

Description of *Rhabditis* (*Caenorhabditis*) *drosophilae* n. sp. and *R. (C.) sonora* n. sp. (Nematoda : Rhabditida) from saguaro cactus rot in Arizona

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Summary – Two gonochoristic species, *Rhabditis* (*Caenorhabditis*) *drosophilae* n. sp. and *R. (C.) sonora* n. sp. are described from decaying saguaro cactus tissue in Arizona, USA. They are characterized by an anteriorly open bursa with a smooth edge; the spicule tips in both species are not pointed and are complex in shape. The dauerlarvae of *R. drosophilae* n. sp. are phoretic on the cactophilic fly *Drosophila nigrospiracula*. Arguments for the placement of both species in the subgenus *Caenorhabditis* of *Rhabditis*, and a list of autapomorphic characters are presented, as well as considerations on the colonization of cactus rot by *Rhabditis* (*Caenorhabditis*) species.

Résumé – *Description de Rhabditis* (*Caenorhabditis*) *drosophilae* n. sp. et de *R. (C.) sonora* n. sp. (Nematoda : Rhabditida) associés aux racines du cactus "Saguaro" en Arizona – Description est donnée de deux espèces gonochoriques, *Rhabditis* (*Caenorhabditis*) *drosophilae* n. sp. et *R. (C.) sonora* n. sp., provenant de tissus de cactus "Saguaro" en décomposition en Arizona, États-Unis d'Amérique. Elles sont caractérisées par une bourse ouverte antérieurement et à marge lisse; chez les deux espèces, les spicules, de forme complexe, ne sont pas pointus. Les dauerlarvae de *R. drosophilae* n. sp. sont phorétiques sur la mouche *Drosophila nigrospiracula* associée aux cactus. Des arguments sont avancés pour l'inclusion de deux espèces dans le sous-genre *Caenorhabditis* du genre *Rhabditis*; une liste de caractères autoapomorphiques est donnée, de même que des considérations sur la colonisation des racines de cactus par les espèces de *Rhabditis* (*Caenorhabditis*).

Key-words : Arizona, *Rhabditis* (*Caenorhabditis*), saguaro cactus, SEM, Sonoran Desert, nematodes.

Species of the subgenus *Caenorhabditis* Osche, 1952 of *Rhabditis* Dujardin, 1845 are of particular interest since *Rhabditis* (*Caenorhabditis*) *elegans* Maupas, 1899 became one of the model organisms for developmental and genetic research. In recent papers, the interest focused also on comparative studies of *R. elegans* and its relatives (Baird *et al.*, 1992; Fitch & Emmons, 1995; Fitch *et al.*, 1995; Sommer & Sternberg, 1995; Fitch & Thomas, 1997). With the exception of *R. plicata* Völk, 1950 (Sudhaus, 1974), all species designated to the subgenus *Caenorhabditis* are morphologically very similar to *R. elegans*. In fact, most species are hardly distinguishable. During a survey of the nematode fauna of rotting saguaro cactus (*Carnegiea gigantea*), two new *Rhabditis* (*Caenorhabditis*) species have been discovered. These two species differ in some important features from *R. elegans* and its presumed (Sudhaus, 1976; Fitch *et al.*, 1995; Kiontke & Sudhaus, 1996; Sudhaus & Kiontke, 1996) closest relatives. They are described in this paper.

Methods

R. drosophilae n. sp. dauerlarvae were picked from their phoretic associates *Drosophila nigrospiracula* Patterson & Wheeler, 1942, and reared on agar plates to which a small piece of saguaro cactus tissue was added.

R. sonora n. sp. specimens were isolated from saguaro cactus rot. Both species were cultured on agar plates and saguaro cactus tissue. Heat relaxed or glutaraldehyde fixed specimens from laboratory cultures were examined by light microscopy. Measurements were taken with a compound research microscope equipped with a camera lucida and a digitizing board. For scanning electron microscopy (SEM) study, *R. drosophilae* n. sp. adults and juveniles were picked from a laboratory culture plate; dauerlarvae were removed from *D. nigrospiracula* individuals. The nematodes were transferred to cold 0.05 M phosphate buffered 2.5 % glutaraldehyde at pH 7.2 for 24 h. *R. sonora* n. sp. specimens were fixed using cold 0.5 % glutaraldehyde in 0.05 M phosphate

buffer. The specimens were washed in phosphate buffer, processed gradually to absolute ethanol, critical point dried using CO₂, mounted on stubs and sputter coated with gold. Specimens were examined with a Philips SEM 515.

***Rhabditis (Caenorhabditis) drosophilae** n. sp.**

= species 2 in Kiontke & Sudhaus, 1996;

Sudhaus & Kiontke, 1996

(Figs 1, 2)

MEASUREMENTS

See Table 1.

DESCRIPTION

Adults: Cuticle about 1 µm thick, smooth, with faint annules, which are not visible on lateral field. Three lateral ridges extending posteriorly to a point about 75 µm anterior to anus. Deirids situated in the dorsal-most ridge. Lips closed; each lip with one inner labial sensillum in both sexes. Lip region sexually dimorphic: males with prominent cephalic sensilla on the subdorsal and subventral lips at the level of the amphids; females without cephalic sensilla. Amphid openings at the base of the lateral lips, not visible with light microscope. Each lip with a semicircular flap projecting into the mouth cavity. Length of buccal cavity averaging 4.3 times its width in females and males. Buccal cavity comprising 9–11 % of the pharynx length in both sexes. Pharyngeal collar 10–13 (12 ± 1) µm, enveloping 55–70 % of buccal cavity. Metarhabdions isomorphic and isotopic each with one triangular tooth projecting into the mouth cavity. Corpus 94–114 (104 ± 6) µm, comprising 52–57 % of pharynx length. Width of median bulb 20–27 (24 ± 2) µm in females and 18–23 (21 ± 1) µm in males, almost as wide as terminal bulb measuring 22–30 (26 ± 2) µm in females and 21–27 (23 ± 2) µm in males. Terminal bulb with *duplex haustrulum* posterior to the valvular apparatus. Cardia present and prominent. Cervical (“excretory”) pore 128–193 (151 ± 17) µm from anterior end at 68–91 % of pharynx length. Deirids, “posterior deirids”, and lateral channel conspicuous in glutaraldehyde fixed specimens. Deirids 136–213 (163 ± 21) µm behind the anterior end, at 78–127 % of pharynx length, thus in many cases posterior to cervical pore. “Posterior deirids” visible in some glutaraldehyde fixed specimens, in females 225–350 µm, in males 147–193 µm anterior to anus or cloaca, at about 75 % of body length.

Females: Vulva a transverse slit, the cuticle on both sides of the vulval opening with ridge-like sculptures.

Each end of the slit covered with a broad cuticular flap. Four dilator muscles attached to the vulva lips. Gonad didelphic and dorsally reflexed, anterior branch right, posterior branch left of intestine. Unreflexed part of anterior branch of gonad 230–448 (342 ± 86) µm long, reflexed part measuring 113–236 (166 ± 43) µm. Unreflexed part of the posterior gonad measuring 247–428 (342 ± 67) µm, reflexed part 78–217 (160 ± 48) µm long. Thus, the reflexed part of the anterior branch of the gonad represents 36–92 % of the length of the gonad (38–82 % for the posterior branch). Posterior and anterior branch of almost the same length. Gonad, measured from anterior to posterior flexure, comprising 52–86 (61) % of body length. Oviduct forming a spermatheca containing large sperm cells of about 5 µm diam. Sphincter present between spermatheca and uterus. Four to eighteen developing eggs present in uteri, sometimes also up to eight hatched juveniles. Eggs measuring 48–52 (50 ± 1) µm × 26–31 (27 ± 2) µm (n = 6). Rectum 18–25 (22 ± 2) µm long. Tail elongate with filiform tip. Phasmid openings 38–58 (50 ± 6) µm or 1.7–2.5 times ABW behind anus, at 36–53 (44) % of tail length.

Males: Testis right of intestine, comprising 54–70 (62) % of body length; ventrally reflexed part 73–105 (141 ± 20) µm long, that is 19–34 (25) % of gonad length. Bursa anteriorly open and peloderan with nine pairs of bursal papillae. Arrangement of papillae 2/1 + 3 + 3. Tips of papilla 1, 4, and 7 attached to the dorsal surface of bursal velum, tips of papillae 2, 5 and 8 attached to the ventral surface, papillae 3 and 9 extending to the bursa edge, papilla 6 thicker than others, slightly bottle shaped and embedded in the velum without reaching the edge. Bursa edge smooth. Phasmids (visible on SEM images) situated at the base of papilla 9. Precloacal sensillum on roundish knob with a bulgy basal anterior edge. Subventral postcloacal sensilla filiform. Spicules separate, slightly curved with notched tip, dorsolateral part very thin like a velum; proximal part separated from the distal part by a fine line or seam. Gubernaculum slender and curved; 74–88 (81) % of spicule length, its lateral edges partly folded ventrally. Rectum 30 ± 1 µm long on average.

Second-stage juveniles: Second-stage juveniles (J2) preparing to become dauerlarvae storing lipids as oil droplets in their intestine as well as in the hypodermis. As in other juvenile stages except dauerlarvae, no lateral ridges present on lateral field. Mouth open. Amphid openings inconspicuous. Pharynx with well developed median and terminal bulbs, their width 11–13 µm and 12–15 µm. Distance between anterior end and cervical pore 74–102 (90 ± 9) µm, corresponding to 63–88 (78) % of pharynx length. Genital primordium oval in shape, 9–18 µm long, at about 50 % of body length. Rectum length 13–17 (15 ± 1) µm. Tail with filiform tip. Phasmids 21–28 (24 ± 2) µm or 1.6–2.1 ABW behind anus.

* Named from the phoretic associate *Drosophila nigrospiracula*.

Table 1. Measurements (in μm) of heat relaxed living specimens of *Rhabditis* (*Caenorhabditis*) *drosophilae* n. sp. and *Rhabditis* (*Caenorhabditis*) *sonorae* n. sp.

	<i>R. (C.) drosophilae</i> n. sp.				<i>R. (C.) sonorae</i> n. sp.	
	Females	Males	J2 that will become dauerlarvae	Unsheathed dauerlarvae	Females	Males
n	10	10	8	11	11	11
Body length	1088 \pm 117 (947-1308)	781 \pm 72 (717-946)	464 \pm 17 (441-496)	395 \pm 19 (360-425)	651 \pm 68 (564-749)	617 \pm 97 (412-737)
Body width	56 \pm 6 (50-66)	40 \pm 3 (37-45)	21 \pm 2 (19-24)	20 \pm 2 (18-23)	36 \pm 5 (30-45)	32 \pm 4 (24-37)
Width of lip region	14 \pm 1 (12-16)	13 \pm 1 (11-14)	6	6 (6-7)	11 (11-12)	12 \pm 1 (10-14)
Buccal cavity length	21 \pm 1 (20-22)	19 \pm 1 (17-22)	16 \pm 1 (14-17)	16 \pm 1 (14-17)	17 \pm 1 (15-19)	16 \pm 2 (14-20)
Buccal cavity width	5 \pm 1 (4-6)	5 \pm 1 (4-6)	1	1	4 (3-4)	4 (3-4)
Pharynx length*	197 \pm 10 (183-213)	183 \pm 7 (173-193)	115 \pm 2 (113-118)	116 \pm 5 (111-125)	164 \pm 7 (160-181)	155 \pm 11 (133-168)
Tail length	116 \pm 18 (89-150)	37 \pm 2 (33-38)	86 \pm 6 (76-95)	45 \pm 3 (40-49)	53 \pm 4 (45-60)	36 \pm 4 (30-43)
ABW	23 \pm 1 (22-26)	22 \pm 1 (20-24)	12.5 \pm 0.5 (12-13)	11 \pm 1 (10-12)	20 \pm 2 (18-24)	22 \pm 1 (19-23)
Vulva in % distance anterior end to anus	60 \pm 1 (58-62)				65 \pm 1 (63-67)	
V	54 \pm 1 (52-56)				60 \pm 1 (58-61)	
Gonade length**	701 \pm 153 (478-874)	481 \pm 76 (410-644)			308 \pm 48 (250-383)	314 \pm 76 (158-399)
Spicules		31 \pm 1 (28-32)				27 \pm 4 (22-33)
Gubernaculum		25 \pm 2 (23-27)				19 \pm 2 (15-22)
a	19.4 \pm 1.2 (17.9-21.6)	19.4 \pm 1.3 (18.0-21.4)	22.1 \pm 1.6 (19.9-25.0)	20.1 \pm 1.3 (17.7-22.1)	19.4 \pm 2.3 (17.3-24.1)	20.5 \pm 2.1 (17.0-24.0)
b	5.5 \pm 0.5 (4.6-6.2)	4.3 \pm 0.4 (3.9-4.9)	4.0 \pm 0.2 (3.8-4.2)	3.4 \pm 0.2 (3.2-3.8)	4.0 \pm 0.3 (3.6-4.6)	3.9 \pm 0.4 (3.1-4.5)
c	9.5 \pm 1.0 (7.4-11.0)	21.2 \pm 1.8 (19.3-24.5)	5.4 \pm 0.4 (4.9-6.1)	8.8 \pm 0.5 (8.1-9.6)	12.3 \pm 0.9 (10.7-13.2)	17.2 \pm 2.3 (13.4-20.2)
d = c'	5.0 \pm 0.6 (4.0-6.4)	1.7 \pm 0.1 (1.6-1.8)	6.9 \pm 0.5 (6.2-7.5)	4.1 \pm 0.2 (4.1-0.2)	2.7 \pm 0.3 (2.3-3.2)	1.7 \pm 0.2 (1.4-2.1)

* Measured from anterior body end.

** Measured from anterior to posterior flexure in females, from flexure to cloaca in males.

Dauerlarvae: Moulded dauerlarvae differing from J2 in the following characters: mouth closed; amphids conspicuous, on average 3 μm behind anterior end; median and terminal bulb weakly developed, diameter of median bulb 7-8 μm , of terminal bulb 8-11 μm ; deirids and "posterior deirids" conspicuous; deirids situated 83-95 (88 \pm 4) μm behind the anterior end at 20-24 (22) % of body length, "posterior deirids" 39-76 (66 \pm 10) μm anterior to anus at 70-77 (72) % of body

length; lateral field with four lateral ridges; tail conical, tip blunt; phasmids 19-24 (22 \pm 2) μm or 1.7-2.2 ABW behind anus. Distance from lips to cervical pore 83-93 (89 \pm 4) μm corresponding to 73-83 (77) % of pharynx length.

TYPE SPECIMENS

Holotype and paratypes in the collection of the Museum für Naturkunde der Humboldt-Universität Berlin,

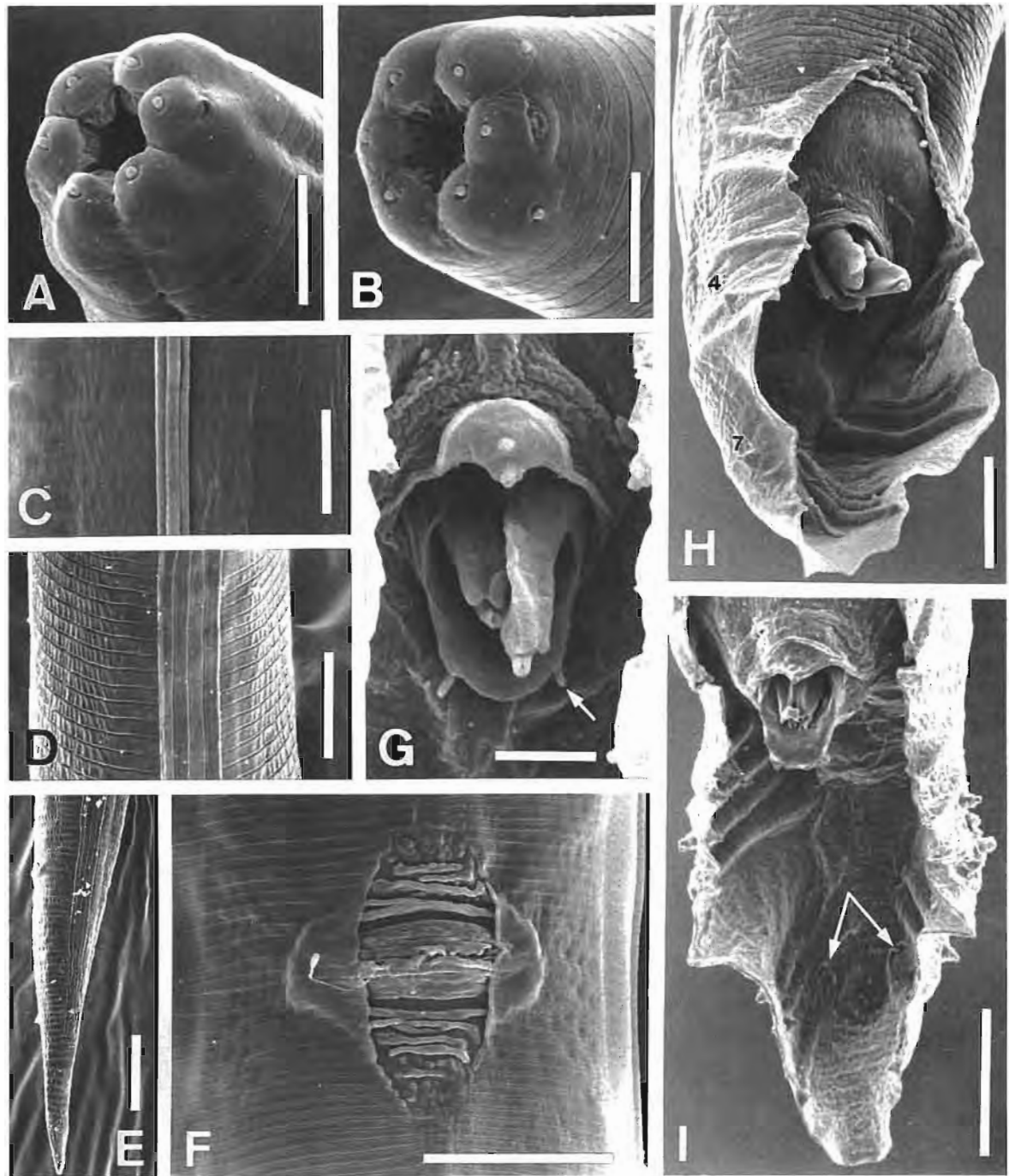


Fig. 1. *Rhabditis* (*Caenorhabditis*) *drosophilae* n. sp. *A, B*: Anterior end of female and male, respectively, showing left lip with amphid opening; *C*: Adult lateral field; *D*: Lateral field of dauerlarva; *E*: Dauerlarva tail; *F*: Female vulva; *G*: Precloacal region with precloacal sensillum, spicule tips, gubernaculum, postcloacal sensilla (arrow); *H*: Male bursa, with bursal papillae 4 and 7 indicated; *I*: Bursa (arrows point to phasmid openings). (Scale bars: *A-D* = 5 μ m; *E, F, H, I* = 10 μ m; *G* = 2 μ m).

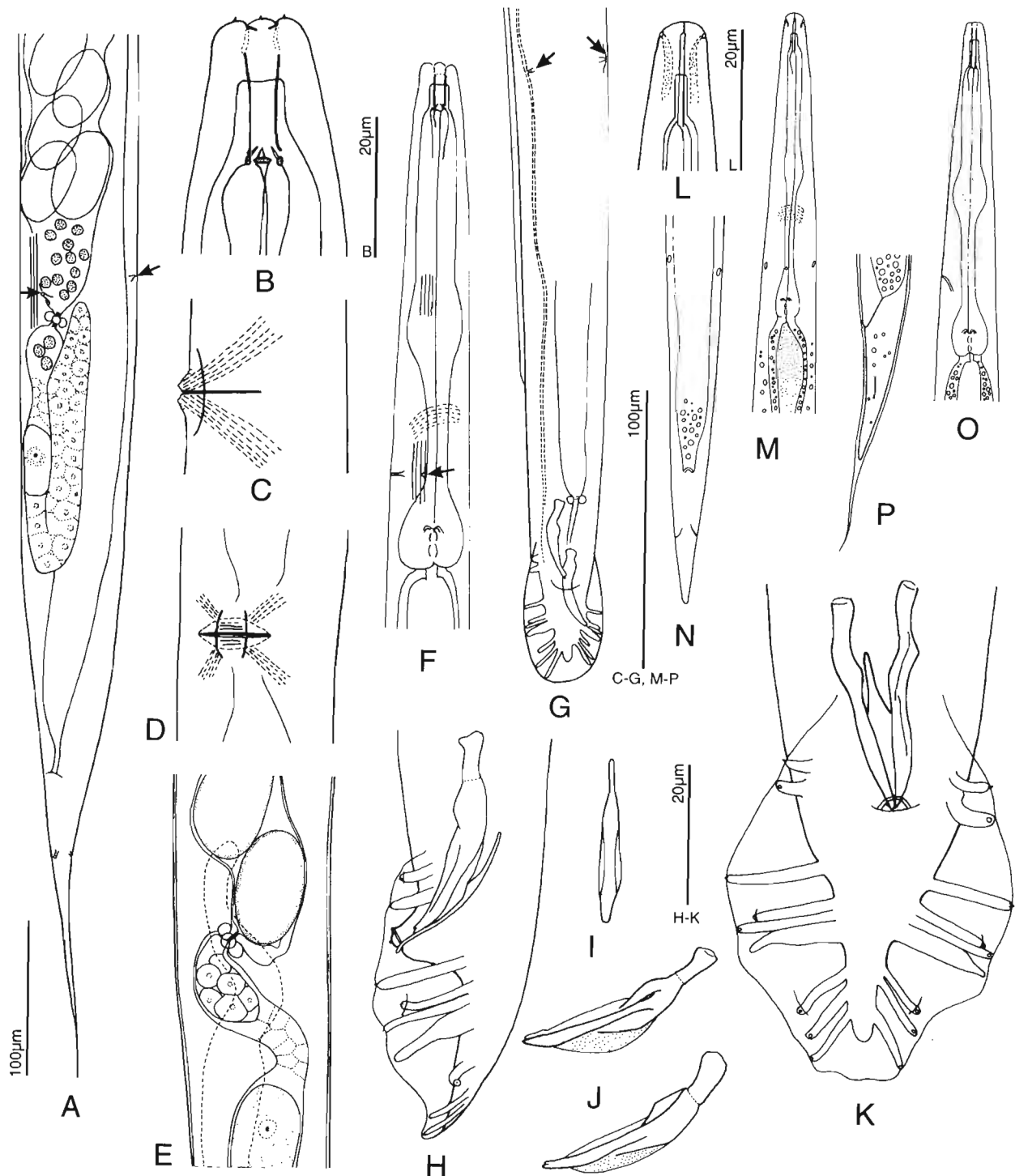


Fig. 2. *Rhabditis* (*Caenorhabditis*) *drosophilae* n. sp. Female. A : Posterior region, subventral, arrows point to posterior deirids ; B : Anterior end, lateral; C : Vulval region, lateral; D : Vulval region, ventral; E : Detail of posterior gonad showing spermatheca. Male. F : Anterior region, lateral (arrow indicates deirid); G : Posterior region showing lateral channel (dashed line) and "posterior deirids" (arrows); H : Bursa, lateral; I : Gubernaculum, ventral; J : Spicules, lateral; K : Bursa, ventral; L, M, N : Unsheathed dauerlarva; L : anterior end, ventral; M : Pharyngeal region, ventral; N : posterior body part, ventral; P : Posterior region of unsheathed dauerlarva, lateral; O : Pharyngeal region of j2, lateral.

Germany (No. 11068 and No. 11069, Generalkatalog Freilebende Würmer), other paratypes in the USDA Nematode Collection, Beltsville, MD, USA; Department of Nematology, University of California, Davis, USA; collection of Prof. Sudhaus, Institut für Zoologie der FU Berlin, Germany.

TYPE LOCALITY AND HABITAT

Arizona, Pima County, University of Arizona "Desert Station", Tucson Mountains. Decaying tissue of saguaro cactus, *Carnegiea gigantea* (Engelm.) Britton & Rose.

DIAGNOSIS

Rhabditis (*Caenorhabditis*) *drosophilae* n. sp. is characterized by the following combination of characters: one triangular denticle on each metarhabdion, pharyngeal sleeve present, open bursa with smooth edge, fourth bursal papilla attached to dorsal surface of bursal velum, spicule tips notched. Phoretic on the cactophilic fly *Drosophila nigrospiracula*.

BIOLOGY AND ECOLOGY

R. drosophilae n. sp. is a gonochoristic species, with males and females in approximately equal numbers (52% of 284 adults were males). Females carry up to eighteen eggs in different stages of development and also several first-stage juveniles in their uteri. Young females are oviparous; in older females juveniles tend to hatch inside the uterus, but are released in an early stage of postembryonal development. Development from egg to adult takes about 4 days, from dauerlarva to adult less than 24 h at 24 °C.

R. drosophilae n. sp. is a specialized coloniser of decaying saguaro cactus tissue. The species is among the firsts in a succession of nematodes in cactus rot. Phoretic dauerlarvae are transported to the rotten parts by the cactophilic fruit fly *D. nigrospiracula*, where they develop to adulthood and reproduce. J2 that will become dauerlarvae store oil in the form of droplets and are attracted by the pupae of *D. nigrospiracula*. These individuals accumulate near a pupa and develop into non-waving dauerlarvae without casting the J2 cuticle. They lose this cuticle spontaneously prior to emergence of the fly. When the adult fly emerges from the pupa, the nematodes crawl onto its head and occupy a pouch formed by the retracted ptilinum (an inflatable sac on the head used to open the puparium). Dauerlarvae are thus transported to a new rotting cactus. Phoresy on flies is an obligatory trigger for further development of dauerlarvae. Dauerlarvae that do not have contact with a fly fail to mature. A similar phenomenon is known for *Rhabditis dubia* Boven, 1937 (Sudhaus & Kühne, 1989) and *Diplogaster coprophila* Sudhaus & Rehfeld, 1990 (Kiontke, 1996).

Rhabditis (*Caenorhabditis*) *sonorae** n. sp.

= *Rhabditis* sp. 1 in Kiontke & Sudhaus, 1996;
Sudhaus & Kiontke, 1996
(Figs 3, 4)

MEASUREMENTS

See Table 1.

DESCRIPTION

Adults: Cuticle about 1 µm thick, smooth with faint annules. Lateral field without ridges or lines, but with irregular interruptions and fusions of the annulation. Annules each containing a triple row of fine dots situated within the cuticle, corresponding to the "struts" of the cuticle in *R. elegans* (Edgar *et al.*, 1982); these rows becoming somewhat irregular in the lateral field. Lips closed, each lip with one labial sensillum, males and females with four cephalic sensilla. All sensilla only distinguishable on SEM images. Amphids not visible with the aid of a light microscope. Buccal cavity triangular in transverse section, this feature also visible in living, heat-relaxed specimens. Length of buccal cavity 3.5-6.2 (4.5) times its width. Cheilostom weakly cuticularized. At the base of the cheilostom, rim of the buccal cuticle projecting into the lumen of the buccal cavity. Metarhabdions with one small denticle each, anisomorphic: the dorsal one slightly smaller and the denticle inserted more posteriorly. Pharyngeal collar enveloping 40-47 (43)% of the buccal cavity. Corpus 85-103 (91 ± 5) µm in females and 75-93 (84 ± 5) µm in males comprising 52-58 (55)% of pharynx length. Median bulb roundish, 17-25 (22 ± 2) µm wide, thus only slightly narrower than terminal bulb measuring 19-28 (23 ± 2) µm. Terminal bulb with *duplex haustrulum*. Cardia present. Cervical pore at 68-85 (81)% of pharynx length, 112-153 (129 ± 14) µm posterior to the anterior end in females, and 90-146 (131 ± 18) µm in males. Deirids in females at 70-79 (75)%, in males at 73-86 (77)% of pharynx length. "Posterior deirids" clearly visible in glutaraldehyde fixed specimens, situated in females 108-154 (133 ± 15) µm anterior to anus, in males 92-111 (102 ± 5) µm anterior to cloaca, at 74-79 (77)% of the distance anterior end to anus in females, and 79-82 (81)% anterior end to cloaca in males.

Females: Vulva a transverse slit with cuticular flaps covering the lateral ends. In *R. sonorae* n. sp. the flaps are short, roundish and almost pointed in the middle. Four vulval dilator muscles clearly visible. Gonad didelphic. Anterior branch right of intestine, unreflexed part measuring 107-212 (156 ± 34) µm, dorsal flexure 32-60 (49)% of branch length. Posterior branch left of intestine, 133-190 (152 ± 18) µm long, reflexed part representing 32-64 (45)% of the length of unreflexed part. Gonad measured from anterior to posterior flexure

* Named from Sonoran Desert.

comprising 41-52 (47) % of body length. Oviduct enlarged to a spermatheca with sphincter at junction with the uterus. Large sperm cells with a diameter of approximately 5 μm present in spermatheca and in uterus, between the (one to three) uterine eggs. Eggs measuring $54 \times 28 \mu\text{m}$ ($n = 5$) on average. Rectum 18-25 (22 ± 2) μm long. In some specimens two rectal gland cells visible. Phasmids 19-29 (24 ± 3) μm or 1-1.5 times ABW behind anus, at 39-51 (45) % of tail length. Tail elongate, typically widened at the level of phasmid openings and narrowing down to a point.

Male: Testis right of intestine, ventrally reflexed. Flexure 36-77 μm (59 ± 15) μm long, comprising 14-26 (20) % of testis length. Bursa peloderan and anteriorly open. Bursa edge slightly wavy but not serrate anterior to third bursal papilla. Nine pairs of bursal papillae arranged in a 2/4 + 3 pattern. Papillae 3-6 spaced evenly. Tip of papilla 1, 5, and 7 attached to dorsal surface of bursal velum. Papillae 2, 4 and 8 opening on ventral surface. Papillae 3 and 9 extending to the velum edge. Papilla 6 broader than others but not bottle-shaped as in other *Caenorhabditis* species (see Sudhaus, 1976), its tip embedded within the bursa velum. Phasmids close to tail tip at base of papilla 9. Praecloacal sensillum on smooth bulge. Two filiform postcloacal subventral sensilla visible. Spicules separate, compact, distal part almost straight. Proximal part demarcated by a faint line or seam. Spicule tip dentated. Dorsal part velum-like. Gubernaculum curved, 61-75 (69) % of spicule length, its lateral sides folded ventrally. In glutaraldehyde-fixed specimens, various genital muscles clearly visible: gubernaculum erector, spicule retractor and erector and diagonal muscles (as described for *R. elegans* by Sulston *et al.*, 1980). In glutaraldehyde fixed specimens four pseudocoelomocytes also conspicuous: two situated behind the excretory glands right of the intestine, one near the posterior deirids, and one near the insertion point of the dorsal spicule retractor muscle. Cloaca 23-30 (26 ± 3) μm long. One male with a duplicated first bursal papilla.

TYPE SPECIMENS

Holotype and paratypes in the collection of the Museum für Naturkunde der Humboldt-Universität Berlin, Germany (No. 11066 and No. 11067, Generalkatalog Freilebende Würmer), other paratypes in the USDA Nematode Collection, Beltsville, MD, USA; Department of Nematology, University of California, Davis, USA; collection of Prof. Sudhaus, Institut für Zoologie der FU Berlin, Germany.

TYPE LOCALITY AND HABITAT

Arizona, Pima County, University of Arizona "Desert Station", Tucson Mountains. Decaying tissue of saguaro cactus (*Carnegiea gigantea*).

DIAGNOSIS

Rhabditis (*Caenorhabditis*) *sonorae* n. sp. is a small species, with body length not exceeding 750 μm . Metarhabdions with one small denticle each, dorsal denticle more caudal. Pharyngeal collar enveloping less than 50 % of buccal cavity, mouth opening triangular. No lateral ridges present in adults. Bursa anteriorly open, anterior edge wavy. Tip of fifth bursal papilla on dorsal surface of velum. Spicule tip tripartite. Females never carry more than three fertilized eggs.

ECOLOGY AND BIOLOGY

The species was found in only one of over 130 studied saguaro cactus rot samples. The material of this sample was old and almost dry; it contained adult *R. sonorae* n. sp. The species can be bred on fresh saguaro cactus tissue. Formation of dauerlarvae has not been observed in laboratory cultures. Females are oviparous. Their uterus contained mostly none, sometimes one and seldom up to three developing eggs, but never juveniles.

Discussion

The following characters assign *R. drosophilae* n. sp. and *R. sonorae* n. sp. to the subgenus *Caenorhabditis* of *Rhabditis*: The bursal papillae are arranged in a 2/4 + 3 pattern, the sixth papilla is broader than others, the spicules have a dorsal velum. *R. drosophilae* n. sp. and *R. sonorae* n. sp. differ from all but one described *Rhabditis* (*Caenorhabditis*) species in possessing an anteriorly open bursa. This character is only shared by *R. plicata*. *R. drosophilae* n. sp., *R. sonorae* n. sp. and all *Rhabditis* (*Caenorhabditis*) species with the exception of *R. plicata* possess one single tooth on each metarhabdion (Wright & Thomson, 1981; Baird *et al.*, 1994; De Ley *et al.*, 1995; Sudhaus & Kiontke, 1996; in contrast to Sudhaus, 1976), whereas in *R. plicata* the armature of the metarhabdions consists of three ridges each. *R. drosophilae* n. sp. and *R. sonorae* n. sp. differ from *R. plicata* in the presence of a pharyngeal collar which is lacking in *R. plicata*. A pharyngeal collar is also present in the other *Rhabditis* (*Caenorhabditis*) species where it envelops at least 40 % of the buccal cavity. *R. plicata* is considerably bigger than *R. drosophilae* n. sp. and *R. sonorae* n. sp. (body length in females 1236-1850 μm in *R. plicata*, 947-1308 μm in *R. drosophilae* n. sp. and 564-749 μm in *R. sonorae* n. sp.; body length in males: 1013-1706 μm in *R. plicata*, 717-946 μm in *R. drosophilae* n. sp. and 412-737 μm in *R. sonorae* n. sp.). *R. sonorae* n. sp. differs from all other *Caenorhabditis* species including *R. drosophilae* n. sp. by the shape of the spicules, the lateral field lacking ridges, and the shape of the male and female tail. *R. sonorae* n. sp. is smaller than *R. drosophilae* n. sp., females carry less eggs and the metastomal denticles are smaller.

Sudhaus and Kiontke (1996) showed that *R. sonorae* n. sp. and *R. drosophilae* n. sp. clearly belong to a monophyletic group *Caenorhabditis*. The two species

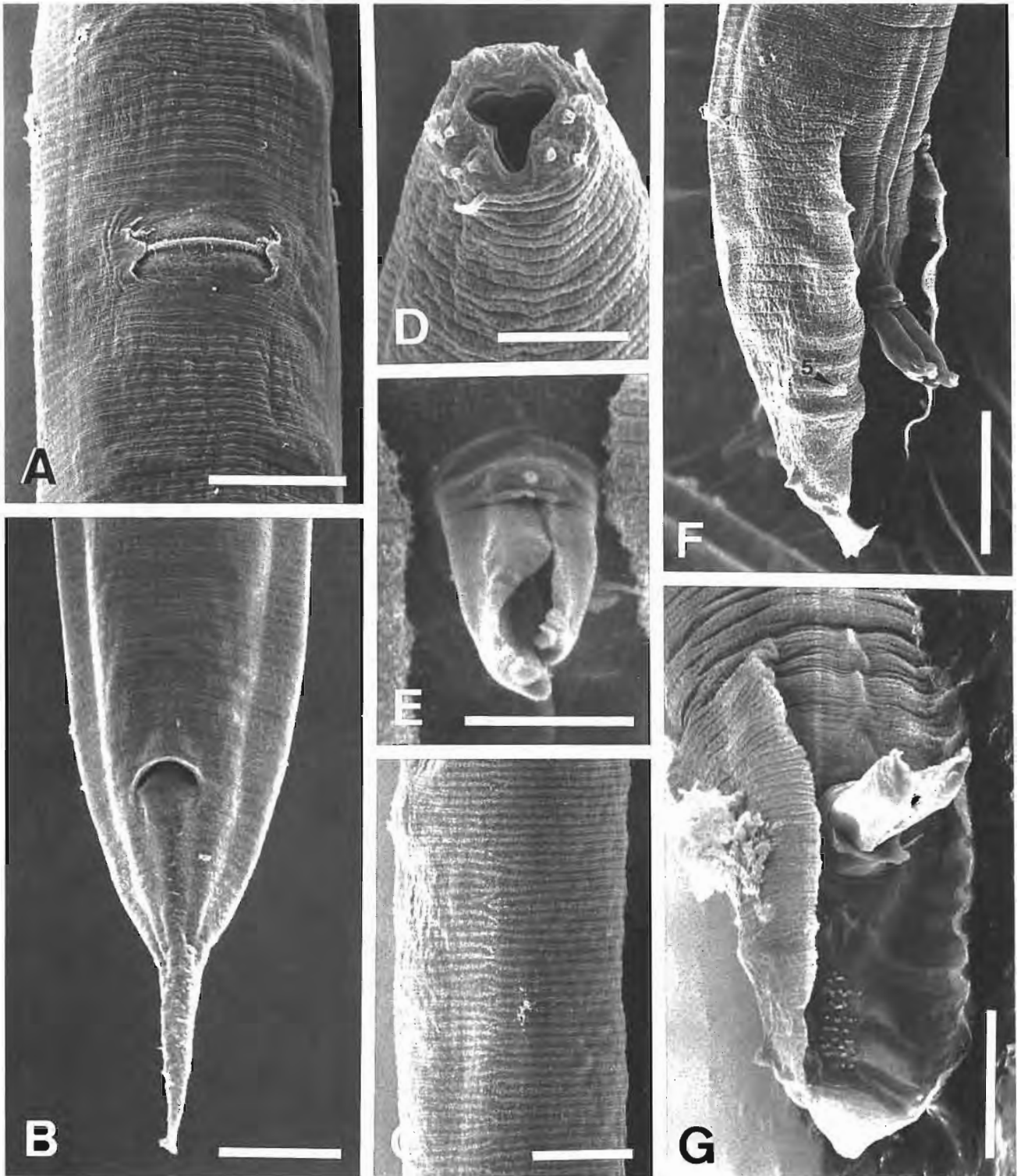


Fig. 3. *Rhabditis* (*Caenorhabditis*) *sonorae* n. sp. Female. A : Vulva region, ventral; B : Tail region, ventral; C : Lateral field in vulva region. Male. D : Anterior end ; E : Spicule tips and precloacal sensillum; F : Bursa, lateral, papilla 5 is indicated; G : Bursa, subventral, showing distal end of gubernaculum. (Scale bars : A-C, F, G = 10 μ m; D, E = 5 μ m).

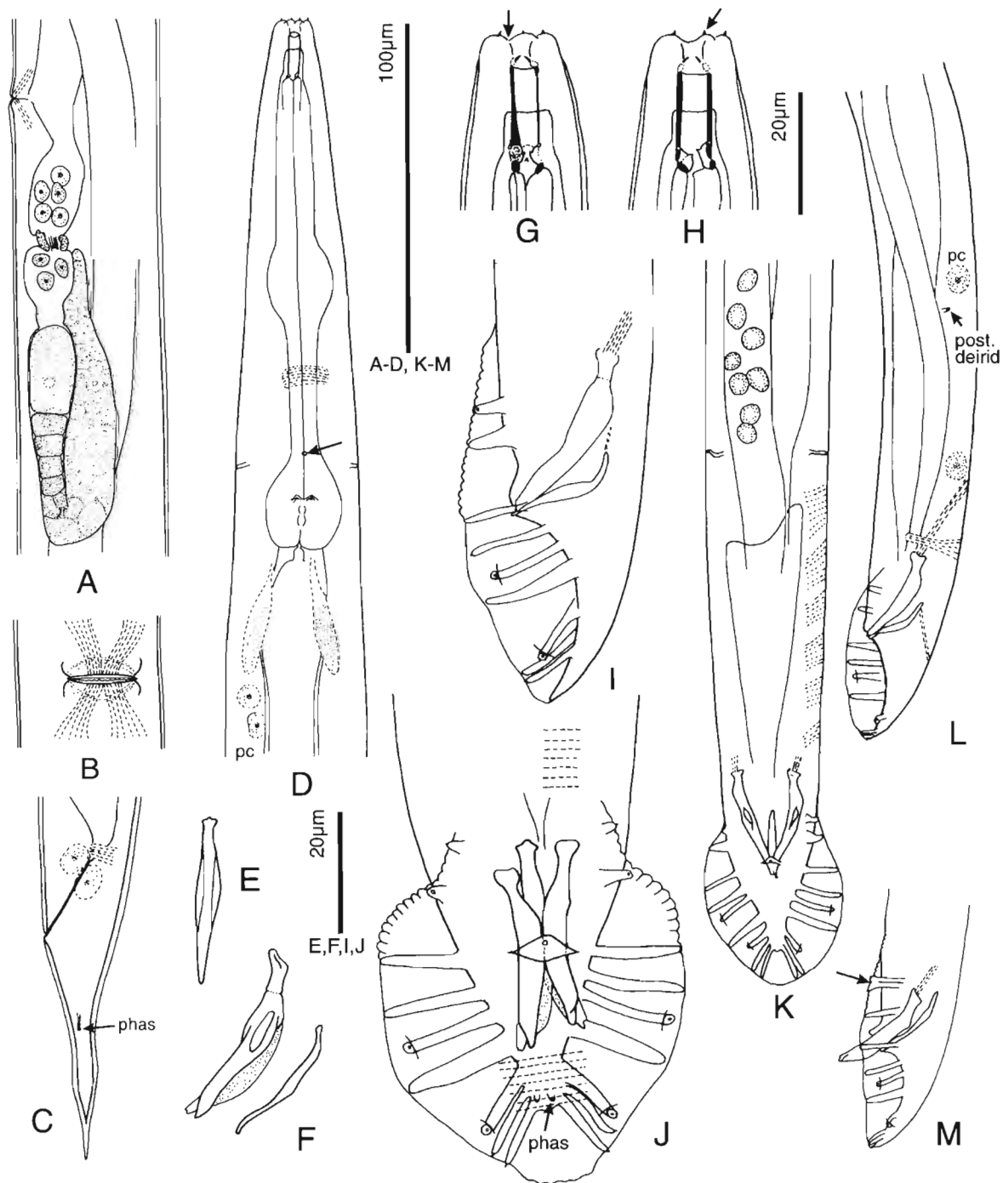


Fig. 4. *Rhabditis (Caenorhabditis) sonoreae* n. sp. Female. A : Lateral view of vulva, spermatheca and posterior gonad; B : Vulva, ventral; C : Tail region, lateral (phas = phasmid); D : Anterior body region, ventral (pc = pseudo-coelomocytes). Male. E : Gubernaculum, ventral; F : Spicule and gubernaculum, lateral; G : Anterior end, arrow points to gap between the two subventral lips; H : Anterior end, arrow points to right lateral lip; I : Bursa, lateral; J : Bursa, ventral, showing cuticular striation (phas = phasmids); K : Posterior body region, ventral, showing "posterior deirids" and diagonal muscles; L : Posterior body region, lateral, showing "posterior deirids", two pseudo-coelomocytes (pc) and the spiculum retractor and gubernaculum erector muscle; M : Bursa aberration : papilla 1 duplicated.

diverged at early and separate times during the *Caenorhabditis* lineage (sp. 1 and sp. 2). In other words, despite their similar habitat, *R. sonoreae* n. sp. and *R. drosophilae* n. sp. are not sister species. Four synapomorphic characters demonstrate that *R. sonoreae* n. sp. is the sister species of all other *Caenorhabditis* species (or all species except *R. plicata*).

On the basis of the cladogram and the data compiled for other *Caenorhabditis* species (Sudhaus & Kiontke, 1996), it is now possible to list autapomorphic characters for the two new species: autapomorphies for *R. sonoreae* n. sp. are the smooth lateral field without lateral ridges, the tridentate spicule tip, and perhaps the triangular mouth opening. For *R. drosophilae* n. sp. the shape of the spicule tip and the unique life cycle are considered autapomorphic. Sexually dimorphic cephalic sensilla are present in all *Caenorhabditis* species except *R. sonoreae* n. sp. However, *R. sonoreae* n. sp. exhibits the plesiomorphic situation within *Caenorhabditis* with regard to the cephalic sensilla.

The position of *R. sonoreae* n. sp. and *R. drosophilae* n. sp. in the phylogenetic tree has consequences for the evolutionary interpretation of their ecology. *R. drosophilae* n. sp. is clearly a specialized inhabitant of cactus rot. *R. sonoreae* n. sp. was found only once. However, the sample which contained the species was rather big, and the worms were present as adults in several subsamples together with other cactus-specific nematode species. There was no other decaying organic material near the sample site from which the worms could have invaded the cactus rot. In general, habitats for rhabditid nematodes seem to be rather rare in the Sonoran Desert. These arguments lead me to assume that *R. sonoreae* n. sp. is indeed a cactus rot dweller. If this assumption holds true, the colonization of cactus rot must have occurred twice within *Caenorhabditis*. There is no reason to believe that the stem species of *Caenorhabditis* lived in cactus rot. Rhabditid nematodes colonized cactus rot at least eight times, judging from the number of unrelated species that have been found in cactus rot: two *Rhabditis* (*Caenorhabditis*) species, one *Rhabditis* (*Rhabditella*) species, one *Rhabditis* (*Cephaloboides*) species, one *Prodonatorhabditis* species, *Diplogaster* (*Diplogastrellus*) *cerea* Kiontke & Sudhaus, 1996, three *Diplogaster* species belonging to the *Nudicapitatus*-group *sensu* Weingärtner (1955) and two *Mononchooides* species (unpubl.).

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