Three New Species of Heteroderoidea (Nematoda) from the Aleutian Islands

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Abstract: Three new species of Heteroderoidea are described from Adak and Amchitka Islands in the Aleutian chain. Second-stage juveniles of *Thecavermiculatus crassicrustata,* n. sp., differ from those of *T. gracililancea* Robbins by having longer stylets (40–45 μm vs 19–22 μm). The female of *T. crassicrustata* has a longer neck, a more posterior excretory pore, and lacks a posterior protuberance. *Meloidodera eurytyla,* n. sp., differs from other *Meloidodera* spp. in that second-stage juveniles have longer stylets (32–35 μm) and much more massive stylet knobs, while males have a longitudinally striated basal head annule. *Meloidogyne subarctica,* n. sp., can be separated from other *Meloidogyne* spp. by combinations of the following characteristics: perineal pattern with large oval areas in the tail region devoid of striae, arch with few unbroken striae; female excretory pore 1.5–2.5 × the stylet length from the anterior end; haploid chromosome number = 18; the spermatheca filled with sperm; stylet length of second-stage juveniles 13.5–15.4 μm. *Key words:* endoparasites, taxonomy, cystoid nematode, root-knot nematode.

During the summer of 1977, M. P. Williams of the University of Tennessee Ecology Program collected in the Aleutian Islands galled roots of a dunegrass, *Elymus mollis* Trin., which were found to contain females of an undescribed *Meloidogyne* sp. Subsequently, Williams in 1978 and Raymond McCord in 1979 collected and sent numerous soil and root samples for detection and identification of nematodes. Among the many species found were three new species of Heteroderoidea, described herein. Later papers will deal with Hoplolaimoidea and Criconematoidea.

MATERIALS AND METHODS

Soil samples were generally of a loamy medium sand (Typic Cryopsamment) and were washed through a sieve (38 μm pore) with water to collect nematodes. Soils of finer texture were processed by a centrifugal-flotation method (2). Roots were examined with a stereoscope to find females *in situ*. All extracted nematodes were killed and fixed in hot 4% formalin, then processed to glycerin by a rapid method (5). Measurements were made on specimens mounted in glycerin or glycerin jelly. The necks of some females of each species were severed from the bodies and mounted in glycerin for better observation of esophageal structures. Perineal patterns were photographed with the aid of an interference contrast microscope. Male tails of each species were severed and mounted in a lateral orientation to study reproductive structures. Female gonads were dissected from females in glycerin, then mounted in glycerin on slides. Chromosome squashes were prepared with a propionic orcein method (7). Seedlings of oat (*Avena sativa* L.), fescue (*Festuca elatior* L. 'Ky 31') and tomato (*Lycopersicon esculentum* L. 'Rutgers') were each inoculated with about 5,000 eggs of the root-knot nematode and grown in the greenhouse. Type material for all species consisted only of nematodes collected directly from Aleutian soils. Holotypes, allotypes, and some paratypes, as well as posterior cuticular regions of the root-knot nematodes, have been deposited in the USDA Nematode Collection (USDANC), Beltsville, Maryland.

Meloidodera eurytyla, n. sp.
Figs. 1–10, Table 1

Measurements and ratios for paratypes and second-stage juveniles are given in Table 1.

DESCRIPTION: Mature *females* yellow, broadly oval to pear shaped (Fig. 10), with relatively short necks that are frequently twisted or asymmetrically swollen. Body covered with a transparent, light yellowish, leathery coat, usually with thicker, brown patches. Neck secured to roots by brittle brownish substance apparently exuded by nematode. Head not offset, four annules present (Fig. 9). Face view not seen clearly, but lip region apparently consisting of four

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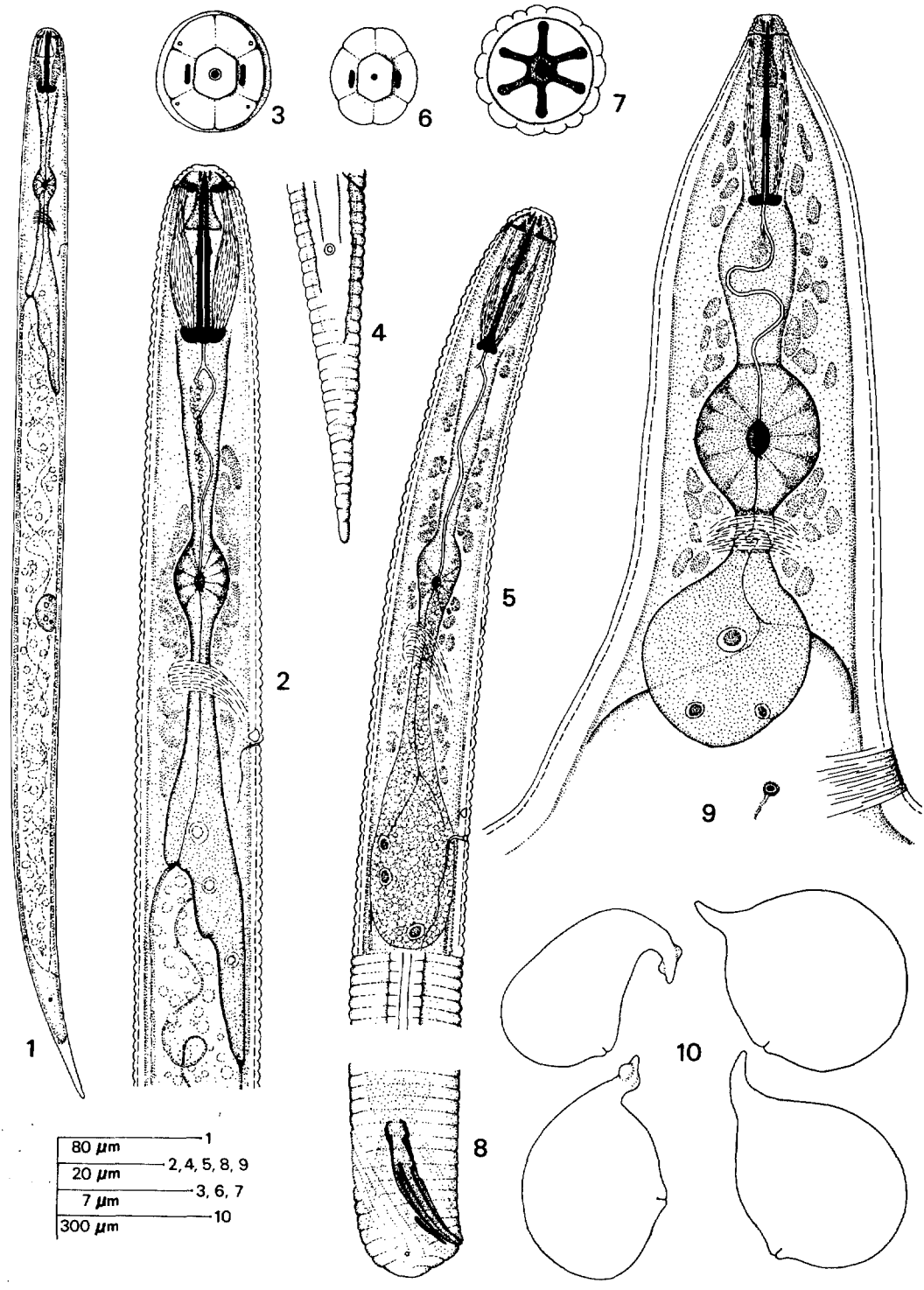


Figs. 1–10. *Meloidodera eurytyla* n. sp. 1) Second-stage juvenile, entire. 2) Second-stage juvenile, anterior region. 3) Second-stage juvenile, face view. 4) Second-stage juvenile, tail. 5) Male, anterior region. 6) Male, face view. 7) Male, optical cross section at basal lip annule. 8) Male, tail. 9) Female, anterior region. 10) Females, body outlines. (Scales in µm).

Table 1. Measurements and ratios for *Meloidodera eurytyla*, n. sp.

	Paratype ♀♀ (n = 7)				Paratype ♂♂ (n = 11)				Second-stage juveniles (n = 17)			
	Mean	Range	SD*	CV*	Mean	Range	SD	CV	Mean	Range	SD	CV (%)
Length (μm)	469	375 -583	63.8	13.6	732	583 -865	98.6	13.5	580	556 -607	14.5	2.5
Width (μm)	224	177 -255	25.4	11.3	22	16.3- 27.2	3.51	16.0	23.4	21.1- 25.9	1.81	7.7
Stylet length (μm)	34.1	32.2- 36.6	1.58	4.6	27.9	24.3- 33.4	2.82	10.1	33.1	32.2- 34.8	0.84	2.5
Stylet base height (μm)	2.3	2.2- 2.5	0.12	5.3	2.4	1.9- 2.9	0.30	12.6	3.0	2.6- 3.5	0.29	9.8
Stylet base width (μm)	6.7	6.5- 7.1	0.26	3.8	4.1	3.7- 5.0	0.37	9.0	7.8	7.4- 8.4	0.27	3.5
Dorsal esophageal gland orifice to stylet base (μm)	4.4**	3.5- 5.6	-----	-----	3.5	2.0- 5.1	1.14	32.2	5.3	4.2- 7.0	0.72	13.7
Excretory pore to head end (μm)	152	139 -162	8.69	5.7	117	103 -143	14.4	12.3	119	110 -124	3.81	3.2
Excretory pore to head end as % of body length	31.9	27.3- 38.9	4.49	14.1	17.0	15.2- 18.7	0.80	4.7	20.5	19.5- 21.2	0.43	2.1
Valve to head end as % of body length	15.0	11.7- 18.9	2.47	16.5	10.6	7.4- 11.9	1.34	13.6	14.2	13.2- 14.6	0.56	3.9
a	2.1	1.9- 2.5	0.21	10.1	33.5	28.8- 37.2	2.39	7.1	24.9	21.0- 28.3	2.26	9.1
b	-----	----------	-----	----	5.8	5.1- 7.3	0.69	11.8	4.2	4.0- 4.3	0.10	2.4
b′	-----	----------	----	---	4.3	3.7- 5.6	0.53	12.3	3.2	3.0- 3.5	0.15	4.7
c									8.8	8.5- 9.4	0.24	2.7
Tail length/body width at anus									4.4	4.1- 5.0	0.25	5.6
Neck length (μm)	82.8	71.9-108.8	13.6	16.4								
Vulva-anus distance (μm)	134	100 -178	30.1	22.5								
Testis length as % of body length					42.8	38.3- 47.2	3.29	7.7				
Spicule length (μm)					25.4	23.6- 28.0	1.49	5.9				
Gubernaculum length (μm)					6.9†	----------	-----	----				
Genital primordium to tail end (μm)									225	206 -245	9.87	4.4
Phasmid to tail end (μm)									55.0	50.5- 58.2	2.25	4.1

*SD: Standard deviation; CV: Coefficient of variation.
**Four specimens.
†One specimen.

rounded lobes. Stylet long, slender, anterior surface of knobs flattened and extending laterally (Fig. 9). Esophageal glands formed as a large lobe partly overlapping the intestine. Excretory pore at or slightly behind the distal end of the esophageal glands.

Males longer but proportionally more slender than juveniles, assuming a nearly straight shape when heat relaxed. Head region with 2–4 annules, annulations incomplete on some individuals (Fig. 5). Labial disc hexagonal, surrounded by six lips, lip region wider dorso-ventrally (Fig. 6); amphidial apertures appearing small. Basal head annule longitudinally striated, divided into about 14 sectors (Fig. 7). Cephalic framework moderately developed. Stylet slender, knobs sloping posteriorly and rounded. Median bulb and valve reduced (Fig. 5); esophageal glands pyriform, overlapping intestine; apparent gland secretion leading to subventral orifices (Fig. 5) but not to dorsal orifice. Excretory pore at level of most anterior gland nucleus, two annules behind the hemizonid. Lateral field composed of four incisures, the outer bands incompletely areolated (Fig. 5). Spicules and gubernaculum typical of the genus (Fig. 8), phasmids located subterminally.

Second-stage juveniles: Body relatively stocky (Fig. 1), rounded anteriorly, tapering posteriorly. Head region not offset (Fig. 2), with four annules, basal annule not striated longitudinally. Head in face view (Fig. 3) similar to male's but larger. Stylet heavy, knobs very large, inclined slightly forward (Fig. 2); stylet protractors massive. Valve of median bulb small; esophageal glands overlapping intestine sublaterally and ventrally. Excretory pore midway between median bulb and esophago-intestinal junction, just behind the hemizonid. Lateral canals present in the intestine. Lateral field with four incisures, similar to male's. Phasmid 6–8 annules behind anus and with a subcuticular, lens-like structure (Fig. 4). Tail elongate-conoid, tapering to a finely rounded apex (Fig. 4), last half of tail hyaline.

HOLOTYPE (female): Length 559 μm; width 374 μm; neck length 143 μm; stylet length 35 μm; stylet base 2.2 μm high × 5.6 μm wide; DGO to stylet base 4.8 μm; excretory pore to head end 157 μm; valve to head end as percentage of body length 16%; vulva-anus distance 127 μm; a = 1.5; b′ = 3.4.

ALLOTYPE (male): Length 739 μm; width 20.4 μm; stylet 25.2 μm; stylet base 2.1 μm high × 3.8 μm wide; DGO to stylet base 4.0 μm; excretory pore to head end 112 μm; valve to head end as percentage of body length 9.6%; a = 36.2; b = 6.1; b′ = 4.3; testis length as percentage of body length 44%; spicule length 23.9 μm.

DIAGNOSIS: In Wouts' key (9), *M. eurytyla* n. sp. keys to *M. floridensis* Chitwood, Hannon & Esser, 1956 but differs from this species in many respects. In *M. eurytyla,* the basal head annule of the male is longitudinally striate (smooth in *M. floridensis*), the males and juveniles have longer bodies and stylets, the juvenile stylet knobs are much larger and wider, and the juvenile tail is longer, than in *M. floridensis*. Females of *M. eurytyla* have a generally shorter distance between the vulva and anus, and the stylet knobs have lateral anterior surfaces rather than posteriorly sloping surfaces.

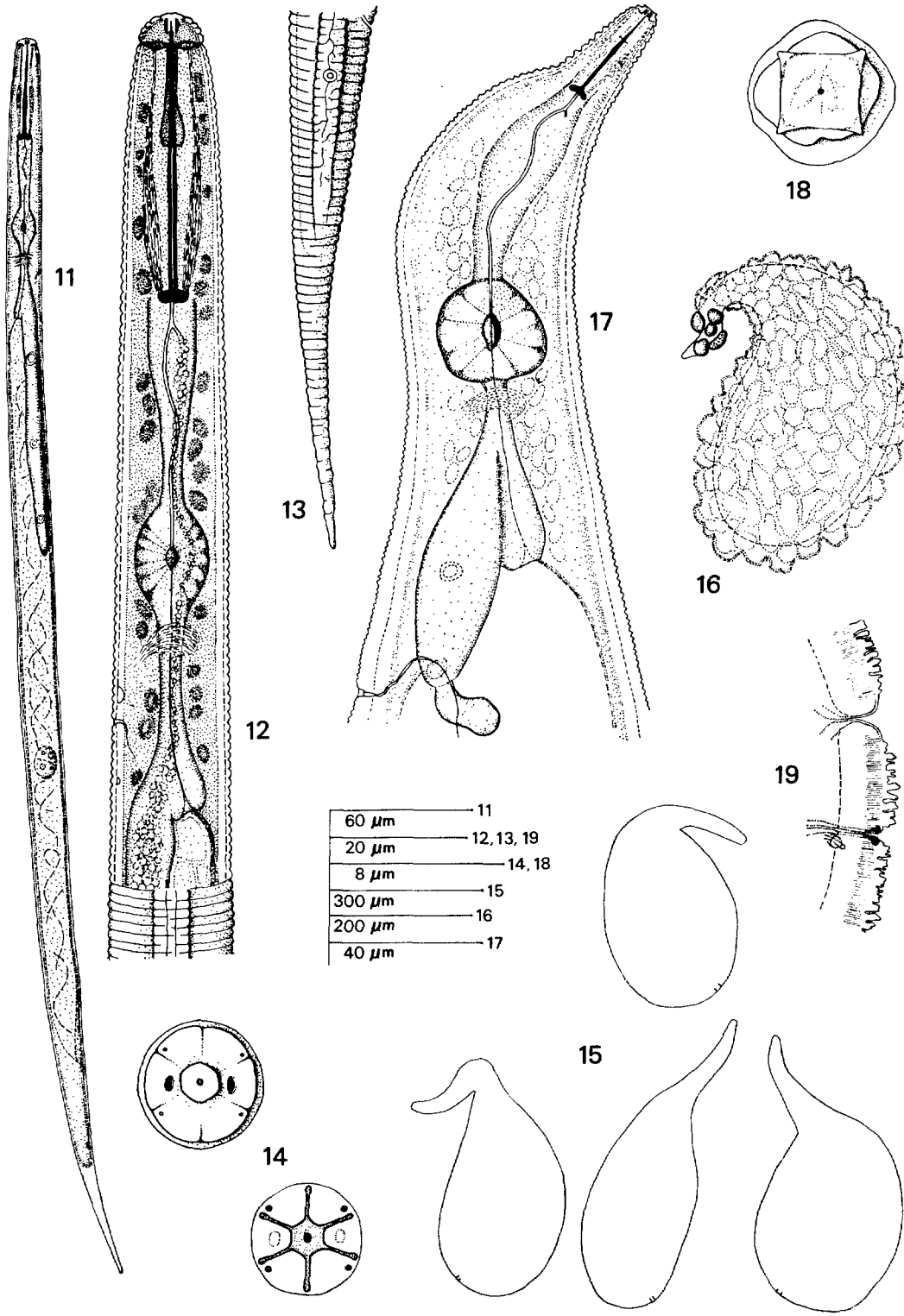
From *M. sikhotealiniensis* Eroshenko, 1978 (1), *M. eurytyla* differs in that females and juveniles are longer; the juvenile stylet is longer and much more massive, while the esophageal glands and tail are shorter; the female cephalic region is high and conoid-truncate with four annules, rather than low and flattened with a prominent second annule; and the juvenile cephalic region is not offset.

TYPES, TYPE HOSTS and LOCALITY: Holotype (T-327t), allotype (T-328t), and paratype females, males, and second-stage juveniles (T-2517p-T-2528p) collected at Kuluk Bay, Adak Island, Alaska, July-August 1978, from the roots and rhizospheres of *Elymus mollis* Trin. (Poaceae), and *Honckenya peploides* ssp. *major* (Hook.) Hult. (Caryophyllaceae); other specimens collected from the same locality and host plants 11 August 1979.

The specific name is derived from two Greek words: *eurys*—wide and *tylos*—knob.

Thecavermiculatus crassicrustata n. sp.
Figs. 11–19, 39–45; Table 2

Measurements and ratios for paratypes



Figs. 11–19. *Thecavermiculatus crassicrustata* n. sp. 11) Second-stage juvenile, entire. 12) Second-stage juvenile, anterior region. 13) Second-stage juvenile, tail. 14) Second-stage juvenile, face view and cephalic framework. 15) Females, body outlines. 16) Female, body with subcrystalline layer and neck secretions. 17) Female, anterior region. 18) Female, face view. 19) Female, vulval-anal region. (Scales in µm.)

Table 2. Measurements and ratios for *Thecavermiculatus crassicrustata*, n. sp.

	Paratype ♀♀ (n = 8)				Paratype ♂♂			Second-stage juveniles (n = 20)			
	Mean	Range	SD*	CV*	n	Mean	Range	Mean	Range	SD	CV
Length (μm)	592	459 -799	108	18.2	6	1,420	1,067 -1,739	538	501 -612	34.2	6.4
Width (μm)	232	140 -323	60.0	25.9	6	30.5	29.2- 33.0	16.4	15.0- 19.0	1.23	7.5
Stylet length (μm)	26.4	24.3- 27.7	1.21	4.6	6	30.4	28.7- 31.6	42.4	39.7- 44.8	1.54	3.6
Stylet base height (μm)	2.3	1.9- 2.8	0.28	12.2	6	2.2	2.0- 2.4	1.7	1.4- 2.1	0.21	12.1
Stylet base width (μm)	5.3	3.7- 6.4	0.89	16.7	6	5.0	4.1- 5.7	5.0	4.7- 5.9	0.25	4.9
Dorsal esophageal gland orifice to stylet base (μm)	4.4**	2.5- 6.1	1.27	29.0	4	4.9	2.9- 6.5	4.4	2.7- 6.5	1.09	24.8
Excretory pore to head end (μm)	153†	131 -200	28.1	18.4	4	148	136 - 156	110	100 -121	5.65	5.1
Excretory pore to head end as % of body length	25.9†	19.0- 37.0	5.93	22.9	4	10.0	8.5- 10.8	20.5	19.5- 21.8	0.60	2.9
Valve to head end as % of body length	15.6**	9.9- 22.0	4.44	28.5	5	6.6	5.5- 8.0	15.6	14.7- 16.1	0.40	2.6
a	2.7	1.9- 4.0	0.65	24.4	6	46.8	36.8- 52.7	32.8	28.8- 36.7	2.33	7.1
b	4.2**	3.1- 5.6	0.81	19.1	3	11.6	10.8- 12.7	4.3	4.0- 4.4	0.19	4.4
b′	3.7**	2.6- 4.6	0.66	17.9	5	6.3	6.0- 6.9	2.4	2.3- 2.7	0.12	4.9
c								6.7	6.0- 7.3	0.33	5.0
Tail length/body width at anus								6.8	5.6- 7.7	0.61	9.0
Neck length (μm)	215	175 -303	40.4	18.8							
Vulva–anus distance (μm)	18.0	12.0- 30.0	6.4	35.6							
Testis length as % of body length					5	53.7	50.3- 59.2				
Spicule length (μm)					3	33.2	33.0- 33.5				
Gubernaculum length (μm)					1	8.3	----------				
Genital primordium to tail end (μm)								222	209 -243	14.2	6.4
Phasmid to tail end (μm)								69.4	58.8- 81.0	6.04	8.7

*SD: Standard deviation; CV: Coefficient of variation.
**Seven specimens.
†Six specimens.

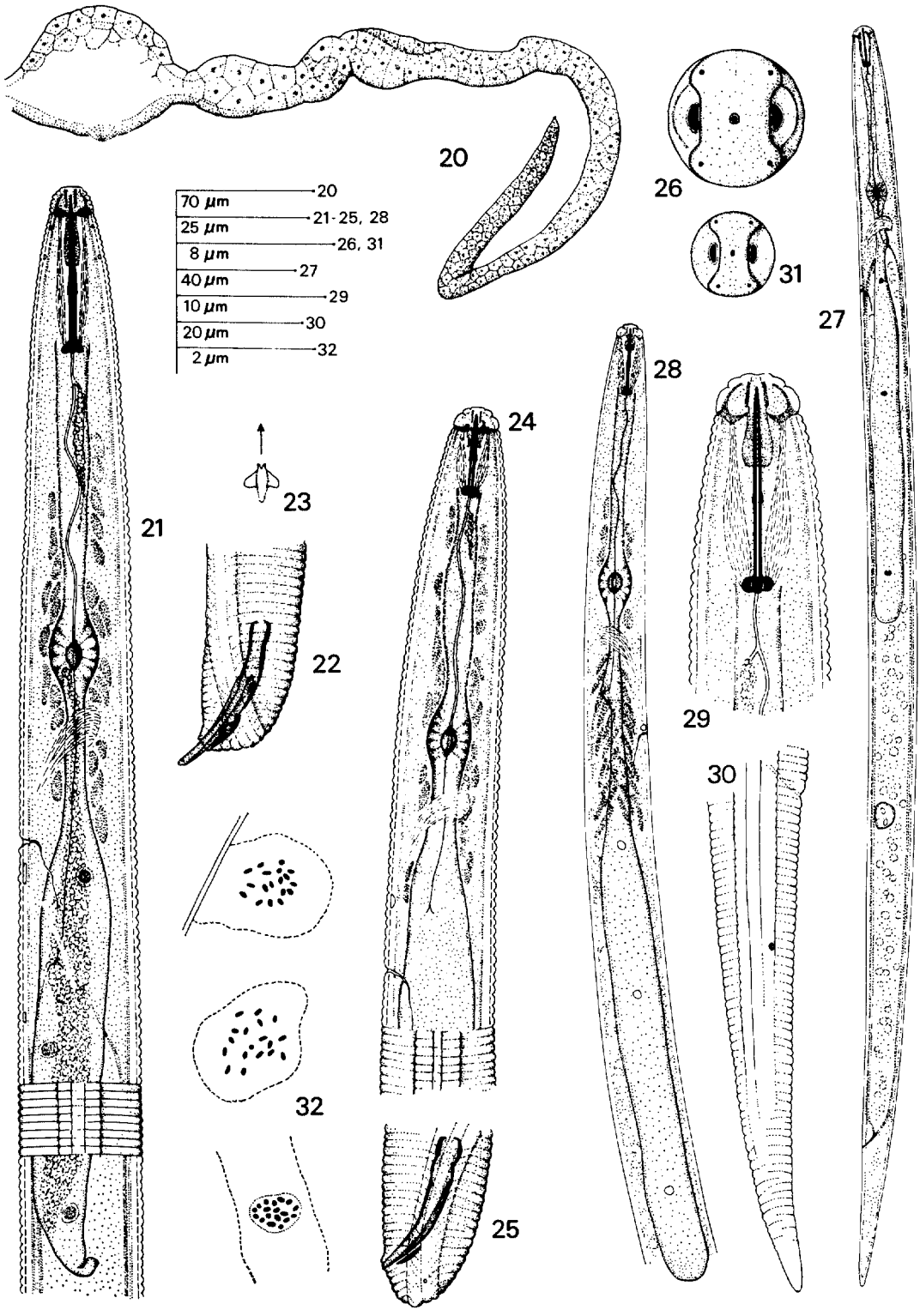
and second-stage juveniles are given in Table 2.

DESCRIPTION: Mature *females* white, broadly to narrowly ovate (Fig. 15), usually with long, ventrally-directed necks. Body covered with a variably thick, pearly-white subcrystalline layer (Figs. 16, 41) composed of many thickened plates (Fig. 42); anterior neck region held in place in the root by brittle, brown substance. Cuticle annulated in region of stylet (Fig. 17), but otherwise with a zig-zag pattern (Fig. 44). Perineal region with more circular pattern around vulva (Fig. 43). Head not offset, with one or two annules. In face view, lip region quadrate with corners slightly protuberant (Fig. 18). Amphidial apertures not seen. Stylet slender, knobs sloping posteriorly (Fig. 17). Orifice of dorsal esophageal gland about one-tenth the stylet length behind the knobs. Median bulb ovate, valve large; nerve ring encircling isthmus just behind the bulb. Esophageal glands long, with a narrow posterior end, overlapping intestine subventrally and ventrally. Excretory pore near level of posterior terminus of glands. Vulva and anus close (Figs. 15, 19), not on protuberance; phasmids embedded near anus but not seen in surface view. Female gonads (Fig. 20) poorly differentiated into constituent parts: ovary long; spermatheca poorly defined and empty; uterus short but distally expanded to receive eggs, and continuing to enlarge with increasing egg production; eggs hatching *in utero* and juveniles remaining within female body; young females with eggs or eggs and juveniles; older females containing juveniles only. Chromosomes not seen in the few recovered oocytes. In oogonia, about 17 chromosomes seen in maturation divisions (Fig. 45), but only three good figures observed.

Males long, body tapering anteriorly, slightly tapering posteriorly, usually curving into a U-shape when heat relaxed. Head region offset, with five annules (Fig. 21) not longitudinally striated. Face view not clearly seen, apparently similar to that of second-stage juvenile. Cephalic framework strong. Male stylet longer than female's; knobs rounded, sloping posteriorly. Distance from dorsal gland orifice to stylet knobs about one-sixth the stylet length. Valve of median bulb large; nerve ring encircling isthmus just behind median bulb. Esophageal glands overlapping intestine ventrally and subventrally, often with a recurved posterior tip (Fig. 21). Apparent glandular secretion leading primarily to subventral gland orifices. Cephalids approximately three and eight annules behind the head region; hemizonid flattened in optical cross-section, two annules wide, and about two annules behind the excretory pore (Fig. 21); hemizonion near the middle of the glands. Lateral field with four incisures, outer bands areolated, middle band incompletely aeolated (Fig. 21). Cloacal opening ventroterminal (Fig. 22), spicules similar in structure to those of other heteroderids. Phasmids not seen. Gubernaculum about one-fourth the length of the spicules, with two anterior, divergent projections, lateral wings, and an indistinct posterior projection (Fig. 23).

Second-stage juveniles (Fig. 11) slender, tapering slightly anteriorly, more posteriorly. Head region offset, with four smooth annules (Fig. 12). Labial plate hexagonal and lip region divided into six sectors (Fig. 14). Amphidial apertures oval, small. Cephalic framework moderately developed (Fig. 12), the radii thin, apically clavate, the subventral and subdorsal arms on each side closer to each other (Fig. 14). Stylet slender, much longer than that of female or male (Fig. 12; Table 2), knobs weakly sloping posteriorly, anterior surfaces nearly flat. Dorsal gland orifice about one-tenth the stylet length behind the knobs. Valve of median bulb small. Esophageal glands overlapping intestine ventrally and subventrally, extending almost to middle of body. Gland secretion leading primarily to dorsal orifice. Excretory pore near proximal end of isthmus, two annules behind hemizonid; hemizonion 5–8 annules behind excretory pore. Lateral field similar to that of male, with four incisures reduced to three in vicinity of anus. Tail elongate-conoid (Fig. 13), tapering to a finely rounded tip, annulated over its entire length. Phasmid a few annules behind the anus, with a subcuticular lens-like structure. Hyaline region of tail occupying the distal 50–70% of the tail.

HOLOTYPE (female): Length 608 μm; width 247 μm; neck length 268 μm; stylet



Figs. 20–32. *Thecavermiculatus crassicrustata* n. sp. 20) Female, gonad. 21) Male, anterior region. 22) Male, tail. 23) Gubernaculum, dorsal view. *Meloidogyne subarctica* n. sp. 24) Male, anterior region. 25) Male, tail. 26) Male, face view. 27) Second-stage juvenile, entire. 28) Second-stage juvenile, anterior region. 29) Second-stage juvenile, head region. 30) Second-stage juvenile, tail. 31) Second-stage juvenile, face view. 32) Oocytes, metaphase chromosomes. (Scales in µm.)

length 25.2 μm; stylet base 2.0 μm high × 4.2 μm wide; DGO to stylet base 5.5 μm; excretory pore to head end 145 μm; valve to head end as percentage of body length 16.1%; vulva-anus distance 13.6 μm; a = 2.5, b′ = 3.3.

ALLOTYPE (male): Length 1,590 μm; width 36 μm; stylet length 29.9 μm; stylet base 2.1 μm high × 5.2 μm wide; DGO to stylet base 5.0 μm; excretory pore to head end 178 μm; valve to head end as percentage of body length 6.6%; testis length as percentage of body length 51%; a = 44.2; b = 11.4; b′ = 6.1.

DIAGNOSIS: *T. crassicrustata* n. sp. differs from the only other known species, *T. gracililancea* Robbins, 1978 (4), in that the females of *T. crassicrustata* have long necks, the excretory pore is further from the head, and a posterior protuberance is absent. Juveniles of *T. crassicrustata* have longer, more slender tails and much longer stylets. Males of *T. gracililancea* are unknown. This new species is unusual in that the juvenile stylet is considerably longer than that of the female.

TYPES and LOCALITIES: Holotype (T-329t), allotype (T-330t), paratype females, males, and second-stage juveniles (T-252p-T-2538p) collected from roots and rhizosphere of *Elymus mollis* Trin. growing on beach terraces at Kuluk Bay, Adak Island, Alaska, July-August 1978; other juveniles also collected from rhizosphere of *E. mollis* on dunes at Andrew Bay, Adak, 11 August 1979, and on beach terrace on Amchitka Island, 8 August 1979.

The specific name is formed from the Latin words *crassus*—thick, and *crustatus*—crusted.

BIOLOGY: Females lie on the surface of the host roots with only the necks embedded in root tissue (Figs. 39, 40). No galls are formed, but the pearly-white subcrystalline layer makes females on the root surface rather conspicuous. Only the fine feeder roots are attacked; females have not been found on coarser roots or rhizomes. This species has been maintained on *E. mollis* for 2 yr at 15 C and continuous light in a growth chamber.

Meloidogyne subarctica n. sp.
Figs. 24–38, 46–57; Tables 3, 4

Measurements and ratios for paratypes and second-stage juveniles are given in Table 3; selected measurements of perineal patterns are given in Table 4.

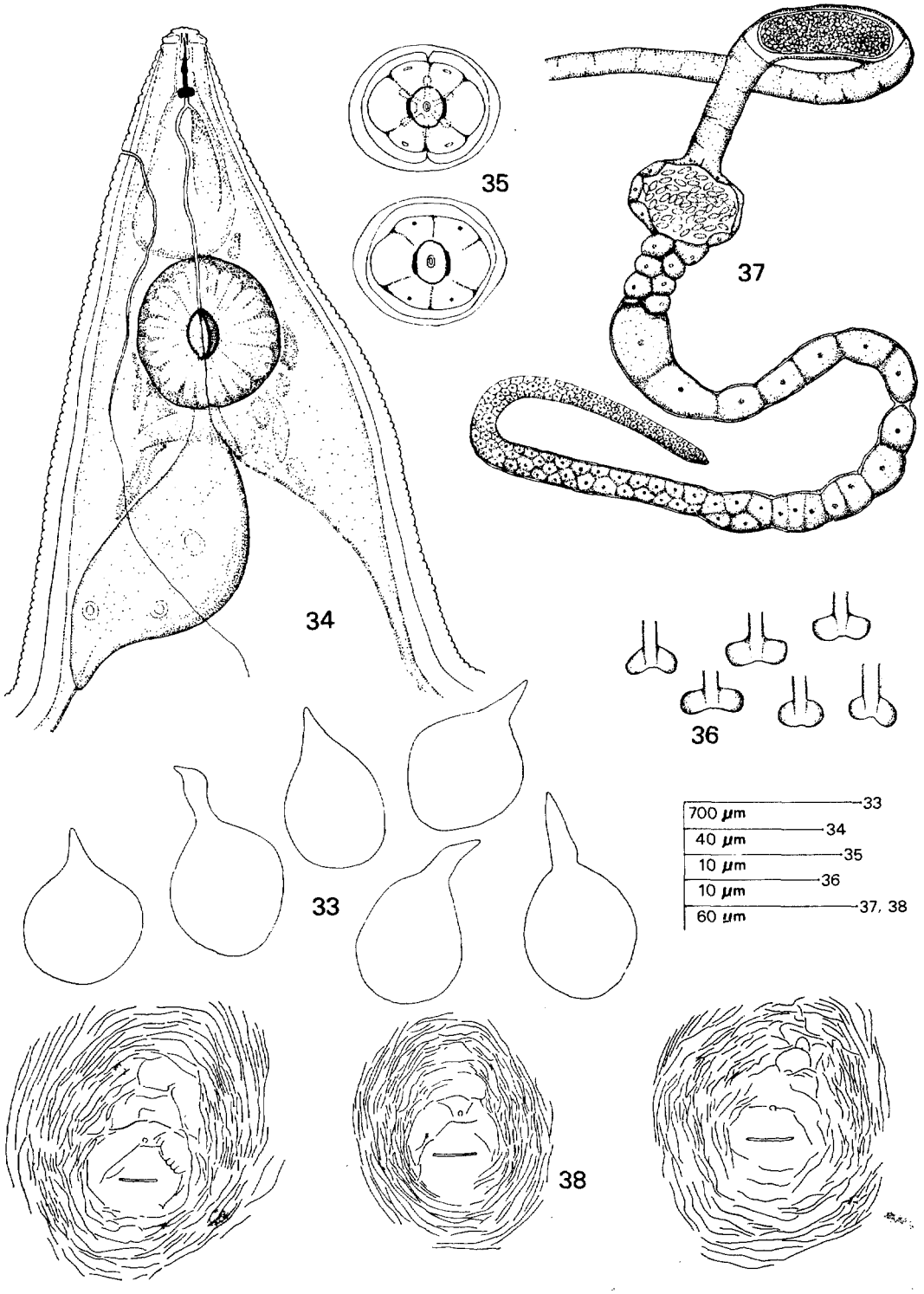
DESCRIPTION: *Females* milky-white, spheroid or ovoid (Fig. 33); necks short to long, not directed ventrally. Posterior protuberance absent. Face view (Fig. 35) showing small labial disc surrounded by six lips; lip region wider laterally. Lip region with one wide annule, somewhat angular in profile (Fig. 34). Stylet knobs variable in shape (Fig. 36), occasionally asymmetric. Dorsal gland orifice slightly behind the stylet knobs. Ampulla often very large. Excretory pore about 1.5–2.5 × the stylet distance from the anterior end. Median bulb ovate to round, the valve large. Esophageal glands distinct and overlapping intestine ventrally. Each gonad highly differentiated (Fig. 37), spermatheca enlarged and filled with sperm. Perineal pattern generally oval to rounded (Figs. 38, 49–57); arch with few unbroken striae, resulting in large, oval or angular regions devoid of striae; tail region without tail whorl. Lateral fields marked by short, broken striae, or devoid of striae. Vulval width and perivulval height (Table 4) less variable than other morphometric perineal characters. Chromosomes of oocytes very small and rather difficult to distinguish (Fig. 32), numbering 18 (chromosomes of six oocytes counted).

Males vermiform, nearly straight to strongly curved when heat relaxed. Face view (Fig. 26) showing fused labial disc and medial lips; laterally, amphidial apertures large, lip margins present; four cephalic sensilla present. Head region slightly offset, with one annule dorsally and ventrally, one or two laterally (Fig. 24). Stylet with rounded knobs. Dorsal gland orifice about one-fourth the stylet length behind the knobs. Median bulb reduced, valve large. Junction of esophagus and intestine not clearly seen, terminating in vicinity of hemizonid. Excretory pore 5–8 annules behind the hemizonid. Esophageal glands indistinct distally. Lateral field with four incisures and areolated; occasionally, short, shallow incisures sporadically present to give the effect of six incisures. Spicules and gubernaculum similar to those of other *Meloidogyne* spp., the cloacal opening oc-

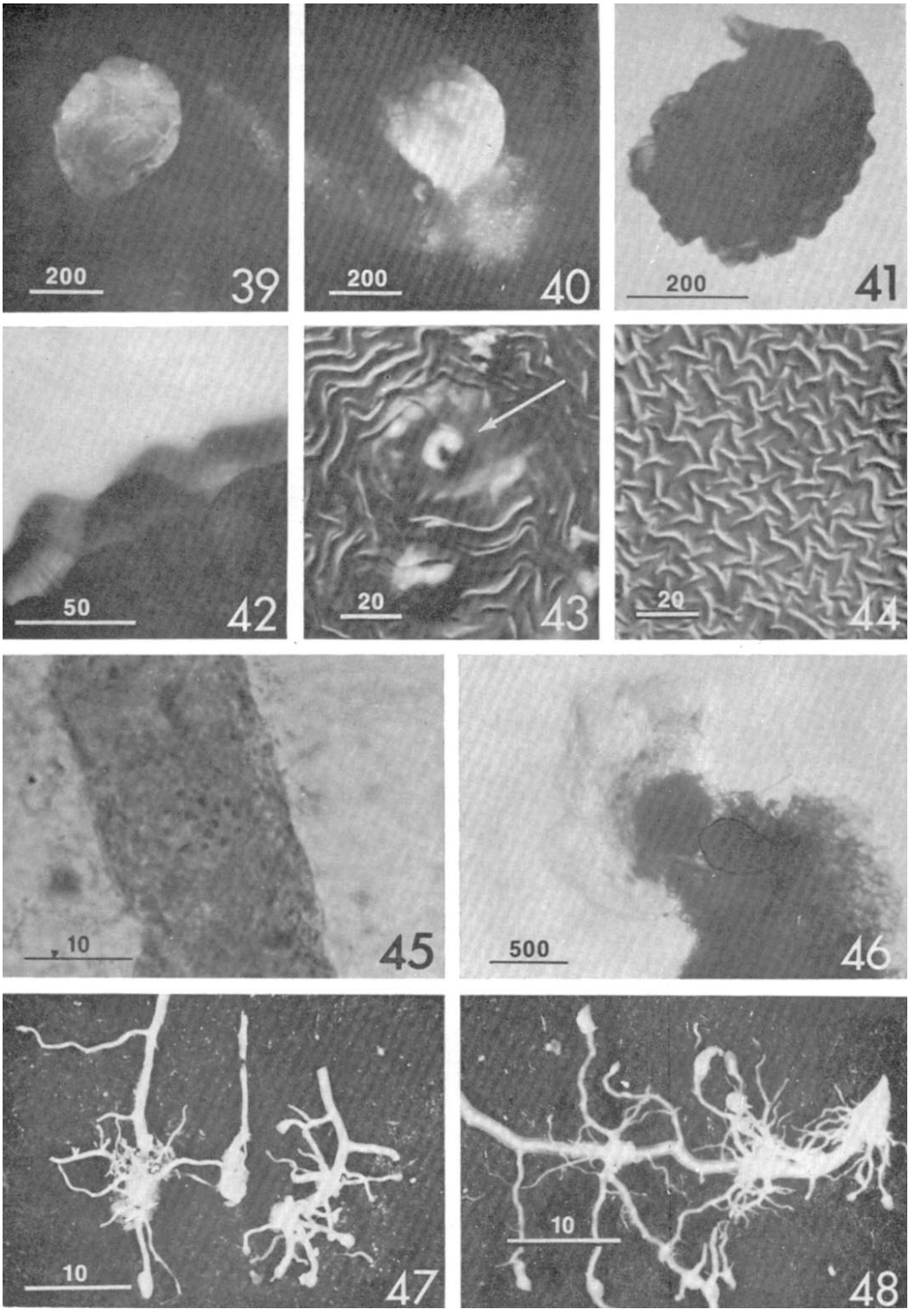
Table 3. Measurements and ratios for *Meloidogyne subarctica*, n. sp.

	Paratype ♀♀ (n = 12)				Paratype ♂♂			Second-stage juveniles (n = 20)			
	Mean	Range	SD*	CV*	n	Mean	Range	Mean	Range	SD	CV
Length (μm)	709	608 -836	82.5	11.6	6	1,648	1,403 -1,755	439	349 -507	30.1	6.9
Width (μm)	466	356 -622	69.8	15.0	6	31.4	27.2- 36.9	15.0	12.2- 17.0	1.42	9.5
Neck length (μm)	194	173 -231	23.4	12.1							
Stylet length (μm)	14.2	12.7- 15.7	0.73	5.1	6	18.9	17.2- 19.7	14.4	13.5- 15.4	0.44	3.1
Stylet base height (μm)	2.0	1.7- 2.3	0.20	9.9	6	2.5	2.0- 2.8	1.2	1.0- 1.4	0.16	13.2
Stylet base width (μm)	4.0	3.7- 4.4	1.20	5.0	6	3.4	3.1- 4.8	2.1	1.9- 2.5	0.17	7.9
Dorsal gland orifice to stylet base (μm)	5.2	3.7- 7.1	1.04	19.8	6	4.7	4.1- 5.8	3.9	2.9- 4.8	0.62	15.9
Excretory pore to head end (μm)	31.3	22.4- 38.5	3.97	12.7	5	138	125 - 141	79.8	64.1- 86.0	4.87	6.1
Excretory pore to head end as % of body length	4.4	2.9- 5.2	0.75	17.0	5	8.5	8.0- 10.0	18.3	16.6- 19.3	0.67	3.7
Annules from excretory pore to head	16.8	12 - 23	2.68	16.0							
Valve to head end as % of body length	9.8	7.4- 12.8	1.77	18.0	5	4.9	4.5- 5.6	12.6	11.6- 13.6	0.47	3.7
a	1.5	1.3- 1.8	0.14	9.2	6	53.0	45.3- 61.0	29.4	24.7- 34.8	2.5	8.5
b	------	----------	------	----	2	13.6	12.7- 14.5	6.6	6.5- 6.9	0.16	2.4
b′	4.9	4.2- 5.7	0.53	10.8	3	8.2	7.6- 9.0	2.1	2.0- 2.5	0.14	6.5
c								9.2	8.2- 11.0	0.64	6.9
Tail length/body width at anus								4.5	3.9- 5.2	0.42	9.3
Testis length as % of body length					6	48.5	31.7- 61.5				
Spicule length (μm)					2	34.9	32.9- 36.9				
Gubernaculum length (μm)					2	8.0	7.7- 8.4				
Genital primordium to tail end (μm)								163	137 -200	19.0	11.6
Phasmid to tail end (μm)								34.6	27.2- 38.8	2.43	7.0

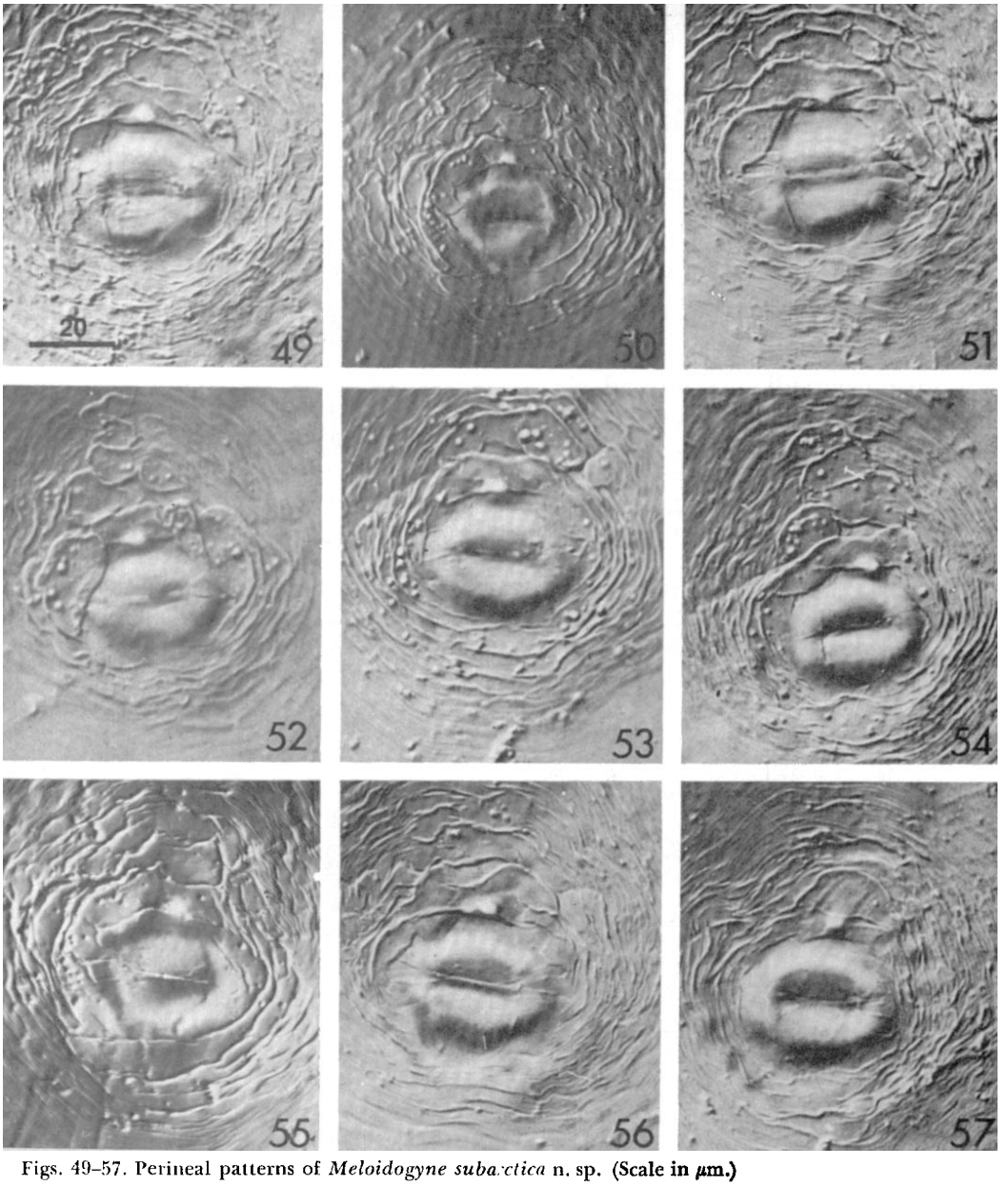
*SD: Standard deviation; CV: Coefficient of variation.



Figs. 33–38. *Meloidogyne subarctica* n. sp. 33) Females, body outlines. 34) Female, anterior region. 35) Females, face views. 36) Females, stylet knob variation. 37) Female, gonad. 38) Females, perineal patterns.



Figs. 39–48. *Thecavermiculatus crassicrustata* n. sp. 39, 40) Females on roots. 41) Female with intact subcrystalline layer. 42) Subcrystalline plates. 43) Posterior region (arrow: vulva). 44) Cuticular pattern. 45) Oogonial metaphase chromosomes. *Meloidogyne subarctica* n. sp. 46) Females and egg mass stained with acid fuchsin (female outline enhanced). 47, 48) Galling on roots of *Elymus mollis*. (Scales of Figs. 39–46 in μm; scales of Figs. 47–48 in mm.)



Figs. 49–57. Perineal patterns of *Meloidogyne subarctica* n. sp. (Scale in μm.)

Table 4. Measurements for twenty perineal patterns of *Meloidogyne subarctica*, n. sp.

	Mean	Range	SD*	CV*
Vulval width (μm)	20.9	18.0-25.3	1.86	8.9
Perivulval height (μm)	34.1	29.9-38.6	2.56	7.5
Perivulval width (μm)	40.8	29.9-46.0	4.39	10.8
Perivulval height/width	0.84	0.7- 1.1	0.12	13.8
Interphasmidial distance (μm)	22.1	11.4-28.8	4.85	21.9
Distance from anus to vulva (μm)	19.2	12.8-23.4	2.48	12.9

*SD: Standard deviation; CV: Coefficient of variation.

curring a little anterior to the phasmids. Tail broadly conoid-rounded (Fig. 25).

Second-stage juveniles nearly straight when heat relaxed (Fig. 27). In face view (Fig. 31), labial disc thinner than in male and fused with medial lips; margins of lateral lips not seen. Four cephalic sensilla present. Head region slightly offset, with one annule (Fig. 29). Stylet slender, with rounded knobs. Dorsal gland orifice about one-fourth the stylet length behind the knobs. Valve of median bulb in a central position (Fig. 28). Excretory pore placed just behind hemizonid. Esophageal gland lobe very long, extending to middle of body; gland nuclei evenly distributed. Rectum not inflated. Lateral field similar to that of male. Tail tapering evenly to a finely rounded tip. Phasmids offset, near ventral edge of lateral field (Fig. 30).

HOLOTYPE (female): Length 629 μm; width 393 μm; neck length 226 μm; stylet length 13.6 μm; stylet base 1.8 μm high $\times$ 3.5 μm wide; DGO to stylet base 3.8 μm; excretory pore to head end 27.2 μm; annules from excretory pore to head = 14; valve to head as percentage of body length 10.8%; a = 1.6; b = 6.8; b′ = 4.1.

ALLOTYPE (male): Length 1,870 μm; width 35 μm; stylet length 19.6 μm; stylet base 2.7 μm high $\times$ 4.2 μm wide; DGO to stylet base 4.9 μm; excretory pore to head end 150 μm; valve to head end as percentage of body length 4.5%; testis length as percentage of body length 49%; spicule length 35.5 μm; gubernaculum length 8.4 μm; a = 53.4; b = 14.4; b′ = 9.0.

DIAGNOSIS: The multiple oval or angular areas in the arch and tail region of the perineal pattern, devoid of striae, separate *M. subarctica* n. sp. from most other species of root-knot nematodes. The offset phasmids of *M. subarctica* juveniles may also differentiate this species from other *Meloidogyne* spp. The perineal region of *M. sewelli* Mulvey and Anderson, 1980 (3) resembles that of *M. subarctica,* but the peripheral striae are less distinct and the pattern is a more flattened oval in *M. sewelli.* In addition, the second-stage juvenile of *M. subarctica* is stockier, has a longer stylet, and has the dorsal gland orifice closer to the stylet knobs. Females of *M. subarctica* are much larger and have longer necks, while males are more slender and possess longer spicules. The perineal regions of *M. litoralis* Elmiligy, 1968 and *M. deconincki* Elmiligy, 1968 are somewhat similar to those of *M. subarctica,* but in *M. litoralis* and *M. deconincki* females the excretory pore is anterior to the stylet base. *Meloidogyne artiellia* Franklin, 1961 also has a clear region in the tail vicinity, but striae are even fewer and broken more frequently than in *M. subarctica.* From the three cool-climate species listed by Taylor and Sasser (6) as occurring on grasses (*M. microtyla* Mulvey, Townshend, and Potter, 1975, *M. naasi* Franklin, 1965, *M. ottersoni* [Thorne, 1969] Franklin, 1971), *M. subarctica* can be easily differentiated by perineal patterns. None of the species listed by Triantaphyllou (7) as having n = 18 chromosomes can be confused with *M. subarctica.* In Whitehead's keys (8), females key to couplet 13 but fit neither of the choices; juveniles key to *M. megadora* Whitehead, 1968, but in *M. subarctica* the stylet is longer and the tail is more regular in outline. The *Meloidogyne* sp. reported from American beachgrass (10,11), but not yet formally described, differs from *M. subarctica* in that it does not form terminal galls. The juveniles of *M. subarctica* are generally much shorter than the American beachgrass species.

TYPES and LOCALITY: Holotype (T-331t), allotype (T-332t), paratype females, males, and second-stage juveniles (T-2539p-T2551p), and paratype slides of perineal patterns (T-2552p-T2557p), collected at Kuluk Bay, Adak Island, Alaska, July 1978, from roots of *Elymus mollis* Trin.

BIOLOGY: *M. subarctica* form large terminal and intercalary galls on the roots of *E. mollis* (Figs. 47, 48). Intercalary galls usually contain only one female, but terminal galls each may have a dozen or more females and numerous swollen juveniles. Males are found most often in small, terminal galls. Egg masses produced by mature females are very large (Fig. 46). No females were observed to protrude from root tissue. Eggs maintained in water at room temperature hatched into normal juveniles, but cultures of *M. subarctica* on *E. mollis* died out in the greenhouse (24–26 C). However,

cultures were increased in a growth chamber at 15 C. No galling was observed on oat, fescue, or tomato, but these cultures were kept in the greenhouse and thus may have been grown at unsuitable temperatures.

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