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Terrestrial Nematodes of Alaska I. Trichodoridae (Nemata)

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Abstract: Four species of Trichodoridae, two of them new and belonging to the *T. aequalis* complex, are reported from Alaska. *Trichodorus carlingi* n. sp. differs from all other species of the genus in having conspicuously hamate spicules. Vaginal sclerotizations are trapezoidal to rectangular. *Trichodorus paucisetosus* n. sp., which resembles *T. sparsus* Szczygiel, 1968 and *T. nanjingensis* Liu & Cheng, 1990, has sparsely setose, noncephalated spicules partially striated in one or two zones, oval to round vaginal sclerotizations, sperm in discrete spermathecae, and onchiostyle 57–72 µm long. *Trichodorus californicus* Allen, 1957 is reported from many sites in Alaska, and *T. aequalis* Allen, 1957 is reported from one site. *Trichodorus californicus* was collected almost exclusively from glacial refugial regions north of the Alaska Range.

Key words: Biogeography, dispersal, distribution, nematode, stubby-root nematode, taiga, taxonomy, *Trichodorus aequalis, T. californicus, T. carlingi, T. paucisetosus,* tundra.

The recognition and documented importance of *Meloidogyne chitwoodi* Golden et al., 1980 on Pacific Northwest crops led to concern in Alaska that *M. chitwoodi* could occur in Alaskan potato and grain fields. In 1983 and 1984, through Dr. D. E. Carling, Alaska Agriculture and Forestry Experiment Station (AAFES), Palmer, I received numerous samples from potato, barley, and oat fields in southern and northwest Alaska for nematode analysis. In 1985, AAFES provided funds through a grant from the Alaska Department of Natural Resources, Division of Agriculture, for a large-scale sampling of south-central Alaska, resulting in 540 samples collected from diverse plant associations and localities. Other samples have been received since then, so that about 700 soil samples have been examined and sorted.

Although *M. chitwoodi* was not found in these extensive surveys, the samples have abundant material for documenting the highly diverse nematofauna of Alaska. A summary of this diversity for plant parasites has been published (8). The Alaskan nematode fauna has hitherto been little studied, but some species have been described or recorded from the Aleutian Islands (5–7) and the mainland (3,17). This paper, the first in a series, describes and differentiates the Trichodoridae collected in Alaska.

Materials and Methods

Nematodes were extracted from soil collected at numerous sites in Alaskan agricultural fields or near roads throughout south-central Alaska, in an area roughly bounded by the Gulf of Alaska, the Yukon River, George Parks Highway (Alaska Route 3), and the U.S.–Canada border. Soil samples were also collected along the Dalton Highway (formerly the North Slope Haul Road), at Prudhoe Bay, along the Kobuk River near Noorvik, at Unalakleet, and on the eastern side of Kodiak Island. Most sample sites are listed as mileposts (MP) on roads near which the sample was collected; some sites near which mileposts were not seen are given as road-travel kilometers from a town or city. Reference to spruce refers to *Abies* sp., no distinction being made between black and white spruce. Nematodes were extracted with a sugar flotation-centrifugation technique (13), fixed in hot (60 C) 4% formalin, then processed to pure glycerin according to Seinhorst's rapid method (20),

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and mounted in glycerin on permanent slides. Drawings and measurements were made from glycerin-mounted specimens with the aid of a drawing tube.

SYSTEMATICS

Trichodorus carlingi n. sp. (Figs. 1–7, 21)

Measurements of holotype male, paratype males, and paratype females in Tables 1 and 2.

Male: Posterior half moderately curved (Fig. 1); cuticle usually swollen after fixation, in three layers, the middle layer thinner than the others. Onchiostyle slightly arcuate. Anterior ventromedian cervical papilla posterior to onchiostyle base, level with or slightly behind nerve ring and lateral cervical pore (Fig. 2); position of posterior ventromedian cervical papilla highly variable but closer to the excretory pore than to the anterior papilla. In esophageal corpus, anterior ventrosublateral nuclei slightly posterior to excretory pore; posterior ventrosublateral nuclei near esophagus base, about level with the dorsal gland nucleus. Esophageal glands not overlapping intestine. Excretory pore closer to intesting than to onchiostyle base. Nerve ring less than one body-width behind onchiostyle; lateral cervical pore just behind nerve ring.

Sperms large, ovate, surface-striated, nuclei spindle-shaped or rounded (Fig. 21). Spicules not cephalated, tips strongly recurved ventrally (Figs. 6, 7); spines and striae absent; small ventrodistal velum often visible (Fig. 7); spicule tips strongly bifid. Three preanal supplements; posteriormost supplement anterior to proximal ends of spicules; anteriormost supplement reduced. Bursa not seen. Tail tip cuticle thickened, bluntly digitate (Fig. 6). One pair of subventral papillae posterior to cloaca, one pair of ventrosubterminal pores.

Female: Body slightly curved ventrally when heat-relaxed (Fig. 1). Cuticle three-layered as in male, but middle layer often as thick as the other two; four layers apparently present on posterior regions of some females, created by subdivision of the inner layer. Onchiostyle as in male; esophageal gland nuclei positioned as in male; esophagus not overlapping intestine. Excretory pore about midway between onchiostyle base and intestine (Fig. 3). Nerve ring position as in male. Reproductive system typical of other *Trichodorus* spp.; sperm present in oval spermathecae. Vulva porelike. Vaginal region wider than high in lateral view; vaginal sclerotizations

TABLE 1. Morphometrics of male holotype and seven male paratypes of *Trichodorus carlingi*.

Measure	Holotype	Paratypes			
		Mean	Range	SD	CV
		Measurements in µm			
Length	813	828	682–955	84.6	10.2
Width	29	35	29–39	3.6	10.3
Onchiostyle length	61	62	57–67	3.7	6.0
Esophagus length	171	167	141–180	14.3	8.6
Head to excretory pore	120	116	106–127	8.4	7.2
Head to CP1	83	87	83–98	6.0	6.9
CP1 to CP2	26	18	11–26	5.4	30.0
CP2 to excretory pore	13	10	7–13	2.8	28.0
Spicule length	44	46	44–47	0.9	2.0
Gubernaculum length	17	16	15–18	1.4	8.8
Cloaca to SP1	39	39	34–46	3.6	9.2
SP1 to SP2	44	42	34–48	5.5	13.1
SP2 to SP3	45	44	37–53	5.7	13.0
		Ratios and percentages			
a	28	24	20–28	3.3	13.8
b	4.8	5.0	4.8–5.4	0.3	6.0
T	60	59	55–63	2.5	4.2

TABLE 2. Morphometrics of eight female paratypes of *Trichodorus carlingi*.

	Mean	Range	SD	CV
	Measurements in µm			
Length	801	711–886	53.4	6.7
Width	37	34–39	2.6	7.0
Onchiostyle length	59	56–65	3.2	5.4
Esophagus length	158	146–171	11.3	7.2
Head to excretory pore	109	103–118	5.4	5.0
	Ratios and percentages			
a	22	20–24	1.3	5.9
b	5.1	4.5–5.5	0.4	7.8
V	54	50–57	2.2	4.1
G_1	17	15–20	1.8	10.6
G_2	18	15–21	2.6	14.4

in optical cross-section trapezoidal or rectangular (Fig. 4). Two pairs of midbody lateral pores, one pair three to four body widths anterior to the vulva, one pair less than one body width behind vulva. Tail broadly rounded, anus ventrosubterminal (Fig. 5). One pair of subterminal pores.

Diagnosis

Trichodorus carlingi n. sp., a member of the *T. aequalis* complex (16), is distinguished from all other *Trichodorus* spp. by its possession of hamate spicules and oval, striated sperms with pediform nuclei.

Relationships

Trichodorus carlingi n. sp. is morphologically quite similar to *T. aequalis* Allen, 1957, but in *T. aequalis* the spicule tips are straight, not hamate, as in *T. carlingi;* sperms are elliptical with elongated nuclei in *T. aequalis* (Fig. 23) but are ovate with striated surfaces and pediform nuclei in *T. carlingi.* The sperms of *T. carlingi* are very similar to those of several species illustrated by Decraemer (10), but spicule shapes and ornamentation are distinctly different. Females of *T. carlingi* are very similar to those of *T. aequalis* and *T. sparsus* Szczygiel, 1968 and cannot be reliably separated from them.

Type host and locality

Holotype male and paratype female collected in rhizosphere of black spruce (*Picea mariana* (Mill.) Britt., Sterns & Pogg) with moss groundcover, near MP 1370, Alaska Highway near Tanana River, 5 August 1985; three male and three female paratypes in mixed black spruce-willow (*Salix* sp.)-aspen (*Populus tremuloides* L.) rhizosphere with Labrador tea (*Ledum decumbens* (Ait.) Lodd. ex Steud.) groundcover, MP 1372, Alaska Highway at Sears Creek, 5 August 1985; one paratype male in mixed paper birch (*Betula papyrifera* Marsh.)-black spruce rhizosphere, 116 km southeast of Fairbanks, Alaska Highway, 27 July 1985; two males and four female paratypes, mixed grass rhizosphere, Unalakleet River, 32 km from Norton Sound, August 1984.

Type specimens

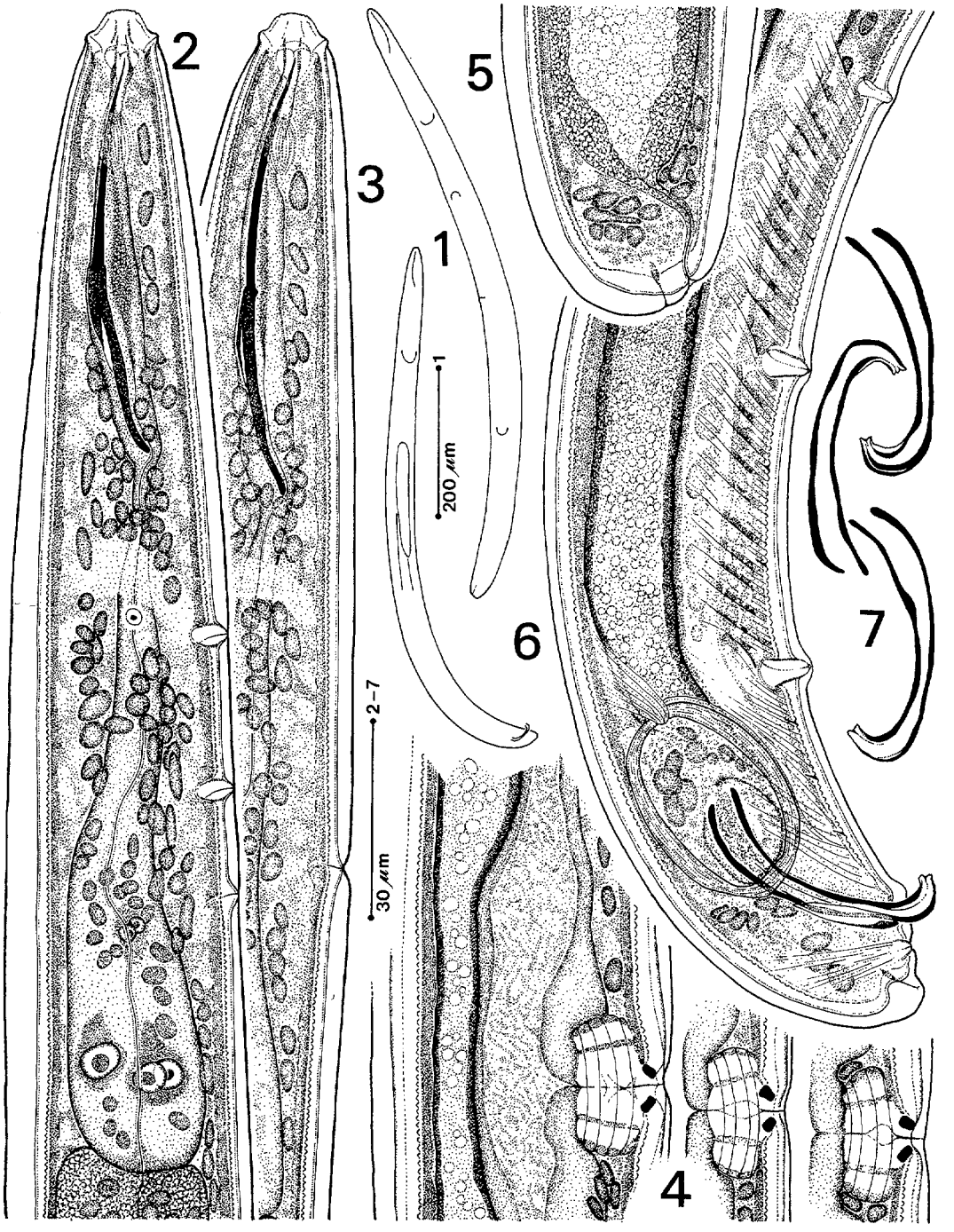
Holotype male, two paratype males, and one paratype female deposited in the USDA Nematode Collection, Beltsville, Maryland; four paratype males and seven paratype females deposited in the Tennessee Nematode Collection, University of Tennessee, Knoxville.

Etymology

This species is named with pleasure for Dr. D. E. Carling, whose arrangements, assistance, and interest were indispensable in the collection of Alaskan nematodes.

Trichodorus paucisetosus n. sp.
(Figs. 8–15, 22)

Measurements of holotype male, paratype males, and paratype females are presented in Tables 3 and 4.



FIGS. 1–7. *Trichodorus carlingi.* 1) Habitus of heat-relaxed male and female. 2) Male, anterior region. 3) Female, anterior region. 4) Female, vulval regions. 5) Female, posterior region. 6) Male, posterior region. 7) Spicules.

Male: Posterior half strongly curved (Fig. 8), cuticle slightly swollen after fixation. Onchiostyle arcuate. Two ventromedian cervical papillae; anterior papilla near level of nerve ring well behind onchiostyle base; posterior papilla closer to excretory pore than to anterior papilla; lateral cervical pore pair usually between the ventro-

TABLE 3. Morphometrics of male holotype and nine male paratypes of *Trichodorus paucisetosus*.

	Holotype	Paratypes			
		Mean	Range	SD	CV
		Measurements in μm			
Length	696	771	638–911	76.5	9.9
Width	39	37	34–44	3.4	9.2
Onchiostyle length	71	67	57–71	4.7	7.0
Esophagus length	166	165	146–175	8.7	5.3
Head to excretory pore	110	117	100–124	7.5	6.4
Head to CP1	92	93	79–99	6.0	6.5
CP1 to CP2	19	18	14–26	3.6	20.0
CP2 to excretory pore	6	8	5–11	2.6	32.5
Spicule length	46	46	41–50	3.1	6.7
Gubernaculum length	18	19	17–22	1.8	9.5
Cloaca to SP1	33	37	33–41	2.8	7.6
SP1 to SP2	35	40	27–51	7.7	19.3
SP2 to SP3	46	50	39–66	8.0	16.0
		Measurements and ratios			
a	18	21	17–27	2.9	13.8
b	4.2	4.7	4.2–5.7	0.4	8.5
T	59	60	56–64	2.4	4.0

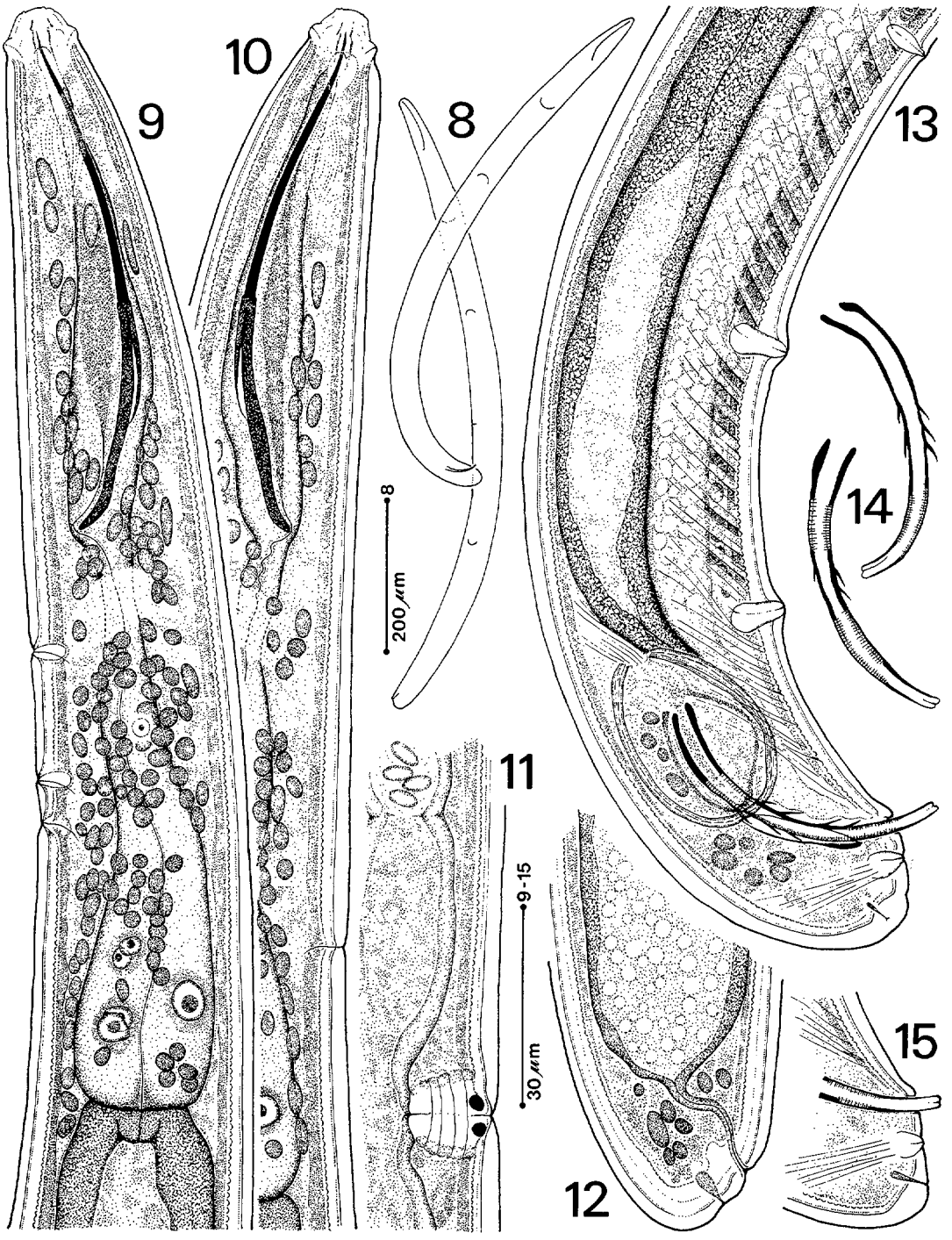
median papillae (Fig. 9). Excretory pore about midway between onchiostyle base and esophageal base. Esophageal gland nuclei usually closely associated in posterior half of corpus; glands not overlapping intestine. Nerve ring less than one body width behind the onchiostyle base.

Sperms globular, surfaces smooth; nuclei pediform (Fig. 22). Spicules slender, smoothly curved, not cephalated, tips bifid (Figs. 13, 14); each spicule with a few strong spines on middle third, and finely striated, striae grouped proximally and distally to spined region, but sometimes striated only on the distal third (Fig. 14). Three preanal supplements, posteriormost near the proximal ends of the fully retracted spicules, anteriormost supplement reduced. Tail tip cuticle slightly thickened, rounded to bluntly protuberant (Figs. 13, 15). One pair of subventral papillae posterior to cloaca, one pair of terminal to ventrosubterminal pores.

Female: Body slightly curved ventrally when heat-relaxed (Fig. 8). Onchiostyle as in male; esophageal gland nuclei positioned as in male; esophagus not overlapping intestine. Excretory pore closer to in-

TABLE 4. Morphometrics of eight female paratypes of *Trichodorus paucisetosus*.

	Mean	Range	SD	CV
	Measurements in μm			
Length	805	706–882	64.6	8.0
Width	40	34–44	3.1	7.8
Onchiostyle length	67	58–72	5.1	7.6
Esophagus length	168	156–185	9.2	5.5
Head to excretory pore	126	119–131	5.6	4.4
	Ratios and percentages			
a	20	16–23	2.3	11.5
b	4.8	4.4–5.8	0.3	6.3
V	54	52–58	2.3	4.3
G_1	18	12–23	3.5	19.4
G_2	20	15–25	3.4	17.0



FIGS. 8–15. *Trichodorus paucisetosus* n. sp. 8) Habitus of heat-relaxed male and female. 9) Male, anterior region. 10) Female, anterior region. 11) Female, vulval region. 12) Female, posterior region. 13) Male, posterior region. 14) Spicules. 15) Male tail variation.

testine than to onchiostyle base (Fig. 10). Nerve ring position as in male. Reproductive system typical for the genus; sperm present, spermathecae oval. Vulva pore-like. Vaginal region trapezoidal, depth and width about equal; vaginal sclerotizations in optical cross section spherical to broadly oval (Fig. 11). Two pairs of midbody later-

al pores, one pair about four body widths anterior to vulva, the other pair one body width or less posterior to vulva. Tail rounded, anus ventral to ventrosubterminal (Fig. 12); one pair of subterminal pores.

Diagnosis

Trichodorus paucisetosus n. sp., a member of the *T. aequalis* complex (16), is distinguished from other *Trichodorus* spp. by the following characteristics in males: body length 638–911 μm, onchiostyle length 57–71 μm, two ventral cervical papillae anterior to the excretory pore, three preanal supplements with the posteriormost supplement near the spicule base, not cephalated but with numerous striae and few strong medial spines, and sperms spherical with pediform nuclei; in females body length 706–882 μm, onchiostyle length 58–72 μm, vaginal sclerotizations spherical or broadly oval, two pairs of midbody lateral pores.

Relationships

Trichodorus paucisetosus n. sp., is morphologically similar to *T. sparsus* Szczygiel, 1968 (24) and *T. nanjingensis* Liu and Cheng, 1990 (15). Males of all three species possess striated, spined spicules, two ventral cervical papillae anterior to the excretory pore, and three preanal supplements with the most posterior supplement near the spicule base. From *T. sparsus, T. paucisetosus* can be separated by its possession of a few prominent spines restricted to the middle part of the spicules (spines numerous, finer, and distributed over most of the spicule length in *T. sparsus*); noncephalated spicules (cephalated in *T. sparsus*); and oval or round vaginal sclerotizations (angular in *T. sparsus*). *Trichodorus paucisetosus* differs from *T. nanjingensis* as follows: onchiostyle longer, in males 57–71 μm, in females 58–72 μm (in *T. nanjingensis,* onchiostyle length 43–48 μm in males, 42–46 μm in females); vaginal sclerotizations oval or round (angular in *T. nanjingensis*); sperm contained in spermathecae (sperm in uteri, spermatheca absent in *T. nanjingensis*).

Type host and locality

Holotype male, one paratype male, and three paratype females collected in white spruce (*Picea glauca* (Moench) Voss) forest with rose (*Rosa acicularis* Lindl.) groundcover, near a pond at MP 48, Steese Highway, northeast of Fairbanks, 25 July 1985; Paratypes from the following locations; one male, spruce-Labrador tea rhizosphere, 0.5 km south of MP 41, Elliott Highway north of Fairbanks, at base of White Mountains Trail, 25 July 1985; one male and a female, spruce rhizosphere, Steese Highway, MP 60, at Cripple Creek campground, 26 July 1985; three males and four females in a mixed aspen-spruce stand with rose groundcover, Steese Highway at the Chatanika River crossing, MP 39, 26 July 1985; one male, spruce-birch woods with *Equisetum* sp. groundcover, Alaska Highway at the Salcha River crossing 64 km south of Fairbanks, 26 July 1985.

Type specimens

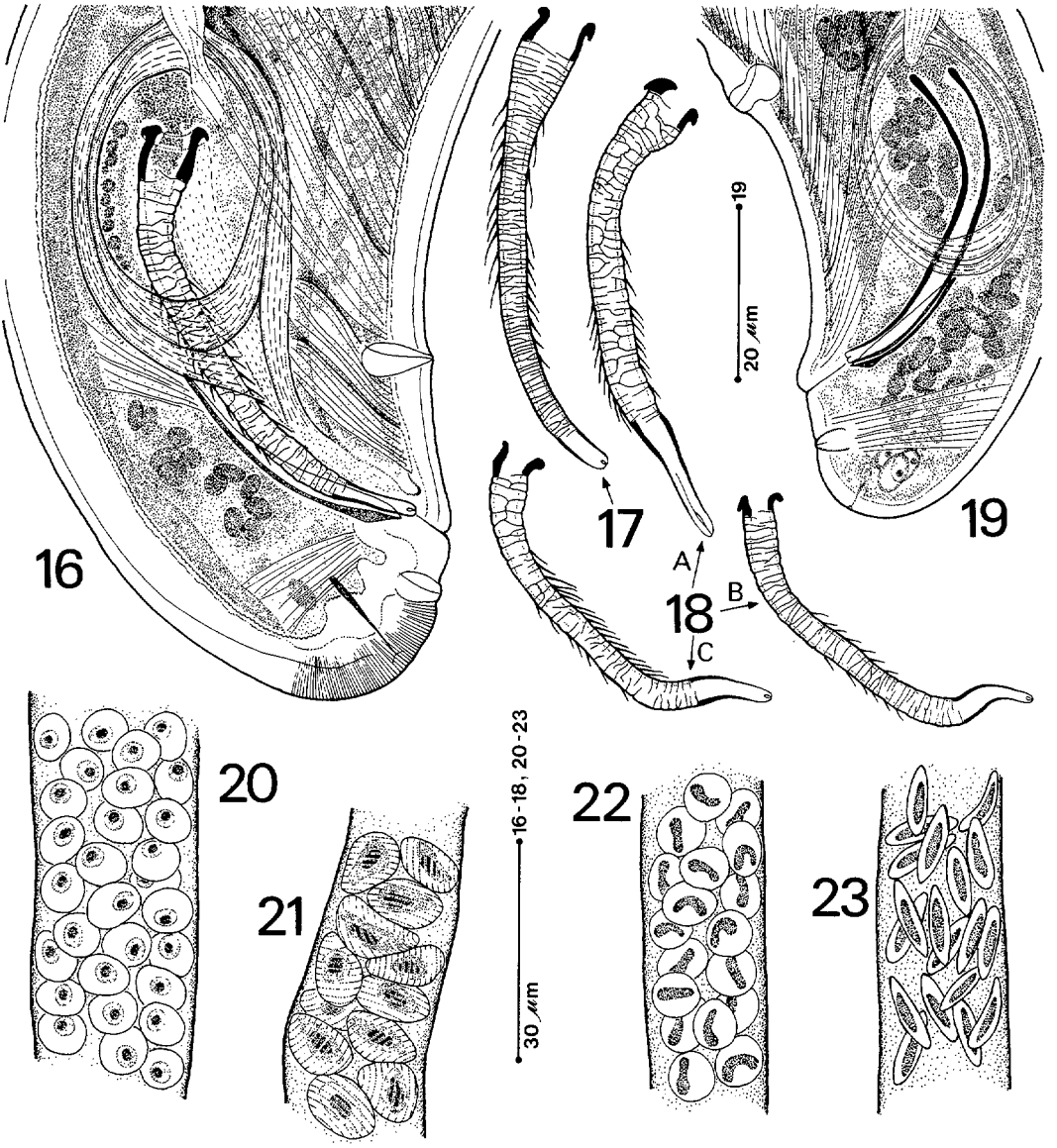
Holotype male, two paratype males, and four paratype females deposited in the USDA Nematode Collection, Beltsville, Maryland; six paratype males and three paratype females deposited in the Tennessee Nematode Collection, University of Tennessee, Knoxville.

Etymology

This species epithet refers to the few spines found on the spicules.

Trichodorus californicus Allen, 1957
(Figs. 16–18, 20)

Specimens identified as this species were collected from many sites in Alaska. Morphometric data, vulval sclerotization shape, location and number of cervical, vulval, and preanal papillae were all identical to previous descriptions (2,9,10) and to paratype specimens lent by E. Mae Noffsinger. Spicule morphology was similar but not identical to the male *T. californicus* paratype examined. In both the paratype (Fig. 17) and Alaskan specimens (Figs, 16, 18), spicules are usually densely spi-



FIGS. 16–18. *Trichodorus californicus.* 16) Posterior end of male from Dalton Highway, MP 113. 17) Spicule of paratype male. 18A) Spicule of male from Unalakleet River. 18B) Spicule of male from Copper Center. 18C) Spicule of male from Alaska Highway, MP 1364. 19) *Trichodorus aequalis,* posterior end of male. 20–23) Sperm cells of Alaskan *Trichodorus* spp. 20) *T. californicus.* 21) *T. carlingi.* 22) *T. paucisetosus.* 23) *T. aequalis.*

nose and prominently striated. However, in Alaskan specimens, the spicules are often bent ventrally in their posterior third, then recurved dorsally, and the distal region of the spicule tapers noticeably to the tip. Spicular striae also appear to be less dense in Alaskan *T. californicus,* and are absent in the tapered distal region. However, the spicules of other specimens of *T. californicus* from California, lent by R. T. Robbins, have a greater degree of tapering than the paratype and approximate in other details the spicule illustrated in Figure 16. Sperm shape (Fig. 20) of Alaskan specimens is quite similar to that illustrated for *T. californicus* by Decraemer (10). Thus it appears that these Alaskan specimens represent a distinctive population of the

more southern typical *T. californicus*. Alaskan *T. californicus* also resemble *T. dilatatus* Rodriguez-M. and Bell, 1978 in the tapering distal portion of the spicules, which in the five *T. dilatatus* paratype males examined possess greatly expanded proximal ends as illustrated by Decraemer (9). In Alaskan *T. californicus*, the spicules exhibited little or no proximal expansion.

Collection Data

Potato field, Copper Center, 16 August 1983; grasses, near Unalakleet River 32 km from Norton Sound, August 1984; grasses, Dalton Highway, MP 113, August 1984; tundra, Prudhoe Bay at ARCO spill site, 22 July 1985. Along George Parks Highway (Alaska Route 3), 23 July 1985: MP 269, spruce; MP 314-315, willow; MP 330, poplar (*Populus balsamifera* L.). Along Elliott Highway (AK 2): MP 82, spruce near unnamed stream feeding into Brooks Creek, 24 July 1985; MP 73, willow and spruce near crossing at West Fork, 24 July 1985; near bridge across Tolovana River, spruce stand with no groundcover, 25 July 1985; MP 71 at Livengood Turnoff, spruce and alder (*Alnus* sp.), 25 July 1985; MP 45, birch, 25 July 1985; crossing at Tatalina River, riverbank with alder, willow, and *Equisetum* sp., 25 July 1985. Along Dalton Highway, 25 July 1985: between MP 60 and MP 61, birch and willow; MP 7, spruce. Along Steese Highway (AK 6), 26 July 1985: MP 60, Cripple Creek campground, rose and willow; MP 57, southeast area of tundra-like region with bunchberry (*Cornus canadensis* L.) and birch near dirt road leading from U.S. Creek turnoff; MP 39 at Chatanika River, spruce. Along Alaska Highway (AK 2) north of Delta Junction, 26 July 1985: 67 km south of Fairbanks at Sewell Lane turnoff, poplar, aspen, birch; 128 km south of Fairbanks on Tanana River bank, willow, alder, aspen. Along Richardson Highway (AK 4), 26 July 1985: MP 253, birch and mixed herbaceous groundcover; MP 251, tundra-like rocky meadow; MP 238, Donnelly Wayside, willow in boggy area; MP 105, aspen with lingonberry (*Vaccinium vitis-idaea* L.) groundcover, 7 August 1985. Along Alaska Highway (AK 2) south of Delta Junction 5 August 1985: MP 1374 at Sears Creek, spruce, willow, grassy groundcover; MP 1369, birch and spruce; MP 1364, willow and poplar; MP 1360, paper birch; MP 1357 and 1344, paper birch and spruce; MP 1335, spruce with moss and lichen groundcover; MP 1334, aspen with lingonberry groundcover; MP 1325 and 1319, spruce and paper birch. Along Alaska Highway south of Delta Junction, 6 August 1990: MP 1249, spruce in bog; MP 1255, willow; MP 1257 at Lakeview State Recreation Site, spruce and willow at lake margin; MP 1269, poplar and spruce near bank of Tanana River; MP 1274, spruce and poplar. Along Taylor Highway (AK 5), 6 August 1985: MP 39, spruce over permafrost; MP 35, alpine tundra with glandular birch (*Betula glandulosa* Michx.) and mixed alpine plants; MP 34, tundra-like with stunted spruce and *Vaccinium* sp.; MP 9, mixed meadow of grasses, *Rubus* sp., *Ribes* sp., and fireweed (*Epilobium angustifolium* L.); MP 6, willow and poplar. Along Tok Cut-Off section of Glenn Highway (AK 1), 6 August 1985: MP 89, alder without groundcover; MP 98, on bank of Tok River, willow; MP 117, MP 103, and MP 67 at Carlson Creek, spruce with mixed ericaceous groundcover; MP 52, willow; MP 24, spruce, alder, *Equisetum* sp., and fireweed.

Trichodorus aequalis Allen, 1957
(Figs. 19, 23)

One male was identified from a sample collected along Elliott Highway (AK 2) at the Tolavana River crossing in a white spruce stand lacking groundcover. Dimensions are: Length 891 μm, onchiostyle length 79 μm, esophageal length 171 μm, distance from anterior end to excretory pore 133 μm, anterior end to CP1 91 μm, CP1 to CP2 25 μm, CP2 to excretory pore 17 μm, spicule length 47 μm, gubernaculum length 19 μm, cloaca to SP1 38 μm, SP1 to SP2 43 μm, SP2 to SP3 43 μm, a = 20, b = 5.2, T = 57%. Spicule and tail shape (Fig. 19) agreed closely with those

illustrated by previous authors (2,10). Sperms (Fig. 23) were elliptical with elongated nuclei, resembling those of *T. coomansi* De Waele and Carbonell, 1982 (10).

Discussion

Localities listed in the species descriptions are those in which adult males were found. Trichodorid juveniles and females were found at more than forty additional sites, but except for *T. californicus* could not be identified to species.

The distribution of *T. californicus* is of particular interest. This species was collected almost always from boreal forest (taiga) between the Alaska Range and the Yukon River. No *T. californicus* were found in samples from the Denali Highway region, Matanuska River Valley, Kenai Peninsula, Kodiak Island, Palmer-Anchorage area, Copper River valley southwest of Bartell Creek, the Valdez area, George Parks Highway region south of Bear Creek (MP 269), or Richardson Highway area south of Donnelly. These regions where *T. californicus* was not found were all totally glaciated (Wisconsin Interval) 15–18,000 years ago (1,11); thus *T. californicus* distribution in Alaska and nonglaciation are highly correlated. *Trichodorus californicus* was found at only two sites within the former ice sheet expanse: a sample from a potato field near Copper Center, and an aspen–lingonberry site about 5 km north of Copper Center. This apparently isolated population could have been the result of human activity or of flood deposition by the Copper River, whose tributary system just reaches the Mentasta Lake–Bartell Creek area. North and west of the Yukon River, *T. californicus* was found rarely, although the total number of samples collected was far smaller. *Trichodorus californicus* occurred at Prudhoe Bay in arctic tundra, under grasses along the Unalakleet River in western Alaska, and at two sites (taiga) on Dalton Highway just north of the Yukon River. None of these sites is believed to have been glaciated. Ten samples collected along Dalton Highway in the Brooks Range and on the north slope did not contain *T. californicus*. In other regions of North America, *T. californicus* has been recorded from California, primarily in forest and mixed tree-range biotopes in the Pacific Coast Range (2,21), Colorado (conifers) (2), South Dakota (*Poa pratensis* L.) (22), Wisconsin (*Vaccinium macrocarpon* Ait, *Zea mays* L., *Acer* spp., *Pinus* spp.) (4,12,14,18) and Florida (host unspecified) (23).

The historical biogeography of *T. californicus* can be determined from the current distribution pattern, past glacial events, and morphology. *Trichodorus californicus* is a polyphagous nematode, but it is most abundant and common in taiga and other coniferous rhizospheres, because most of the records from Alaska and many from California are from Pinaceae. The central Alaskan population probably has been isolated from the type population (Contra Costa Co., California) for many thousands of years, because morphology of the distal end of the spicule is different. During Pleistocene glaciations, *T. californicus* distribution in Alaska was severely restricted to a narrow band between the Alaska Range icecap and the Yukon River Valley. Despite the exposure of ice-free Beringia, it seems unlikely that *T. californicus* reached Siberia, because the Beringian landscape was tundra, not taiga (1). Since deglaciation, *T. californicus* in Alaska has apparently spread little; suitable taiga habitat north of the Yukon River and in the Alaska Range has not been colonized to any significant degree. This nematode appears to be a very poor disperser, and it is probably incapable of wind dispersal as anhydrobiotic individuals.

This scenario does not fully explain the reported occurrences of *T. californicus* in more easterly states. The Colorado report, on conifers, is easily reconciled. The report from South Dakota, in Kentucky bluegrass rhizosphere, is intriguing because at the maximum extent of the North American Wisconsin Interval ice sheets, only the northeastern half of South Dakota

was covered, and much of the southwestern part may have been taiga (11). The four reports from Wisconsin, which was totally glaciated, do not fit the historical scenario proposed unless significant movement by human activity is postulated; this solution is not very plausible. The Florida report is anomalous.

A solution, especially with regard to the Wisconsin and Florida reports, may lie in a reevaluation of specimens from those states. The level of taxonomic discrimination within trichodorid genera has increased tremendously in the past 10 years (9,10). For instance, *T. californicus* was described (2) with smooth spicules. Not until 1978 (19) was the striate nature of the spicules recognized, and it was only in 1980 (9) that an accurate LM drawing was published. Thus any records of *T. californicus* other than those of the type locality and Alaska should be considered suspect unless substantiated with specimens fitting the current interpretation of the species.

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