paranema</i> n. sp. (N = 1)	920	42	2	3	108	72	.66	75	129	43	69	20		
<i>pertanema</i> n. sp. (N = 10)	1 747 1 440-2 016	109 88-133	6 3-9	8 5-11	127 120-136	66 54-79	.52 .44-.63	216 159-279	157 133-174	54 38-73	83 63-98	35 32-38	74 63-86	36 25-48
<i>popenema</i> n. sp. (N = 7)	2 001 1 740-2 190	87 75-93	4 3-5	5 4-7	164 144-183	82 69-102	.50 .39-.60	190 150-240	198 159-240	47 37-52	132 105-162	37 33-42	66 60-90	32 24-36
<i>trigonema</i> n. sp. (N = 10)	2 556 2 070-3 330	129 99-156	2 1-3	2 1-3	99 66-120	74 60-90	.73 .65-.88	210 171-279	128 90-159	51 48-55	162 129-180	52 42-63	74 60-90	42 39-45
<i>yoponema</i> n. sp. (N = 5)	1 331 1 088-1 600	51 47-54	4 4-5	7 6-8	142 120-174	57 41-73	.39 .30-.49	122 108-143	117 95-143	50 48-55	87 76-101	24 19-29	64 54-73	34 32-38

Table 2
Morphometric data for males of *Parasitodiplogaster* species.

Species	L	Body width	Stoma width	Stoma L	L. ant. pharynx	L. post. pharynx	Post. pharynx Ant. pharynx	Ant. end to E. P.	Ant. end to N. R.	L tail	Width tail	L spicule	Width spicule	L gubernaculum	Width gubernaculum
	(μm)	(μm)	(μm)	(μm)	(μm)	(μm)		(μm)	(μm)		(μm)	(μm)	(μm)	(μm)	(μm)
<i>citrinema</i> n. sp. (N = 5)	1 835 1 384-2 240	56 45-76	6 4-8	9 6-13	134 126-143	69 60-82	.52 .48-.57	231 171-260	176 153-193	92 77-102	46 41-48	29 26-32	8 7-9	18 16-19	4 3-5
<i>duganema</i> n. sp. (N = 3)	1 888 1 760-1 984	98 88-105	2	4 3-5	92 82-98	80 73-86	.87 .86-.90	187 127-225	129 117-146	83 77-88	42 40-43	45 39-48	9 8-10	20 17-21	4 3-5
<i>maxinema</i> n. sp. (N = 5)	1 098 750-1 350	30 21-42	3 2-3	5 4-6	144 117-156	65 57-75	.46 .38-.59	162 144-198	160 138-180	50 39-54	25 19-29	36 26-41	6 4-8	22 15-26	4 3-5
<i>nymphanema</i> n. sp. (N = 10)	1 150 960-1 520	76 60-92	3 2-4	4 3-5	120 102-141	68 42-90	.56 .41-.70	158 78-210	137 117-156	84 71-105	56 51-64	78 66-84	14 12-15	28 22-33	4 3-6
<i>obtusinema</i> n. sp. (N = 8)	2 670 1 920-3 990	109 84-174	3.3 3-4	3.6 3-4	106 93-120	85 66-99	.80 .65-.90	250 174-315	150 135-186	117 90-153	61 53-75	55 48-68	8 6-9	31 24-36	7 4-8
<i>paranema</i> n. sp. (N = 3)	633 620-640	43 39-48	3 3-4	3 2-4	117	66 63-69	.70 .62-.75	143 135-150	126 115-132	47 39-53	29 21-36	25 24-26	7 6-8	11 10-12	3
<i>pertanema</i> n. sp. (N = 6)	1 360 1 056-1 696	69 63-76	7 6-8	5 4-6	129 115-133	53 47-70	.43 .36-.50	208 153-225	152 135-171	73 59-80	48 45-51	33 32-35	7 6-8	17 16-18	6 5-7
<i>popenema</i> n. sp. (N = 3)	1 984 1 600-2 624	78 63-95	3	5 4-6	181 151-200	98 87-101	.54 .51-.58	195 147-238	185 162-200	110 83-125	56 51-61	52 47-53	10 8-13	25 24-27	6 5-7
<i>trigonema</i> n. sp. (N = 10)	2 528 2 020-3 040	99 79-130	2 1-3	2 2-3	108 88-123	75 63-92	.70 .57-.79	218 187-247	143 110-181	135 115-152	58 48-64	48 36-56	9 8-13	24 21-32	5 3-8
<i>yoponema</i> n. sp. (N = 6)	789 640-864	43 35-48	2 1-3	8 3-11	132 120-142	46 38-60	.34 .29-.43	119 98-133	107 95-120	48 42-53	28 26-30	41 38-45	5 4-6	25 24-26	4 3-5

gubernaculum straight, narrow, genital papillae eight pairs, consisting of four pre-cloacal pairs and four post-cloacal pairs; two pairs at tip of tail; phasmids conspicuous (tubular) at tip of tail; tail tip bearing a fine mucron.

TYPE HABITAT AND LOCALITY

Found in fruits of *Ficus citrifolia* growing in the vicinity of Barro Colorado Island, Republic of Panama.

TYPE MATERIAL

Holotype (male) and *allotype* (female) deposited in the nematology collection of the Department of Nematology, University of California, Davis, California; *paratypes* in the Laboratoire des Vers, Muséum national d'Histoire naturelle, Paris.

DIAGNOSIS AND RELATIONSHIPS

P. citrinema n. sp. is characterized by a well-developed stoma, well-developed muscular anterior and posterior pharynxes, well-developed pharyngeal-intestinal valve,

thickened inner gut wall, well-developed vaginal glands, short, broad spicules, narrow, long gubernaculum and eight pairs of genital papillae.

The following keys separate this species from other Panamanian members of the genus.

Parasitodiplogaster duganema n. sp. (Figs 2C, 3F)

MEASUREMENTS

Adults : See Tables 1 and 2.

DESCRIPTION

Females : Medium to large nematodes; stoma small; anterior and posterior pharynxes almost equal in length, both with distinct bulbs at base; anterior pharynx muscular, lumen expanded at base; distinct isthmus in glandular posterior pharynx; pharyngeal-intestinal valve inconspicuous; excretory pore opposite anterior part of intestine; intestine thin-walled, but walls expanded

around pharyngeal bulb; vulva surrounded with a continuous or broken cuticular ring; vaginal glands distinct, little cuticular modification at vulva; young fully developed in eggs; tail tip pointed.

Males : General features as described under females; testis outstretched; spicules narrow, with a distinct manubrium set off from corpus; gubernaculum swollen in middle; genital papillae seven pairs; three pairs preanal and four pairs postanal; two pairs at tip of tail; phasmids conspicuous (tubular) at tip of tail; tail tip pointed.

TYPE HABITAT AND LOCALITY

Found in fruits of *Ficus dugandii* growing in the vicinity of Barro Colorado Island, Republic of Panama.

TYPE MATERIAL

Holotype (male) and *allotype* (female) deposited in the nematology collection of the Department of Nematology, University of California, Davis, California; *paratypes* in the Laboratoire des Vers, Muséum national d'Histoire naturelle, Paris.

DIAGNOSIS AND RELATIONSHIPS

P. duganema n. sp. is characterized by a small stoma, nearly equal length of the anterior and posterior pharynxes, swollen bases of both anterior pharynxes, reduced pharyngeal-intestinal valve, intestinal cells surrounding pharyngeal base, large thin-walled intestinal cells, excretory pore opposite intestine, slender, narrow spicules, wedge-shaped gubernaculum and seven pairs of genital papillae.

The following keys separate this species from other Panamanian species of the genus.

Parasitodiplogaster maxinema n. sp. (Figs 2E, 3H)

MEASUREMENTS

Adults : See Tables 1 and 2.

DESCRIPTION

Females : Medium to large, slender nematodes; stoma longer than wide; anterior pharynx more than twice as long as posterior pharynx; anterior pharynx faintly muscular, elongate, swollen only slightly at base which contains slender crescent valve plates; posterior pharynx short, slender, glandular, slightly swollen basal bulb area with expanded lumen; pharyngeal-intestinal valve present; excretory pore usually opposite posterior pharynx; intestine thick-walled, containing an amorphous mass of material together with yeast-like cells; vaginal glands reduced; ovaries reflexed; body cuticle not thickened in

region of vulva; tail long, slender, with a small mucron at tip.

Males : General features as described under females; testis outstretched, rarely reflexed; spicules long, narrow, with a small manubrium (width less than that of corpus); gubernaculum long, slightly bent at proximal end; genital papillae six pairs, three pairs pre-cloacal and three pairs post-cloacal; phasmids inconspicuous, tail tip pointed.

TYPE HABITAT AND LOCALITY

Found in fruits of *Ficus maxima* growing in the vicinity of Barro Colorado Island, Republic of Panama.

TYPE MATERIAL

Holotype (male) and *allotype* (female) deposited in the nematology collection of the Department of Nematology, University of California, Davis, California; *paratypes* in the Laboratoire des Vers, Muséum national d'Histoire naturelle, Paris.

DIAGNOSIS AND RELATIONSHIPS

P. maxinema n. sp. is characterized by a well-developed stoma, slender, elongate anterior and posterior pharynxes without noticeable bulbs, a thick-walled intestine, reduced vaginal glands, no obvious cuticular thickening at vulva, slender slightly-bowed spicules with a small rounded manubrium, slender, elongate gubernaculum and six pairs of genital papillae.

The following keys separate this species from other Panamanian members of the genus.

Parasitodiplogaster nymphanema n. sp. (Figs 1C; 3A; 4C, D, E)

MEASUREMENTS

Adults : See Tables 1 and 2.

DESCRIPTION

Females : Medium to large nematodes; stoma distinct, longer than wide; both anterior and posterior pharynxes well-developed and muscular; both with short crescent valve plates at base, basal pharynx with distinct lumen in mid-region; excretory pore opposite posterior pharynx; pharyngeal-intestinal valve distinct; intestine thin-walled, cells large, transparent; ovaries reflexed, sometimes double reflexed; vaginal glands well-developed, cuticle slightly thickened in region of vulva; tail bluntly rounded, sometimes with a terminal minute knob on the tip.

Males : General features as described under females; testis reflexed or outstretched; spicules large, well-devel-

oped, with a distinct manubrium, tips pointed and curved slightly posteriorly; gubernaculum straight; genital papillae seven pairs, four pre-cloacal in a row up the body and three post-cloacal; terminal tail papilla pair have two nerve endings each; tail tip rounded; phasmids inconspicuous.

Juveniles : Some juveniles were found in association with adult wasps (*Pegoscapus* sp.) inside the fig fruits. These juveniles ranged from 222–288 μm in length, 10–13 μm in width, the distance from the head to the base of the posterior pharynx was 80–92 μm and the tail length was 28–29 μm . It is assumed that these are dauer and pre-dauer that developed in the fig from eggs deposited by the females. Similar dauer nematodes were also removed from the genital system of female wasps.

TYPE HABITAT AND LOCALITY

Found in the fruits of *Ficus nymphaeifolia* growing in the vicinity of Barro Colorado Island, Republic of Panama.

TYPE MATERIAL

Holotype (male) and *allotype* (female) deposited in the nematology collection of the Department of Nematology, University of California, Davis, California; *paratypes* in the Laboratoire des Vers, Muséum national d'Histoire naturelle, Paris.

DIAGNOSIS AND RELATIONSHIPS

P. nymphanema n. sp. is characterized by a well-developed stoma, anterior and posterior muscular pharynxes with imperceptible bulb-areas, a distinct pharyngeal-intestinal valve, large, thin-walled intestinal cells, well-developed vaginal glands, body cuticle swollen at vulva, large, well-developed spicules with elongate manubria, spicule tips bent posteriorly and seven pairs of genital papillae.

The following keys separate this species from other Panamanian members of the genus.

Parasitodiplogaster obtusinema n. sp. (Figs 2A, 3J)

MEASUREMENTS

Adults : See Tables 1 and 2.

DESCRIPTION

Females : Large nematodes; stoma small, slightly longer than wide; anterior pharynx well-developed, muscular, with crescent valve plates in the expanded basal portion, clearly set off from muscular posterior pharynx; base of posterior pharynx swollen, with faint crescent valve plates; excretory pore in anterior intestinal

region; small pharyngeal-intestinal valve; intestine with large cells filled with corpuscles ranging from 3–6 μm in diameter; ovaries reflexed; vaginal glands indistinct; body cuticle not or little expanded at vulva; tail tip blunt, with a small mucron.

Males : General features as described under females; testis outstretched; spicules large, slightly curved, with manubrium slightly wider than the corpus, tips blunt; gubernaculum straight, with a medial constriction; genital papillae consist of three pre-cloacal pairs and four post-cloacal pairs (two on tail tip); phasmids distinct, tubular, protruding; tail tip blunt, with a fine mucron.

TYPE HABITAT AND LOCALITY

Found in fruits of *Ficus obtusifolia* growing in the vicinity of Barro Colorado Island, Republic of Panama.

TYPE MATERIAL

Holotype (male) and *allotype* (female) deposited in the nematology collection of the Department of Nematology, University of California, Davis, California; *paratypes* in the Laboratoire des Vers, Muséum national d'Histoire naturelle, Paris.

DIAGNOSIS AND RELATIONSHIPS

P. obtusinema n. sp. is characterized by a small but distinct stoma, well-developed, muscular anterior and posterior pharynxes with distinct swollen basal bulbs; excretory pore opposite intestine, a faint pharyngeal-intestinal valve, thin, but expanded intestinal cells containing small elliptical corpuscles, indistinct vaginal glands, slender, slightly bent spicules, gubernaculum with medial constriction and seven pairs of genital papillae.

The following keys separate this species from other Panamanian members of the genus.

Parasitodiplogaster paranema n. sp. (Figs 1E, 3E)

MEASUREMENTS

Adults : See Tables 1 and 2.

DESCRIPTION

Females : Small nematodes; stoma small; anterior and posterior pharynxes slender, weakly muscled, base of anterior pharynx swollen and containing crescent valve plates; base of posterior pharynx slightly swollen, with indistinct valve plates; excretory pore posterior opposite pharynx; bulb of posterior pharynx inserted into anterior portion of intestine, pharyngeal-intestinal valve present;

intestine with distinct bush border (may be symbiotic bacteria); vaginal glands greatly reduced, cuticle not thickened in region of vulva; tail tip pointed.

Males : General features as described under females; testis outstretched; spicules short and wide, with a large, distinct manubrium; corpus constricted in middle forming two small ventral arches, tip bluntly pointed; gubernaculum short, wide at proximal end and pointed at tip; genital papillae seven pairs, four pairs pre-cloacal in a series and three pairs post-cloacal (one pair at tail tip); tail tip pointed; phasmids inconspicuous.

TYPE HABITAT AND LOCALITY

Found in fruits of *Ficus paraensis* growing in the vicinity of Barro Colorado Island, Republic of Panama.

TYPE MATERIAL

Holotype (male) and *allotype* (female) deposited in the nematology collection of the Department of Nematology, University of California, Davis, California; *paratypes* in the Laboratoire des Vers, Muséum national d'Histoire naturelle, Paris.

DIAGNOSIS AND RELATIONSHIPS

P. paranema n. sp. is characterized by a small stoma, slender weakly muscled anterior and posterior pharynxes with small basal bulbs; intestinal cells surrounding basal bulb of posterior pharynx, intestine tubular, with thick inner walls, short, wide spicules with a distinct manubrium, a short gubernaculum, with the proximal portion greatly swollen and seven pairs of genital papillae.

The following keys separate this species from other Panamanian members of the genus.

Parasitodiplogaster pertanema n. sp. (Figs 1D; 3D; 4A, B)

MEASUREMENTS

Adults : See Tables 1 and 2.

DESCRIPTION

Females : Small to medium-sized nematodes; stoma longer than wide (often coated with a deposit); muscular anterior and weakly muscled posterior pharynxes, both with a basal bulb (containing faint valve plates); excretory pore opposite posterior pharynx; intestine with distinct wall, containing yeast and bacterial cells in lumen; vaginal glands large; cuticle greatly expanded (from 32-70 μm) in region of vulva, ovaries reflexed (sometimes past vulva), reflexed portion of ovary often

expanded, tail bluntly pointed, sometimes terminating in a small button or mucron.

Males : General features as described for females, except stoma is wider than long; testis outstretched, spicules short and broad, with wide manubrium; corpus containing a proximal constriction resulting in a knobbed tip; gubernaculum robust; eight pairs genital papillae, four pairs pre-cloacal and four pairs post-cloacal; tail tips pointed; phasmids inconspicuous.

TYPE HABITAT AND LOCALITY

Found in fruits of *Ficus pertusa* growing in the vicinity of Barro Colorado Island, Republic of Panama.

TYPE MATERIAL

Holotype (male) and *allotype* (female) deposited in the nematology collection of the Department of Nematology, University of California, Davis, California; *paratypes* in the Laboratoire des Vers, Muséum national d'Histoire naturelle, Paris.

DIAGNOSIS AND RELATIONSHIPS

Small to medium-sized nematodes characterized by a stoma wider than long, well-developed anterior and posterior pharynxes with basal bulbs, an indistinct pharyngeal-intestinal valve, small intestinal cells, forming a tube-like intestine with thickened walls; well developed vaginal glands; greatly expanded cuticle in area of vulva; short and broad spicules, with manubrium wider than corpus, gubernaculum with proximal portion bent posteriorly and eight pairs of genital papillae.

The following keys separate this species from other Panamanian members of the genus.

Parasitodiplogaster popenema n. sp. (Figs 1A, 3G)

MEASUREMENTS

Adults : See Tables 1 and 2.

DESCRIPTION

Females : Medium-sized nematodes with stoma slightly longer than wide; anterior muscular pharynx twice as long as posterior weakly muscled pharynx; anterior pharynx with faint crescent valves in unmodified basal portion; posterior pharynx lacking valve plates and only slightly swollen at base which is surrounded by intestinal cells; excretory pore in region of junction between anterior and posterior pharynxes; pharyngeal-intestinal valve inconspicuous; inner lining of intestine thick, outer walls thin; vaginal glands present, body cuticle slightly thickened in region of vulva; eggs deve-

lop to young juvenile stage in uterus; ovaries reflexed, sometimes past vulva; tail tip pointed.

Males : General features as described under females; testis reflexed or outstretched; genital cone present; spicules curved, manubrium large; corpus bent at 22° angle, some sculpturing present on distal portion of corpus, tips acute; gubernaculum straight, proximal portion swollen; genital papillae seven pairs, four pairs pre-cloacal in a series, three pairs post-cloacal (pair of double-nerved papillae on tail tip); phasmids conspicuous, tubular; tail tip with minute mucron.

TYPE HABITAT AND LOCALITY

Found in fruits of *Ficus popenoei* growing in the vicinity of Barro Colorado Island, Republic of Panama.

TYPE MATERIAL

Holotype (male) and *allotype* (female) deposited in the nematology collection of the Department of Nematology, University of California, Davis, California; *paratypes* in the Laboratoire des Vers, Muséum national d'Histoire naturelle, Paris.

DIAGNOSIS AND RELATIONSHIPS

Medium-sized nematodes with well-developed stoma, anterior pharynx approximately twice the length of the posterior pharynx, excretory pore opposite the middle portion of the pharynx; base of posterior pharynx normally surrounded by anterior intestinal cells, intestinal cells thin on the outer side but thick-walled surrounding the lumen; spicules with a large manubrium, corpus with a distinct bend, the tips pointed; gubernaculum straight, proximal portion swollen; seven pairs of genital papillae and tail tip with a small mucron.

The following keys separate this species from other Panamanian members of the genus.

Parasitodiplogaster trigonema n. sp.

(Figs 2B, 3B)

MEASUREMENTS

Adults : See Tables 1 and 2.

DESCRIPTION

Females : Large nematodes with small stoma; both anterior and posterior pharynxes glandular, muscle fibers restricted to swollen basal portion of anterior pharynx (with crescent valve plates); posterior pharynx with basal bulb but valve plates absent; small pharyngeal-intestinal valve; excretory pore in anterior intestinal region or occasionally opposite posterior pharynx; intestinal walls thin, intestinal lumen wide; vaginal glands well developed; cuticle thickened in region of vulva, ridged on the ventral side; ovaries reflexed for a short distance; tail rounded, sometimes with a small mucron on the tip.

Males : General features as described under females; testis outstretched; spicules straight, with a distinct manubrium wider than corpus; spicule tips bluntly pointed; gubernaculum straight, wedge-shaped with proximal end swollen; genital papillae eight pairs, four pairs pre-cloacal in a series up the body, four pairs post-cloacal (double pair of papillae on tail tip); phasmids conspicuous; tail tip with or without mucron.

TYPE HABITAT AND LOCALITY

Found in fruits of *Ficus trigonata* growing in the vicinity of Barro Colorado Island, Republic of Panama.

TYPE MATERIAL

Holotype (male) and *allotype* (female) deposited in the nematology collection of the Department of Nematology, University of California, Davis, California; *paratypes* in the Laboratoire des Vers, Muséum national d'Histoire naturelle, Paris.

DIAGNOSIS AND RELATIONSHIPS

Large nematodes with a small stoma, anterior and posterior pharynxes glandular, both with distinct basal swellings, excretory pore normally opposite the intestine (sometimes posterior pharynx), intestine composed of large, thin-walled cells, vaginal glands well developed, body cuticle expanded in region of vulva, straight spicules with a distinct manubrium, bluntly pointed tips, straight gubernaculum, swollen proximally, eight pairs of genital papillae, tail rounded, sometimes bearing a small mucron.

The following keys separate this species from other Panamanian members of the genus.

Parasitodiplogaster yoponema n. sp.

(Figs 2D, 3I)

MEASUREMENTS

Adults : See Tables 1 and 2.

DESCRIPTION

Females : Small nematodes with stoma longer than wide; anterior pharynx muscular, three times as long as posterior glandular pharynx; basal bulb absent in anterior pharynx but weakly formed in posterior pharynx; valve area in anterior pharynx located some distance from the base; nerve ring encircles anterior pharynx; excretory pore opposite base of anterior pharynx; base

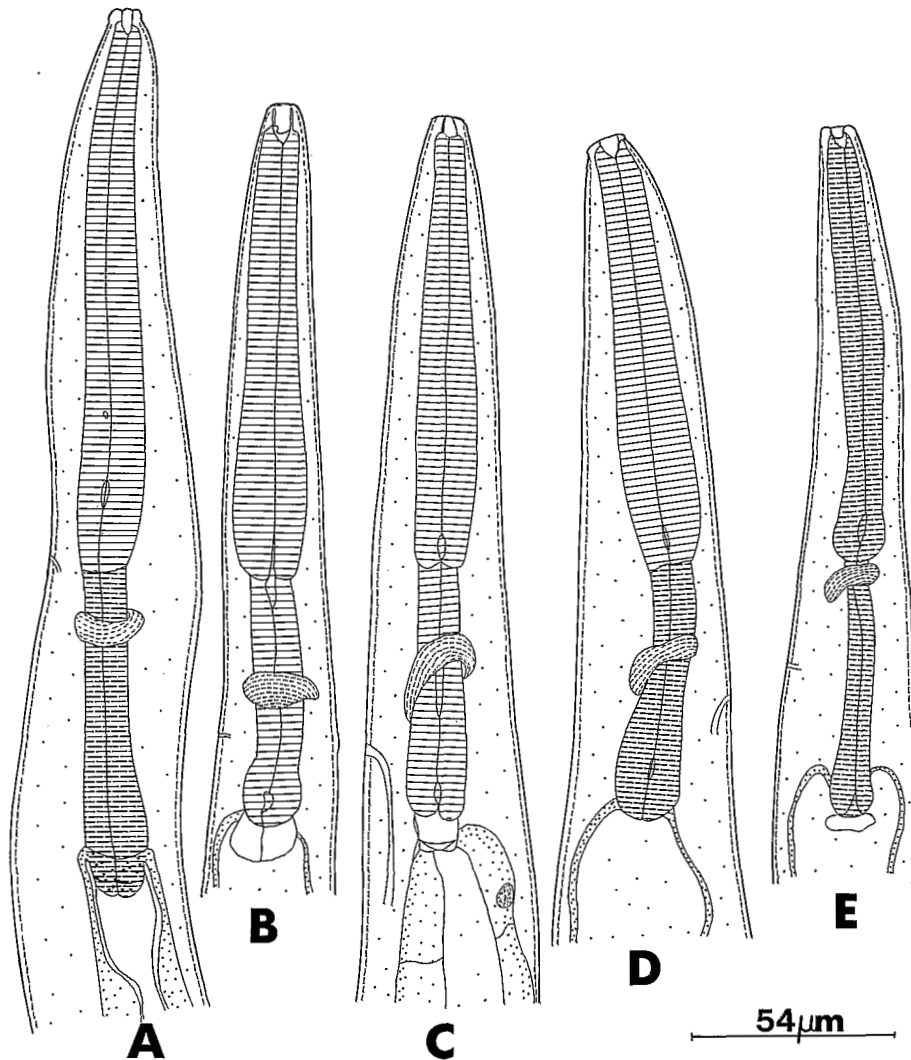


Fig. 1. Anterior portion of male Panamanian *Parasitodiplogaster*. A : *P. popenema* n. sp.; B : *P. c trinema* n. sp.; C : *P. nymphanema* n. sp.; D : *P. pertanema* n. sp.; E : *P. paranema* n. sp.

of posterior pharynx deeply embedded in anterior portion of intestine; pharyngeal-intestinal valve inconspicuous, vaginal glands greatly reduced, vulva inconspicuous, body cuticle not swollen in region of vulva; tail acutely pointed, with a small mucron on tip.

Males : General features as described under females; testis outstretched or reflexed; spicules curved, manubrium small, width less than that of corpus, tips bluntly pointed, slightly expanded; gubernaculum relatively large, proximal portion curved anteriorly; distal portion encloses corpus of spicules, genital papillae eight pairs, three pairs pre-cloacal, extending up body; five pairs

post-cloacal (two ventral pairs on tail tip); tail tip bearing a mucron; phasmids inconspicuous.

TYPE HABITAT AND LOCALITY

From fruits of *Ficus yoponensis* growing in the vicinity of Barro Colorado Island, Republic of Panama.

TYPE MATERIAL

Holotype (male) and *allotype* (female) deposited in the nematode collection at the Department of Nematology, University of California, Davis, California; *paratypes* in

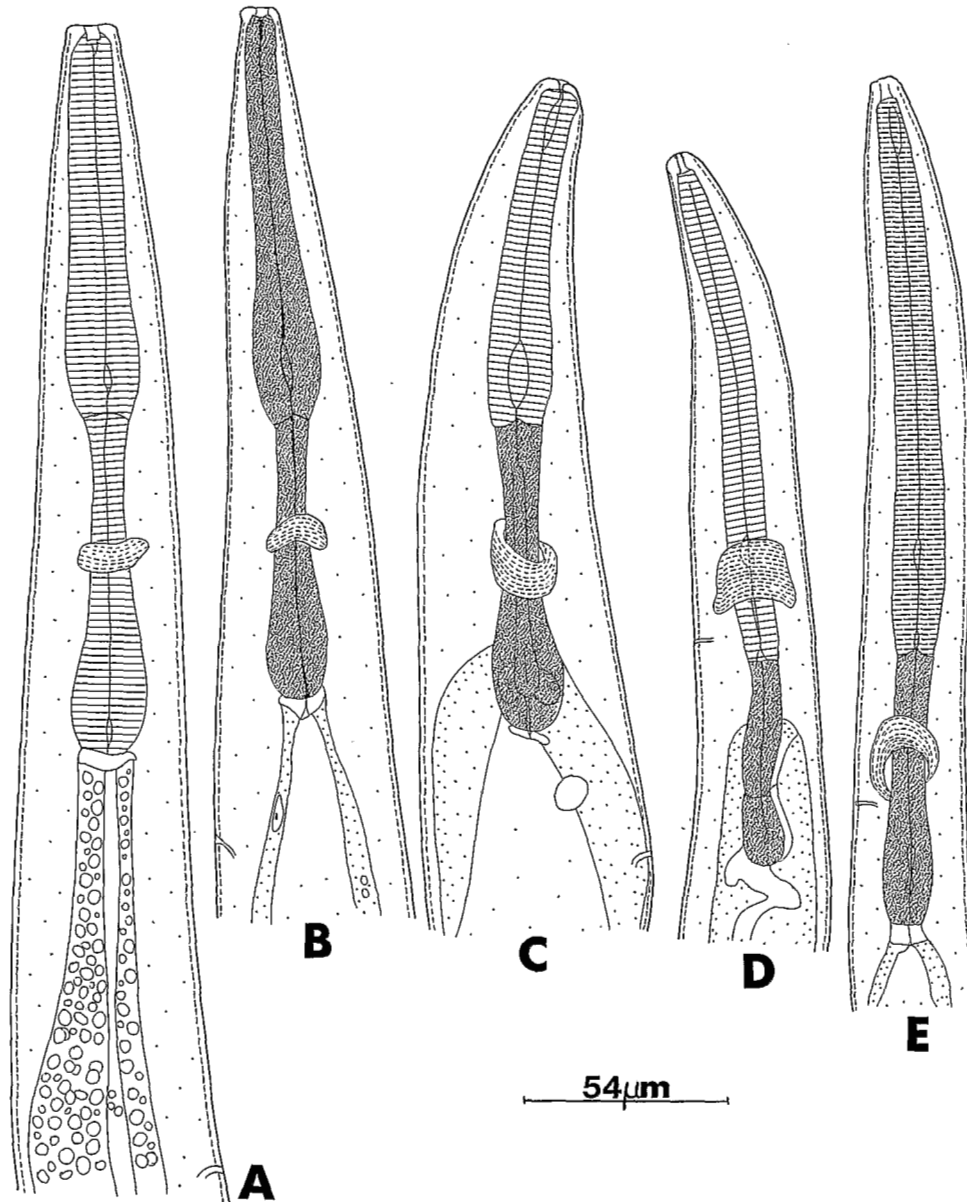


Fig. 2. Anterior portion of male Panamanian *Parasitodiplogaster*. A : *P. obtusinema* n. sp.; B : *P. trigonema* n. sp.; C : *P. duganema* n. sp.; D : *P. yoponema* n. sp.; E : *P. maxinema* n. sp.

the Laboratoire des Vers, Muséum national d'Histoire naturelle, Paris.

DIAGNOSIS AND RELATIONSHIPS

One interesting feature of both sexes is the tendency for the cuticle to separate from the hypodermis. Initially, it was suspected that an extra molt occurred or that the final juvenile cuticle was retained. However, a second

cuticle could not be detected over the hypodermis in the specimens with a loose cuticle.

These are small nematodes with a deep stoma, a muscular anterior pharynx approximately three times the length of the posterior glandular pharynx, the base of the posterior pharynx usually surrounded by the anterior intestinal cells, the excretory pore opposite the anterior pharynx, the intestinal cells large and thin, the vaginal glands indistinct, swollen body cuticle absent in

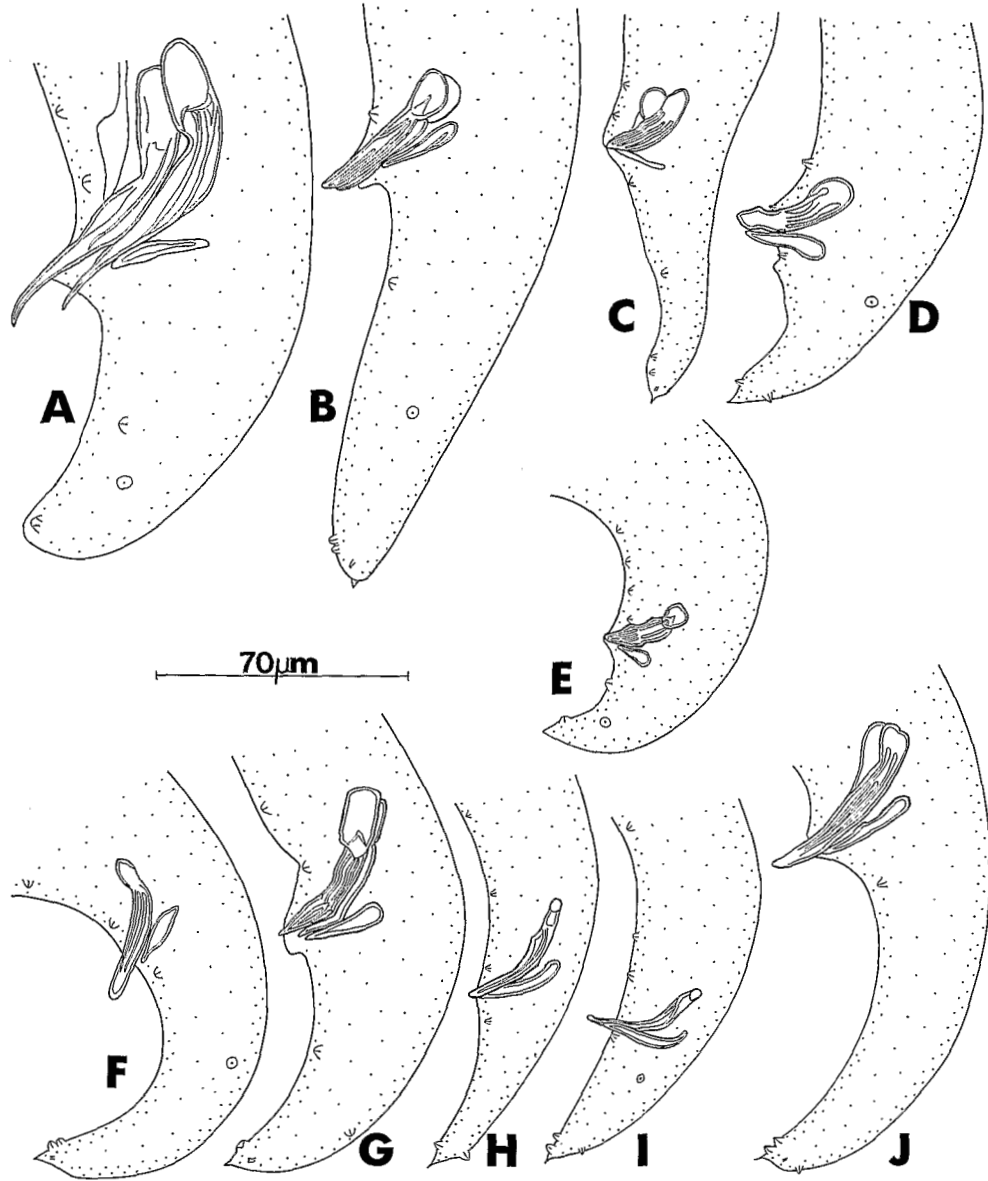


Fig. 3. Lateral view of male tails of Panamanian *Parasitodiplogaster*. A : *P. nymphanema* n. sp.; B : *P. trigonema* n. sp.; C : *P. citrinema* n. sp.; D : *P. pertanema* n. sp.; E : *P. paranema* n. sp.; F : *P. duganema* n. sp.; G : *P. popenema* n. sp.; H : *P. maxinema* n. sp.; I : *P. yoponema* n. sp.; J : *P. obtusinema* n. sp. For the purpose of space, the most anterior pre-cloacal papillae may not be included in the illustrations.

the region of the vulva, narrow spicules, round manubrium, smaller than the corpus diameter, the corpus bow-shaped, a narrow gubernaculum, curved up proximally, eight pairs of genital papillae and the tail tip pointed.

The following keys separate this species from other Panamanian members of the genus.

Key to the females of the Panamanian species of *Parasitodiplogaster*

- 1 — Ratio of posterior pharynx to anterior pharynx 0.68 or greater (0.65-0.90); excretory pore in region of intestine; stoma reduced
- 2 — Ratio of posterior pharynx to anterior pharynx usually less

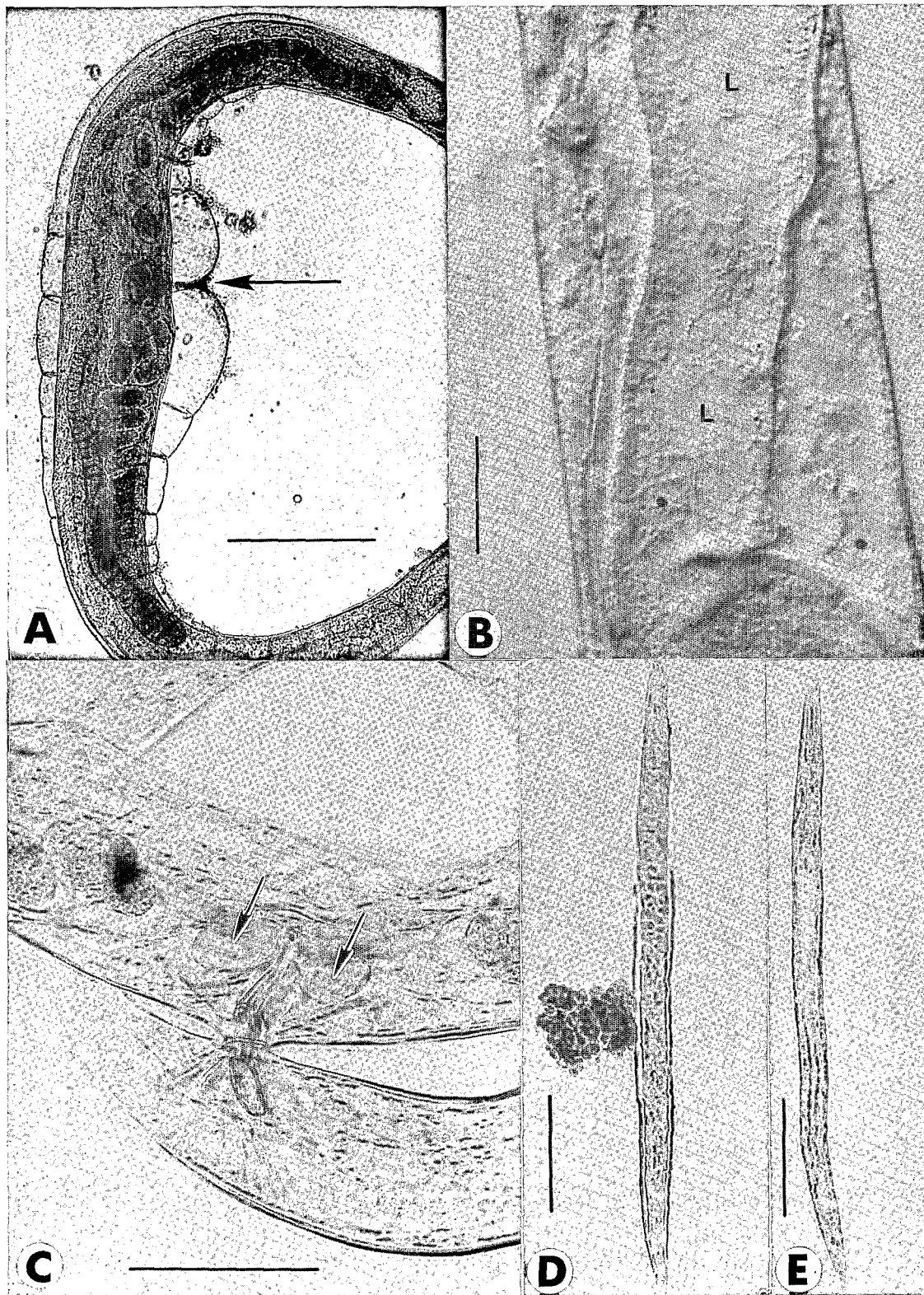


Fig. 4. A : Lateral view of mid-region of *Parasitodiplogaster pertanema* n. sp. showing greatly swollen body cuticle in region of vulva (arrow); B : Bacterial rods in the intestinal lumen (L) of *Parasitodiplogaster pertanema* n. sp.; C : A pair of *Parasitodiplogaster nymphanema* n. sp. " in copula ". Two of the four vaginal glands (arrows) are visible; D : Dauer juvenile of *Parasitodiplogaster nymphanema* n. sp. enclosed in previous juvenile cuticle (from fig fruit); E : Pre-dauer developing juvenile of *Parasitodiplogaster nymphanema* n. sp. (from fig fruit). (Bars equivalent : A = 100 μ m, B = 38 μ m, C = 78 μ m, D = 45 μ m, E = 52 μ m.)

- than 0.68 (0.30-0.69); excretory pore in region of pharynx or if in region of intestine and pharynx ratio is greater than 0.68 (*P. obtusinema* n. sp.) then intestinal cells filled with numerous small globules 3
- 2 — Base of posterior pharynx surrounded by anterior intestinal cells; tail length usually less than 100 μm *P. duganema* n. sp.
— Base of posterior pharynx not or only occasionally surrounded by anterior intestinal cells; tail length usually greater than 100 μm *P. trigonema* n. sp.
- 3 — Excretory pore in region of intestine; stoma reduced
P. obtusinema n. sp.
— Excretory pore in region of pharynx or at pharyngeal-intestinal junction; stoma distinct 4
- 4 — Anterior pharynx usually from two to three times the length of the posterior pharynx (ratio of posterior pharynx to anterior pharynx generally less than 0.50 [range = 0.30-0.60]); vaginal glands reduced 5
— Anterior pharynx usually less than two times the length of the posterior pharynx (ratio of posterior pharynx to anterior pharynx generally greater than 0.50 [range = 0.41-0.66]); vaginal glands well-developed (except in *P. pertanema* n. sp. which has greatly expanded body cuticle in the vulvar region) 7
- 5 — Excretory pore opposite posterior pharynx; base of posterior pharynx rarely surrounded by anterior intestinal cells *P. maxinema* n. sp.
— Excretory pore opposite anterior pharynx, posterior pharynx or pharyngeal-intestinal junction; base of posterior pharynx surrounded (sometimes only slightly) by anterior intestinal cells 6
- 6 — Anterior pharynx approximately twice the length of the posterior pharynx; body cuticle slightly swollen (and often ridged) in region of vulva *P. poponema* n. sp.
— Anterior pharynx approximately three times the length of the posterior pharynx; body cuticle not swollen in region of vulva *P. yoponema* n. sp.
- 7 — Vaginal glands inconspicuous; body cuticle not expanded in region of vulva; base of posterior pharynx surrounded by anterior intestinal cells *P. paranema* n. sp.
— Vaginal glands conspicuous; body cuticle expanded in region of vulva; base of posterior pharynx free or only slightly surrounded by anterior intestinal cells 8
- 8 — Body cuticle greatly expanded (up to 1/2 body width) in region of vulva; pharyngeal-intestinal valve inconspicuous *P. pertanema* n. sp.
— Body cuticle slightly expanded in region of vulva (less than 1/4 body width); pharyngeal-intestinal valve distinct 9
- 9 — Stoma short (3-5 μm); length anterior pharynx from 78-135 μm *P. nymphanema* n. sp.
— Stoma long (5-8 μm); length anterior pharynx from 138-144 μm *P. citrinema* n. sp.
- Length of tail equal to or less than twice spicule length .. 6
- 2 — Excretory pore opposite intestine; average ratio of posterior pharynx to anterior pharynx between 0.70 and 0.80 (range from 0.57 to 0.90) 3
— Excretory pore opposite pharynx or intestine; average ratio of posterior pharynx to anterior pharynx between 0.43 and 0.54 (range from 0.36-0.58) 4
- 3 — Pairs of genital papillae = 8; corpus straight; gubernaculum without medial constriction *P. trigonema* n. sp.
— Pairs of genital papillae = 7; corpus slightly curved; gubernaculum with medial constriction *P. obtusinema* n. sp.
- 4 — Corpus of spicules bent at a 22° angle; borders of manubrium angled; spicule tips pointed, forming an angle of 40° *P. poponema* n. sp.
— Corpus slightly curved, not with an abrupt bend; borders of manubrium rounded; spicule tips rounded or bluntly pointed, forming an angle of 60° or more 5
- 5 — Stoma wider than long; pharyngeal-intestinal valve reduced *P. pertanema* n. sp.
— Stoma longer than wide; pharyngeal-intestinal valve distinct *P. citrinema* n. sp.
- 6 — Excretory pore opposite intestine; ratio of posterior to anterior pharynx = 0.87 (0.86-0.90) .. *P. duganema* n. sp.
— Excretory pore opposite pharynx or rarely intestine; ratio of posterior to anterior pharynx = 0.29-0.70 7
- 7 — Excretory pore opposite anterior pharynx; average ratio of anterior pharynx to posterior pharynx = 0.34 (range = 0.29-0.43); 8 pairs genital papillae .. *P. yoponema* n. sp.
— Excretory pore opposite posterior pharynx or rarely anterior pharynx or intestine; average ratio of anterior pharynx to posterior pharynx = 0.57 (range = 0.38-0.75); 7 pairs genital papillae 8
- 8 — Base of posterior pharynx surrounded by intestinal cells; spicules short and wide, with rounded manubrium as wide as corpus width *P. paranema* n. sp.
— Base of posterior pharynx not surrounded by intestinal cells; spicules long and relatively narrow; manubrium not rounded, or if so then smaller than corpus width 9
- 9 — Manubrium large, elliptical; width nearly equal to that of corpus width; angle between corpus and manubrium = 45°; spicule tips pointed and curved downward *P. nymphanema* n. sp.
— Manubrium small, rounded; width smaller than that of corpus width; angle between corpus and manubrium = 0; spicule tips blunt and straight .. *P. maxinema* n. sp.

Key to the males of the Panamanian species of *Parasitodiplogaster*

- 1 — Length of tail twice or more than spicule length 2

Discussion

The ten species of Panamanian fig wasp nematodes described here present a remarkable picture of adaptive radiation from a single stem species (monophylogeny). This stem species has not been found but may still exist and would be a microbotrophic, free-living diplogasterid feeding on bacteria and other microorganisms in and around fallen fig fruits. The sequence of

development through geologic history might be the following.

Through constant association with the fig fruit, the nematodes encountered the fig wasps as they left some of the fruit that had fallen prematurely. Or the nematodes could have been associated with the above-ground portions of the tree. This would be possible under conditions of high moisture as found in the tropics. The initial association with the fig wasp was probably phoretic, possibly external with the nematodes on or wrapped around the wasp's body. Eventually the association became more complex, with the nematodes exhibiting internal phoresy in the insect's intestinal tract or reproductive system and then invading the hemolymph where development was initiated.

The dauer stage of the nematodes enter the female wasps when they emerge from the gall flowers of the fruit. They then mature inside the fig wasp and by the time the fig wasp is prepared to oviposit in a fig flower, the nematodes have reached the adult or pre-adult stage. After the wasp enters the ostiole of the fig the nematodes leave the wasp and enter the flower cavity where they mate and egg development occurs. The adult nematodes die and the young develop to the third stage dauer (resistant stage) which search for female wasps. The nematodes could reach the female wasp by entering the gall through the hole the male wasp makes for mating or waiting until the wasps emerge.

All ten species of Panamanian fig wasp nematodes show differences in size, digestive system morphology (stoma, pharynx and intestine) and primary and secondary reproductive structures (vaginal glands, modified body cuticle at vulva, spicules, gubernaculum and genital papillae).

This condition of adaptive radiation is analogous to the classical case of Darwin's finches on the Galapagos Islands. There is still discussion on whether the latter is a result of a competitive character displacement (Lack, 1947) or adaptation to an available food source (Bowman, 1961).

With the fig wasp nematodes, only one species of nematode has been found in each fig, so character displacement cannot be used as an explanation for this divergence. The fig trees and fig wasps represent sympatric species since their range overlaps. However each fig species is pollinated by a single fig wasp species (Wiebes, 1979), thus the nematodes in actuality represent allopatric populations since physical overlap never occurs.

What selective forces resulted in these divergent morphological nematode species which obviously arose from a common stem species? In the present situation, it was probably conditions associated with reproduction and feeding in the different fig fruits. The size of the stoma, structure of the pharynx and intestine and microscopic contents of the gut are related to the type of food utilized. In the Panamanian fig wasp nematodes,

there are two distinct morphological types of alimentary tracts. One of these would appear to be for the intake of solid particulate food (medium to large stoma, well muscled pharynxes; gut cells small with distinct border lining the lumen). The other type consists of a small stoma, glandular pharynxes and large, thin-walled gut cells with indistinct borders. A range of intermediary types occur between these two extremes. Such modifications undoubtedly reflect the type of nourishment utilized in the fig fruit and the nature of the physical environment (liquid, moist, or dry).

In microbotrophic species of Diplogasteroidea, one of which was undoubtedly ancestral to these fig wasp forms, the pharynx is usually modified into a robust anterior muscular portion and a smaller posterior glandular portion. These portions are usually not delineated as much as they are in *Parasitodiplogaster* (thus justifying the terms anterior and posterior pharynx for the latter). Spirurid nematodes are also characterized by having the pharynx divided into anterior muscular and posterior glandular sections (Poinar & Quentin, 1972). The presence of glandular pharynxes may be a modification for taking in liquid nourishment, since with *Parasitodiplogaster*, those species with glandular pharynxes also tend to have an intestine composed of large, thin-walled cells. In such species, the intestinal lumen was usually filled with a clear fluid probably originating from the fig fruit. This product could itself serve as a source of nutrients or it could serve as a culture medium for microorganisms inside the nematode's intestinal tract. Bacterial rods were observed in the intestinal lumen of *P. paranema* n. sp. and *P. pertanema* n. sp. (Fig. 4B), cocci in the intestine of *P. yoponema* n. sp. and *P. citrinema* n. sp., undetermined corpuscles in *P. obtusinema* n. sp. and yeast-like cells in *P. maxinema* n. sp.

Many of the Panamanian *Parasitodiplogaster* spp. possess modified crescent-shaped valves in both the anterior and posterior pharynxes. At this time, the presence of a valve in the pharynx is considered to represent a recent modification related to the nematode's behavior and not an indication that the stem species was a member of the Pseudodiplogasteroidea (Goodey, 1963) although this possibility cannot be ruled out.

Further variable modification in female *Parasitodiplogaster* were the vaginal glands and body cuticle in the vulvar region. The vaginal glands varied from very large in *P. citrinema* n. sp., *P. pertanema* n. sp., *P. duganema* n. sp. and *P. nymphanema* n. sp. (Fig. 4) to inconspicuous in *P. yoponema* n. sp., *P. trigonema* n. sp., *P. paranema* n. sp. and *P. maxinema* n. sp. A thick yellowish deposit which plugged the vagina and adhered to the outside of the vulva may have been produced by these glands. A similar deposit frequently surrounded the male cloacal opening.

The modification of the body cuticle in the region of

the vulva varied from nonexistent or barely noticeable in *P. yoponema* n. sp., *P. paranema* n. sp., *P. obtusinema* n. sp. and *P. maxinema* n. sp. to well developed in *P. pertanema* n. sp. (Fig. 4A). The selective pressure for this excess cuticle expansion in *P. pertanema* n. sp. is unknown.

Males varied considerably in the structure of the spicules and gubernaculi. The spicules ranged in length from 24 to 84 µm and varied in curvature, general shape, distal morphology and manubrium structure. During mating, the spicule corpore were inserted into the vagina (Fig. 4C). The gubernaculi ranged from 10 to 36 µm among the species studied and varied in curvature and general shape. The number of genital papillae varied from six to eight pairs. Especially interesting was the pair on the ventral tip of the tail, which was single with a single innervation in *P. paranema* n. sp., *P. pertanema* n. sp., *P. obtusinema* n. sp., *P. duganema* n. sp. and *P. maxinema* n. sp., single with two innervations in each papilla in *P. nymphanema* n. sp. and *P. poponema* n. sp. and double, each with a single innervation in *P. trigonema* n. sp., *P. yoponema* n. sp. and *P. citrinema* n. sp. Eight to nine pairs of caudal papillae are the normal number for diplogasterids (Goodey, 1963). The range in shape and size of the spicules and gubernaculi and the presence of vaginal glands and vulva cuticle expansion must pertain to different mating behavior as reflected by different conditions in the fig fruits.

Representatives of the genus *Parasitodiplogaster* also occur in association with African figs and fig wasps (Poinar, 1979) which brings up the question regarding the origin of this association in time and place. Fossil fig wasps occur in the Oligocene Florissant shales of Colorado (Brues, 1910) and in Dominican amber (A. P. Rasnitsyn, pers. comm.), which ranges from the Lower Miocene to Upper Eocene. This date roughly coincides with the earliest fossil record (mid-Eocene) for

the genus *Ficus* (Müller, 1984). It is quite probable that the relationship between fig wasps and *Ficus* was established by the mid-Cretaceous. Since South America became separated from Africa in the late Cretaceous (Cox & Moore, 1985), this would explain the presence of *Parasitodiplogaster* on both continents today. The Diplogasteridae as a group are quite ancient and probably arose in the early Paleozoic (Poinar, 1983).

REFERENCES

- BOWMAN, R. I. (1961). Morphological variation and adaptation in the Galapagos finches. *Univ. Calif. Publ. Zool.*, 59 : 1-302.
- BRUES, C. (1910). The parasitic Hymenoptera of the Tertiary of Floressant, Colorado. *Bull. Mus. comp. Zool.*, 54 : 1-125.
- COX, C. B. & MOORE, P. D. (1985). *Biogeography*. Boston, Blackwell Scientific Publications, 244 p.
- GOODEY, J. B. (1963). *Soil and freshwater nematodes*. London, Methuen & Co., 544 p.
- LACK, D. (1947). *Darwin's Finches*. Cambridge University Press, 380 p.
- MÜLLER, J. (1984). Significance of fossil pollen for angiosperm history. *Ann. Missouri Bot. Gard.*, 71 : 419-443.
- POINAR, Jr., G. O. (1979). *Parasitodiplogaster sycophilon* gen. n., sp. n. (Diplogasteridae : Nematoda), a parasite of *Elisabethiella stuckenbergi* Grandi (Agaonidae : Hymenoptera) in Rhodesia. *Proc. K. ned. Akad. Wetensch., Ser. C*, 82 : 375-381.
- POINAR, Jr., G. O. (1983). *The Natural History of Nematodes*. Englewood Cliffs, New Jersey, Prentice-Hall, 323 p.
- POINAR, Jr., G. O. & QENTIN, J.-C. (1972). The development of *Abbreviata caucasica* (Von Linstow) (Spirurida : Physalopteridae) in an intermediate host. *J. Parasitol.*, 58 : 23-28.
- WIEBES, J. T. (1979). Co-evolution of figs and their insect pollinators. *Ann. Rev. Ecol. Syst.*, 10 : 1-12.

Accepté pour publication le 21 mai 1990.