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Four New Species of Heteroderidae Including *Ekphymatodera* n. gen. from California[1]

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Abstract: Four new species and a new genus of Heteroderidae from California are described, and their significance for phylogenetic analysis of the family is discussed. The new genus with type species, *Ekphymatodera thomasoni* n. gen., n. sp., shares many characteristics with *Hylonema* Luc, Taylor, & Cadet, 1978, but it is distinguished by its much greater vulva–anus distance and unique cuticular pattern. Hypotheses of relationships of *Ekphymatodera* and *Hylonema* with *Sarisodera* Wouts and Sher, 1971 versus *Heterodera* Schmidt, 1871 are discussed. *Verutus californicus* n. sp. is larger than the type species, *Verutus volvingentis* Esser, 1981, differing in females particularly by the greater distance of its excretory pore from the anterior end. Monophyly of *Verutus,* which may be an outgroup of all other Heteroderidae, is strengthened by description of *V. californicus. Atalodera trilineata* n. sp. differs from other ataloderines by having second-stage juveniles with three lateral lines and from the type, *Atalodera ucri* Wouts and Sher, 1971, by the more subtle cuticular pattern of females and longer juveniles with much longer tails. *Atalodera festucae* n. sp., with four lateral lines in juveniles, has smaller females than *A. trilineata* and has a protruding dorsal vulval lip. A unique common ancestor for *Atalodera–Sherodera–Thecavermiculatus* is supported, and monophyly with *Thecavermiculatus andinus* Golden, Franco, Jatala, & Astocaza, 1973 is considered.

Key words: *Atalodera trilineata* n. sp., *A. festucae* n. sp., *Ekphymatodera* n. gen., *E. thomasoni* n. sp., Heteroderidae, new genus, new species, scanning electron microscopy, taxonomy, *Verutus californicus* n. sp.

A number of unusual heteroderid juveniles have been collected in native habitats of California. These unique forms often remain undescribed, however, because adult stages are usually difficult to obtain in adequate numbers for description. Furthermore, some native populations of heteroderids are sensitive to seasonal conditions or typically occur in low densities, confounding collecting and requiring repeated sampling to obtain sufficient numbers for description. By returning to old sampling sites as well as newer localities, we were successful in obtaining sufficient material to recognize *Ekphymatodera* n. gen. from Yosemite National Park (designated type locality) and Crescent City (near coastal redwoods) in California. Juveniles of the type population were originally collected by I. J. Thomason and curated in the University of California Riverside Nematode Collection (UCRNC). A sample, including similar juveniles from Crescent City, was curated in the mass collection of the California Department of Food and Agriculture, and subsequently all stages were recollected from Crescent City by E. Mae Noffsinger for this study. While sampling at Yosemite for *Ekphymatodera* we also discovered a new species of *Verutus* Esser, 1981, which is described here. Two species of *Atalodera* Wouts and Sher, 1971 were found in conjunction with ecological investigations by D. W. Freckman in the western foothills of the Sierra Nevada mountains at the U.S. Forest Service San Joaquin Experimental Station. *Atalodera trilineata* n. sp. was discovered during surveys for adults of *Atalodera festucae* n. sp.; both new species are described here.

Names of new species are as follows: *Ekphymatodera thomasoni* n. gen., n. sp. (Greek *ekphymatos* = eruption of pimples, describing the unique cuticle pattern of females, and *thomasoni* honoring I. J. Thomason, original collector of the type population); *Verutus californicus* n. sp. (the only species of *Verutus* described from California); *Ata-*

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lodera trilineata n. sp. (Latinized from the Greek *trion* = three and Latin *lineatus* = linear describing the unique three lateral lines in second-stage juveniles); *Atalodera festucae* n. sp. (Latinized from the type host, *Festuca* L.).

Description of these new heteroderids is particularly useful to our ongoing testing of hypotheses of phylogeny of Heteroderidae (1), since phylogenies not readily accommodating such new forms tend to be falsified.

Materials and Methods

Females, males, and second-stage juveniles (J2) of heteroderids were collected from type localities. Additional specimens of *Atalodera* and *Verutus* were obtained from greenhouse cultures on their type hosts. Most specimens were fixed in 5% formalin, slowly infiltrated with glycerin, and mounted for light and scanning electron microscopy (SEM) as previously reported (14). Other specimens were fixed in glutaraldehyde and processed by critical point drying for SEM as previously described (10). These two methods of fixation and infiltration or drying allowed comparison for detecting artifact. For SEM, all specimens were mounted on stubs, sputter-coated with 20 nm gold palladium, and examined with a JEOL 35C at 15 kV. All measurements are in micrometers (μm) unless otherwise specified.

Systematics

Ekphymatodera n. gen.
Heteroderidae
(Filipjev and Schuurmans Stekhoven, 1941)
Skarbilovich, 1947, Wouts and Sher, 1971
(Figs. 1, 2)

Description

Female: Cuticle surface with rough texture composed of minute tubercles; irregular longitudinal striae superimposed over tubercles, becoming deeper and anastomosing near posterior terminus. Cuticle on lips of broad terminal vulva prominence smoother than most Heteroderidae. Distinct anus dorsal to prominence. Labial disc squarish; lips fused, forming a distinct, continuous, plate-like annule. Cysts not formed.

Male: Length at least 1 mm; body slightly twisted. Head region slightly offset without longitudinal striae; labial disc fused with submedial lips. Tail short with bifid spicules.

Second-stage juvenile: Elongate with long, attenuated, hyaline tail terminus; phasmid opening pore-like. Head slightly offset; labial disc fused with submedial lips. Esophageal gland lobe nearly filling body diameter.

Diagnosis and relationships

Ekphymatodera n. gen. shares characters typical of other Heteroderidae, including saccate females with a heteroderid perineal pattern and vermiform males lacking caudal alae. Among heteroderids which do not form a cyst, *Ekphymatodera* is most similar to *Hylonema* in lip patterns of J2 and males (i.e., fusion of submedial lips and labial disc), in the elongate hyaline region of the J2 tail (i.e., 60–103 in *Ekphymatodera* and 55–88 in *Hylonema*), pore-like phasmid and abundant intestinal fasciculi in J2, and bifid spicules in males. Like *Hylonema*, the vulval lips form a smooth contour and are only slightly separated in profile. *Ekphymatodera* is distinguished from *Hylonema* by the much greater vulva–anus distance (73–140 vs. 19) and distinctive female cuticular pattern. *Ekphymatodera* appears to induce a synctium, in contrast to the single uninucleate giant cell of *Hylonema*.

Ekphymatodera thomasoni n. sp.

Female (n = 20): L (including "neck") = 510–790 (mean 630, 95% confidence interval ± 41); width = 210–470 (330 ± 34); neck length = 72–149 (112 ± 11); stylet length = 32.0–35.5 (33.4 ± 1.1); DGO = 2.5–5.0 (3.7 ± 0.7); median bulb (length) = 34.5–45.0 (38.8 ± 1.7); median bulb (width) = 28.0–43.5 (36.8 ± 2.2); excretory pore from anterior end = 94.0–178.0 (129.2 μm ± 16.7); vulva–anus distance (lateral view) 73.5–140.0 (96.2 ± 14.4); vulva length = 40.0–58.5 (49.8 ± 6.0);

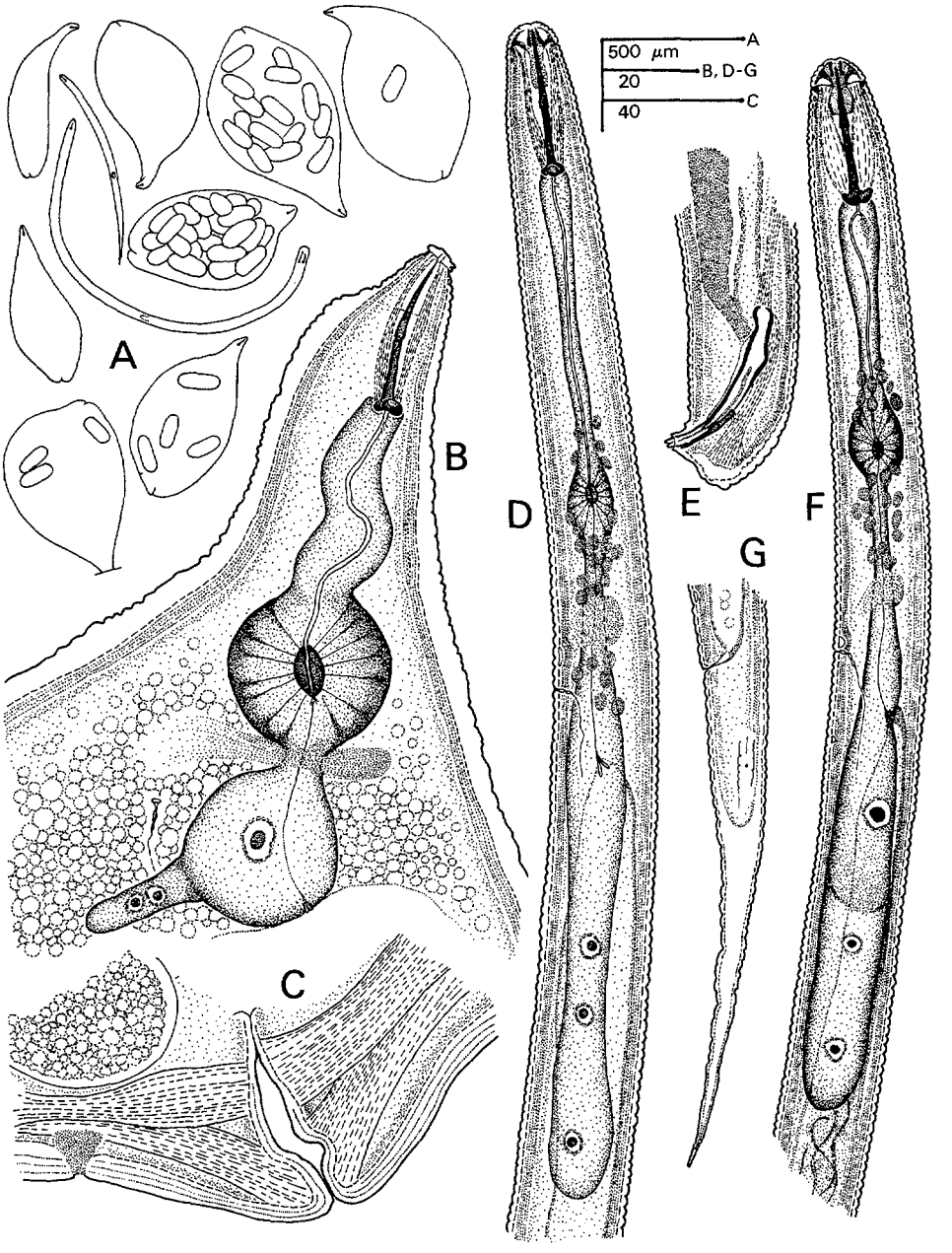

FIG. 1. Line drawings of *Ekphymatodera thomasoni* n. gen., n. sp. A) Overall shape of female, male, second-stage juvenile (J2). B) Anterior end, esophageal region of female (latero-ventral). C) Vulval-anal region (lateral). D) Anterior end, esophageal region of male (lateral). E) Mail tail (lateral). F) Anterior end, esophageal region of J2 (lateral). G) J2 tail (lateral).

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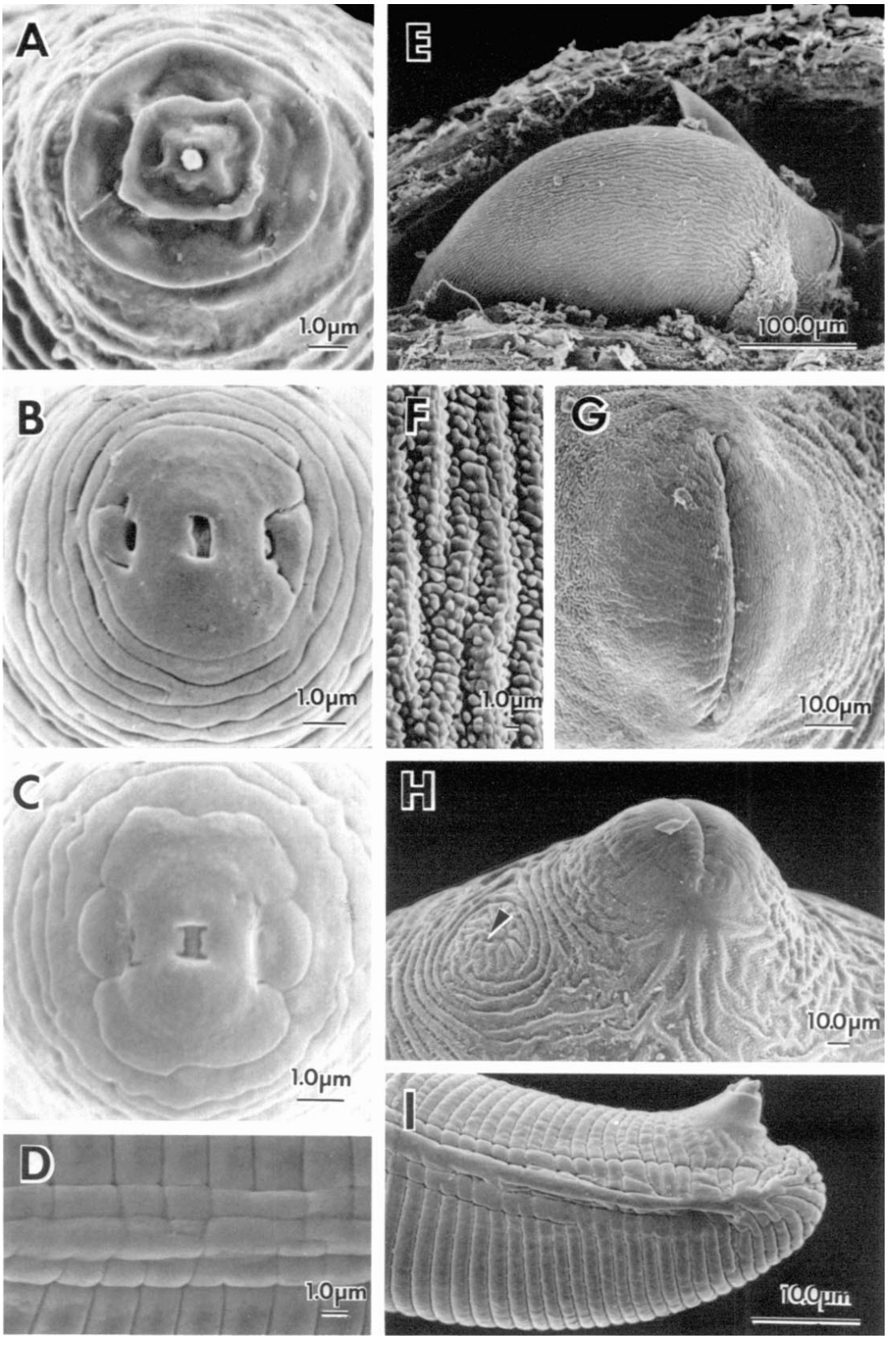
FIG. 2. SEM of *Ekphymatodera thomasoni* n. gen., n. sp. A) *En face* view of female. B) *En face* view of male. C) *En face* view of second-stage juvenile (J2). D) Lateral field of J2. E) Female embedded in host root showing longitudinal striae (latero-ventral). F) Cuticular pattern of female. G) Vulval region (end view). H) Vulval-anal region; arrowhead indicates position of anus (lateral). I) Male tail (lateral).


A
1.0µm
E
100.0µm
B
1.0µm
F
1.0µm
G
10.0µm
C
1.0µm
H
10.0µm
D
1.0µm
I
10.0µm

thickness of cuticle = 6.0–14.5 (9.1 ± 1.0); a = 1.6–2.7 (2.0 ± 0.2); m = 55.0–61.0 (57.3 ± 3.0); o = 7.0–14.9 (11.0 ± 6.0); length median bulb/width median bulb = 0.9–1.4 (1.1 ± 0.1); excretory pore % = 15.3–27.2 (21.3 ± 2.8).

Body typically oval with neck tapering and elongate, posterior protuberance broad. Neck straight or slightly reflexed dorsally. Specimens becoming creamy or light tan after fixation in formalin. Subcrystalline layer thick. Cuticle thinner in neck region and terminal protuberance. Surface consisting of minute tubercles with indistinct longitudinal ridges superimposed. Head region and anterior portion of neck annulated; labial disc squarish with four submedial lobes, lips fused forming large plate-like annule. Stylet with slight ventral curvature; knobs rounded, anterior surface slightly indented. Esophagus short with diminutive isthmus; gland lobe globular, subventral gland nuclei in ventral projection. Excretory pore near level of dorsal gland nucleus. Vulva terminal, anus dorsal.

Holotype (female): L = 593; width = 247; neck length = 124; stylet length = 32.6; DGO = 4.1; median bulb (length) = 35.7; median bulb (width) = 30.6; excretory pore from anterior end = 143.2; vulva–anus distance (lateral view) = 73.0; vulva length (unlike paratypes, calculated from foreshortened lateral view) = 40.8; thickness of cuticle = 9.1; a = 2.3; m = 61.0; o = 12.5; length median bulb/width median bulb = 1.2; excretory pore % = 24.0. Female as in general description; gonads distinct, mature eggs not present. Head sharply turned dorsally with ring of "cement" encircling neck near base of stylet. Excretory pore distinct at level of esophageal gland lobe; dorsal gland nucleus conspicuous; vulva and anus distinct. Cuticular tubercles and longitudinal striae conspicuous.

Male (n = 20): L = 1,070–1,650 (1,420 ± 60) width = 28–38 (33 ± 0.1); stylet = 26.3–33.7 (29.8 ± 3.5); DGO = 1.5–3.5 (2.5 ± 0.3); esophagus length = 178.0–272.5 (236.3 ± 11.6); excretory pore to anterior end = 104.5–188.5 (162.0 ± 8.0); tail length = 8.2–12.2 (9.7 ± 2.8); testis length = 410.0–903.0 (642.3 ± 61.9); spicule length = 34.0–45.5 (38.6 ± 2.3); gubernaculum length = 11.5–16.0 (13.3 ± 1.0); a = 32.2–49.4 (43.1 ± 2.1); b = 7.8–13.0 (9.6 ± 0.5); b′ = 3.9–6.9 (6.1 ± 0.4); m = 47.0–55.0 (51 ± 1); o = 0.05–0.11 (0.08 ± 0.01); T = 30.0–65.0 (45.5 ± 4.5); excretory pore % = 8.5–13.7 (11.5 ± 0.4).

Body cylindrical, tapering slightly anteriorly; posterior half of heat-killed specimens twisting about 90 degrees. Head region slightly offset with 5–7 discontinuous annulations; lips fused with one another as well as with labial disc, lateral lips partially separate. Lateral field with four incisures, areolated anteriorly and posteriorly. Cephalids sometimes observed at second and eighth annule; hemizonid 1.5 annules long and three or four annules anterior to excretory pore. Stylet knobs generally rounded, slightly flattened anteriorly and backward sloping. Esophagus isthmus short. Esophagointestinal valve dorsad about 2.5 median-bulb lengths below bulb. Spicule sheath short. Phasmid openings not observed.

Second-stage juvenile: Measurements are in Table 1. Body cylindrical and tapering especially posteriorly; tail tip long, attenuated. Head region with little or no offset and about five anastomosing annules. Adjacent submedial lips fused with one another and labial disc. Lateral lips fused with labial disc but not with submedial lips. Lateral lines four, areolated. Cephalids sometimes observed at second and eighth annules; hemizonid about two annules long, immediately anterior to excretory pore. Stylet robust, knobs large and anchor-shaped. Esophageal gland region filling body width; large dorsal gland nucleus anteriorly, smaller subventral gland nuclei (two) in tandem. Intestine with abundant fasciculi. Phasmid opening pore-like, duct heavily cuticularized.

Type designations: Collected by I. J. Thomason on 3 July 1957. Holotype (fe-

TABLE 1. Measurements of second-stage juveniles of *Ekphymatodera thomasoni* n. sp. (n = 20).

Character	Range	Confidence interval 95%	Confidence interval 99%	Standard deviation
Linear (μm)				
Body length	560.0–750.0	630.0 ± 18.00	± 28.00	43.00
Body width	19.0–22.0	21.0 ± 0.40	± 0.50	0.80
Stylet length	28.0–32.0	30.0 ± 2.02	± 2.76	0.97
DGO	3.5–11.0	7.7 ± 1.20	± 1.64	2.48
Esophagus length	175.0–235.0	211.0 ± 8.43	± 11.53	18.02
Excretory pore to anterior end	110.0–165.0	123.6 ± 5.11	± 6.99	10.92
Tail length	76.0–110.0	98.4 ± 3.92	± 5.36	8.38
Tail terminus length (hyaline)	60.0–103.0	69.0 ± 4.69	± 6.41	10.02
Phasmid to tail tip	75.0–230.0	166.7 ± 37.50	± 54.60	48.80
Genital primordium to tail tip	210.0–330.0	281.0 ± 24.60	± 34.71	38.71
Ratios				
a	29.0–37.0	31.4 ± 1.05	± 4.90	2.23
b	4.3–5.4	4.9 ± 0.19	± 0.26	0.40
b′	2.5–3.3	3.0 ± 0.14	± 0.19	0.29
c	5.2–8.7	6.4 ± 0.33	± 0.46	0.71
c′	5.8–7.6	6.8 ± 0.35	± 0.48	0.75
Percentages				
m	45.0–50.0	46.6 ± 0.77	± 1.05	1.64
o	8.0–18.0	13.5 ± 1.41	± 1.94	2.93
Excretory pore	16.0–22.0	19.1 ± 0.71	± 0.97	1.52

male) slide number 57 deposited in University of California Riverside Nematode Collection (UCRNC). Paratypes (51 females, 43, males, 35 J2) distributed in type collections as follows: 4 females, 5 males, 6 J2, University of California Davis Nematode Collection (UCDNC); 3 females, 3 males, 3 J2, United States Department of Agriculture Nematode Collection (USDANC), Beltsville, Maryland; 2 females, 1 male, 2 J2, Nematode Collection of the Entomology and Nematology Department, Rothamsted Experimental Station, Harpenden, England; remaining types (42 females, 34 males, 24 J2) in the UCRNC.

Type habitat, host, and locality: Roots and surrounding soil of *Juncus effusus* L. var. *pacificus*, from a meadow on the south bank of the Merced River in Yosemite Valley, Yosemite National Park, California. Additional specimens of *E. thomasoni* collected by personnel at the California Department of Food and Agriculture and by E. M. Noffsinger from the type host near the Oregon coast at Del Norte County Fairgrounds, Crescent City, California; morphometrics of this population do not differ from that of the type.

Verutus californicus n. sp.
(Figs. 3, 4)

Female (n = 20): L (including neck) = 706–966 (mean 851, 95% confidence interval ± 48); width = 147–205 (179 ± 10); neck length not precisely delineated; stylet length = 19.8–30.0 (27.4 ± 4.9); DGO = 4.0–9.5 (6.8 ± 0.8); median bulb (length) = 17.0–27.5 (24.2 ± 1.4); median bulb (width) = 18.5–25.0 (21.1 ± 1.4); excretory pore from anterior end = 194.0–284.0 (219.4 ± 45.6); vulva–anus distance (lateral view) 202.6–722.5 (587.3 ± 41.0); vulva length = 65.5–73.8 (68.9 ± 1.8); thickness of cuticle = 4.0–6.5 (5.2 ± 0.4); a = 3.9–5.3 (4.7 ± 0.2); b = 4.3–7.5 (5.1 ± 0.4); c = 38.5–94.5 (66.9 ± 10.7); m = 50.0–58.0 (53.0 ± 7.0); o = 19.6–39.5 (30.4 ± 3.0); length median bulb/width median bulb = 1.0–1.4 (1.2 ± 0.1); excretory pore % = 21.9–36.4 (28.1 ± 5.4).

Body sausage or reniform-shaped or fre-

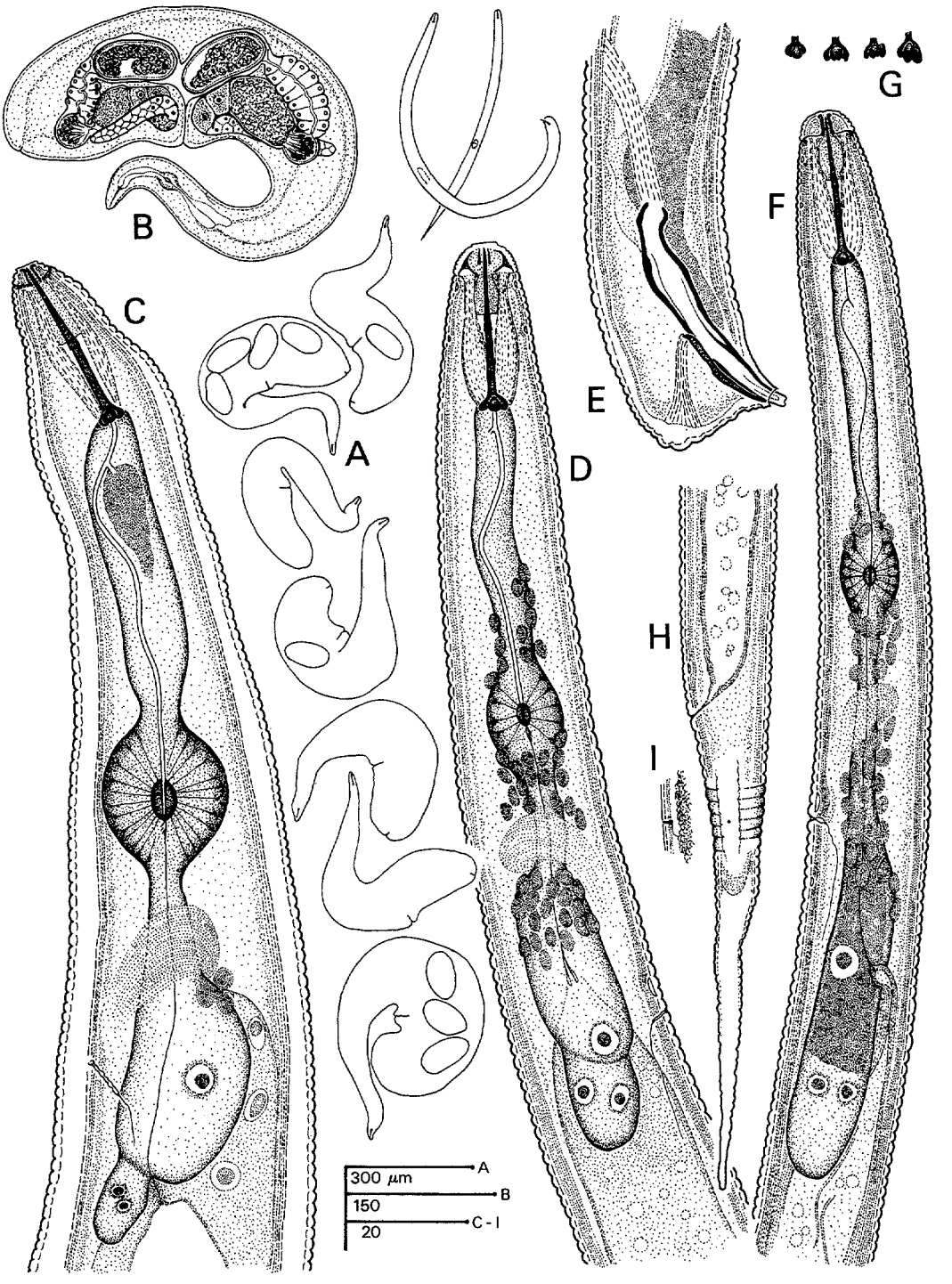


FIG. 3. Line drawings of *Verutus californicus* n. sp. A) Overall shape of females, male, second-stage juvenile (J2). B) Detail of female (lateral). C) Anterior end, esophageal region of female (latero-ventral). D) Anterior end, esophageal region of male (lateral). E) Male tail (lateral). F) Anterior end, esophageal region of J2 (lateral). G) Variation in stylet knob shape of J2 (lateral). H) J2 (lateral). I) Phasmid of J2 (ventral).

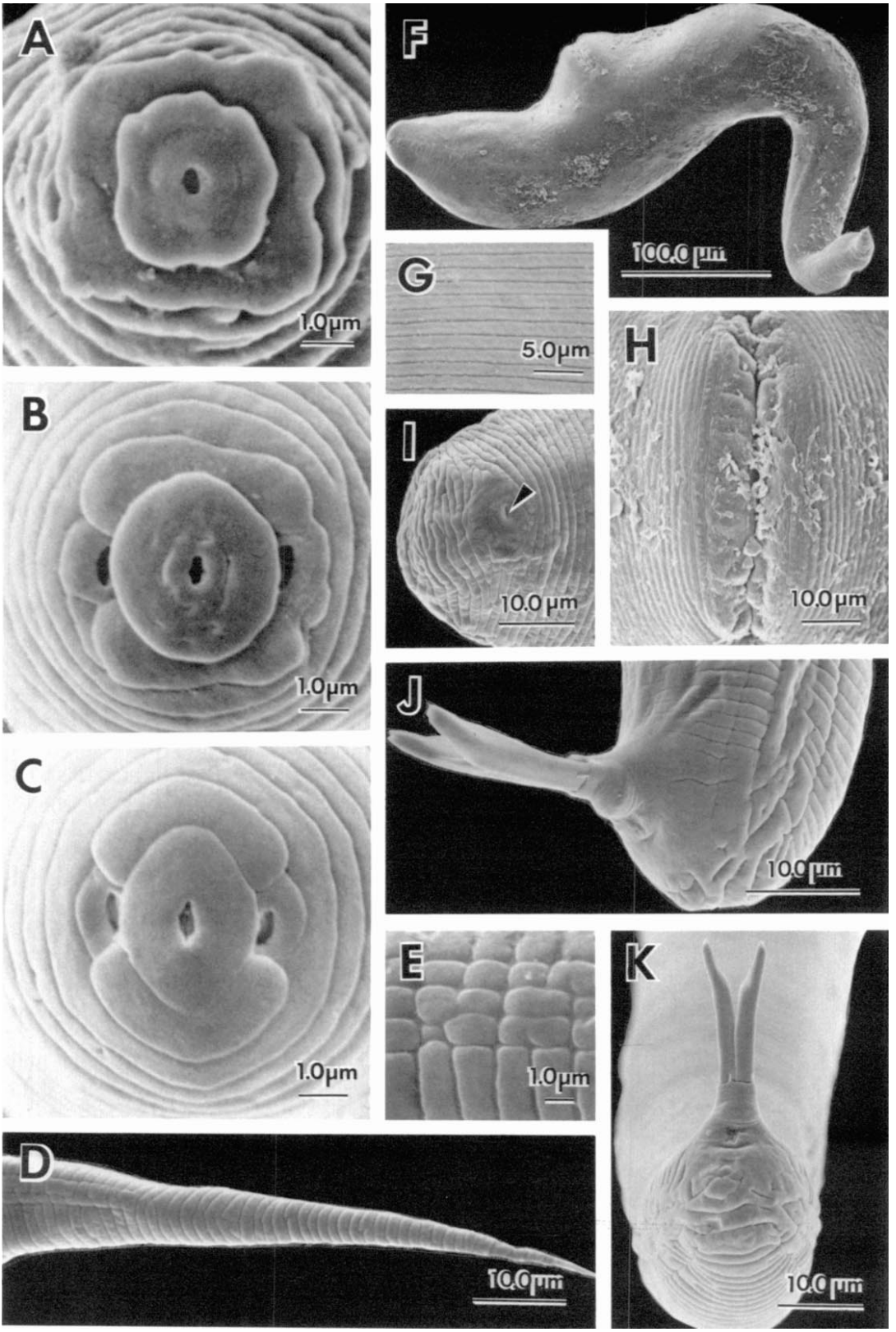


FIG. 4. SEM of *Verutus californicus* n. sp. A) *En face* view of female. B) *En face* view of male. C) *En face* view of second-stage juvenile (J2). D) J2 tail (lateral). E) Lateral field of J2. F) Female (primarily lateral). G) Cuticular pattern at midbody of female. H) Vulval region (end view). I) Female tail; arrowhead indicates anus (end view). J) Male tail (lateral). K) Male tail (ventral and end view).

quently with strong ventral curvature and anterior end recoiled over body; vulva large, subequatorial on slight prominence, anus subterminal, slightly ventral. Fresh specimens pearly white, cuticle with regular transverse striations interrupted laterally to form irregular lateral lines. Cuticle modified to irregular blocks in terminal region surrounding anus; surface pattern often obscured by subcrystalline layer and persistent pieces of molted cuticles. Head region with elevated labial disc, lips fused to form squarish annule, widened in submedial position; lateral lips minute, partially separate in some individuals. Stylet straight, slender with elongate backsloping knobs. Esophagus with elongate procorpus, large metacorpus, distinct narrow isthmus and short, broad gland lobe. Excretory pore near level of gland lobe. Vulva lips smooth, not clearly demarcated from body surface pattern; vagina very deep, paired gonads double-reflexed. Rarely more than three or four embryonic eggs retained per female. Small egg masses with up to 15 eggs associated with mature females.

Holotype (female): L = 706; width = 147; stylet = 20.4; DGO = 7.1; median bulb (length) = 23.5; median bulb (width) = 19.9; excretory pore from anterior end = 166.2; vulva–anus distance (lateral view) = 202.1; vulval length unclear in lateral view; thickness of cuticle = 5.0; a = 4.8; b = 4.8; c = 87.2; o = 0.4; length median bulb/width median bulb = 1.2; excretory pore % = 22.5. Female as in general description; young eggs in embryonic stages. Anterior one-third vermiform, strongly reflexed ventrally; anterior region apparently retaining somatic musculature, surface partially covered with subcrystalline layer and previously molted cuticles. Esophageal gland nuclei distinct; excretory pore posterior to gland lobe. Vagina extending about one-half body width; anus slightly ventral to posterior terminus.

Male (n = 19): L = 770–980 (880 ± 30); width = 28–34 (31.2 ± 0.9); stylet = 25.3–28.2 (26.7 ± 0.4); DGO = 7.2–14.4 (10.3 ± 0.9); esophagus length = 115.0–200.5 (163.5 ± 8.3); excretory pore to anterior end = 130.0–154.5 (143.7 ± 4.2); tail length = 6.1–11.2 (8.5 ± 4.4); testis length = 38.0–67.5 (56.6 ± 3.9); spicule length = 38.0–46.5 (41.4 ± 1.1); gubernaculum length = 12.0–19.5 (15.5 ± 0.9); a = 27.0–36.0 (29.2 ± 1.1); b = 5.7–8.0 (6.6 ± 0.3); b′ = 4.9–6.6 (5.4 ± 0.2); m = 46.5–53.5 (50.0 ± 0.8); o = 13.0–26.4 (19.3 ± 1.8); T = 40.5–75.0 (63.9 ± 3.8); excretory pore = 12.6–16.9 (15.7 ± 0.5).

Body cylindrical, tapering slightly anteriorly; little if any twist of body in heat-killed specimens. Head region slightly offset, with seven or eight annulations. Lip region with rounded labial disc, all six lips generally fused, forming a modified rectangle, one lateral lip sometimes separate or partially separate. Lateral field with four incisures, areolation limited to anterior and posterior ends. Cephalids present at second, and sometimes at eighth annule; hemizonid about two annules anterior to excretory pore. Stylet slender, knobs sloping posteriorly. Median bulb elongate. Esophageal gland lobe short, broad; lumen extending about half length of lobe to esophagointestinal junction. Spicules slightly arcuate, bifid; spicule sheath short with little or no annulation. Phasmid openings not observed.

Second-stage juvenile: Measurements are in Table 2. Elongate with long, attenuated tail; phasmid opening pore-like. Stylet knobs small, backsloping. Adjacent submedial lips fused and broadest sublaterally. Esophageal gland lobe broad; subventral gland nuclei typically near same level in posterior third of lobe.

Type designations: Collected by A. H. Bell on 24 June 1985. Holotype (female), slide number 58 deposited in UCRNC. Paratypes (45 females, 54 males, 95 J2) distributed as follows: 5 females, 4 males, 6 J2, UCDNC; 4 females, 4 males, 6 J2, USDA-NC, Beltsville, Maryland; 2 females, 4 males, 6 J2, Nematode Collection of the Entomology and Nematology Department Rothamsted Experimental Station, Harpenden, England; remaining type material (32 females, 42 males, 77 J2) in the UCRNC.

Type habitat, host, and locality: Roots and

TABLE 2. Measurements of second-stage juveniles of *Verutus californicus* n. sp. (n = 20).

Character	Range	Confidence interval 95%	Confidence interval 99%	Standard deviation
Linear (μm)				
Body length	590.0–670.0	622.2 ± 11.20	± 15.30	24.00
Body width	19.0–22.0	20.8 ± 0.52	± 0.72	1.12
Stylet length	23.0–27.0	24.8 ± 1.99	± 2.73	0.95
DGO	5.5–9.5	6.8 ± 0.51	± 0.70	4.65
Esophagus length	163.0–200.0	183.5 ± 3.45	± 4.84	7.57
Excretory pore to anterior end	110.0–128.0	119.0 ± 2.17	± 2.97	4.65
Tail length	75.0–91.0	81.7 ± 1.99	± 2.71	4.24
Tail terminus length (hyaline)	44.0–66.0	58.7 ± 2.78	± 3.78	5.94
Genital primordium to tail tip	342.0–388.0	364.2 ± 6.68	± 9.13	14.28
Ratios				
a	27.0–34.0	30.4 ± 0.93	± 1.27	1.98
b	3.8–4.5	4.3 ± 0.14	± 0.19	0.29
b′	3.1–3.7	3.4 ± 0.08	± 0.11	0.18
c	7.0–11.0	7.8 ± 0.40	± 0.54	0.85
c′	4.2–6.8	6.0 ± 0.30	± 0.40	0.63
Percentages				
m	44.0–51.0	46.6 ± 1.00	± 1.37	2.14
o	18.0–39.0	26.5 ± 2.10	± 2.87	4.49
Excretory pore	17.0–20.0	19.1 ± 0.20	± 0.28	0.44
Genital primordium	56.0–60.0	58.6 ± 0.49	± 0.67	5.86

surrounding soil of *Carex* L. sp. from a meadow on the south bank of the Merced River in Yosemite Valley, Yosemite National Park, California. Type locality identical to that of *E. thomasoni* n. sp. The samples from which *V. californicum* were recovered included several undetermined species of *Carex*.

Diagnosis and relationships: Verutus californicus n. sp. resembles other species of the genus by the elongate female and a large subequatorial vulva. It is particularly similar to the type species, *V. volvingentis*, although it tends to be larger. The female of *V. californicus* is 851 (706–966) versus 663 (500–930). *Verutus mesoangustus* Minagawa, 1986 is much smaller at 307 (270–342). The anterior end–excretory pore distance in *V. californicus* female is 219 (164–284), whereas that of *V. volvingentis* is 139 (122–183). Second-stage juveniles of *V. californicus* are much longer (622 [590–670]) than those of *V. volvingentis* (492 [430–540]) and the tail is more attenuated (82 [75–91] versus 54 [46–64]). Second-stage juveniles of *V. mesoangustus* are the shortest (346 [320–380]). Lip patterns of *V. californicus* are very similar to those of *V. volvingentis* (10) including fusion of adjacent submedial lips in males and juveniles of both species, but in males of *V. californicus* there is a greater tendency for separation of lateral lips. Published micrographs of *V. mesoangustus* (8) are small and difficult to interpret; however, the squarish, highly fused lip pattern of juveniles resembles males, rather than juveniles, of the other species. *V. californicus* apparently induces a small syncytium (Baldwin and Mundo, unpubl.) similar to that of *V. volvingentis* (4).

Atalodera trilineata n. sp.
(Figs. 5, 6)

Female (n = 17): L (including "neck") = 550–800 (mean 707, 95% confidence interval ± 40); width = 240–470 (366 ± 25); neck length = 67–161 (93 ± 43); stylet length = 26.5–32.0 (29.9 ± 0.8); DGO = 3.5–8.5 (6.0 ± 0.8); median bulb (length) = 19.5–34.0 (27.4 ± 1.4); median bulb (width); = 21.5–32.5 (28.8 ± 1.3); esophagus length = 124.5–185.0 (150.5 ± 17.1);

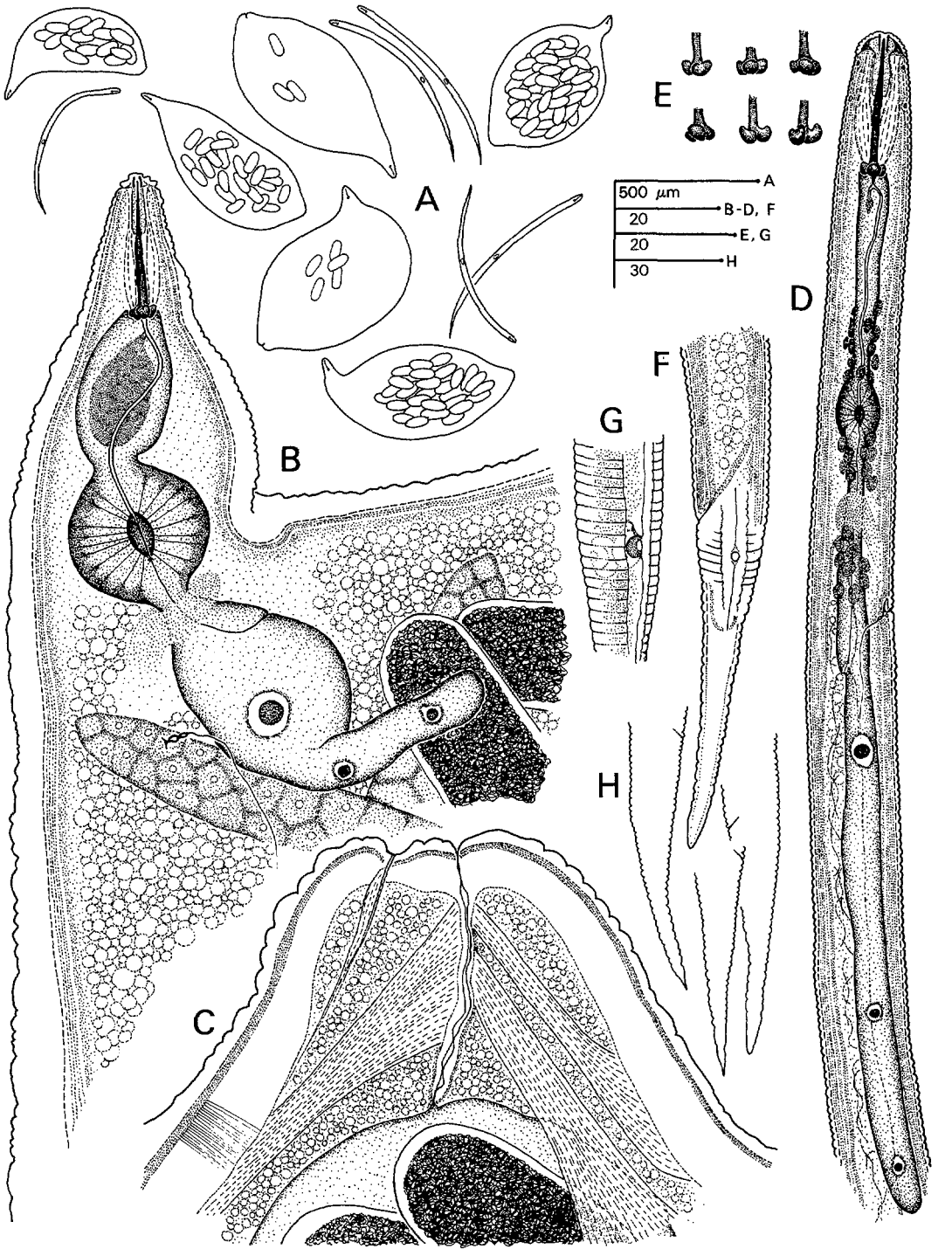


FIG. 5. Line drawings of *Atalodera trilineata* n. sp. A) Overall shape of females, second-stage juveniles (J2). B) Anterior end, esophageal region of female (latero-ventral). C) Vulval-anal region (lateral). D) Anterior end, esophageal region of J2 (lateral). E) Variation in stylet knob shape of J2 (lateral). F) J2 tail (lateral). G) J2 tail in region of ampulla of lens-like phasmid (ventro-lateral). H) Variation in shape of J2 tail (lateral).

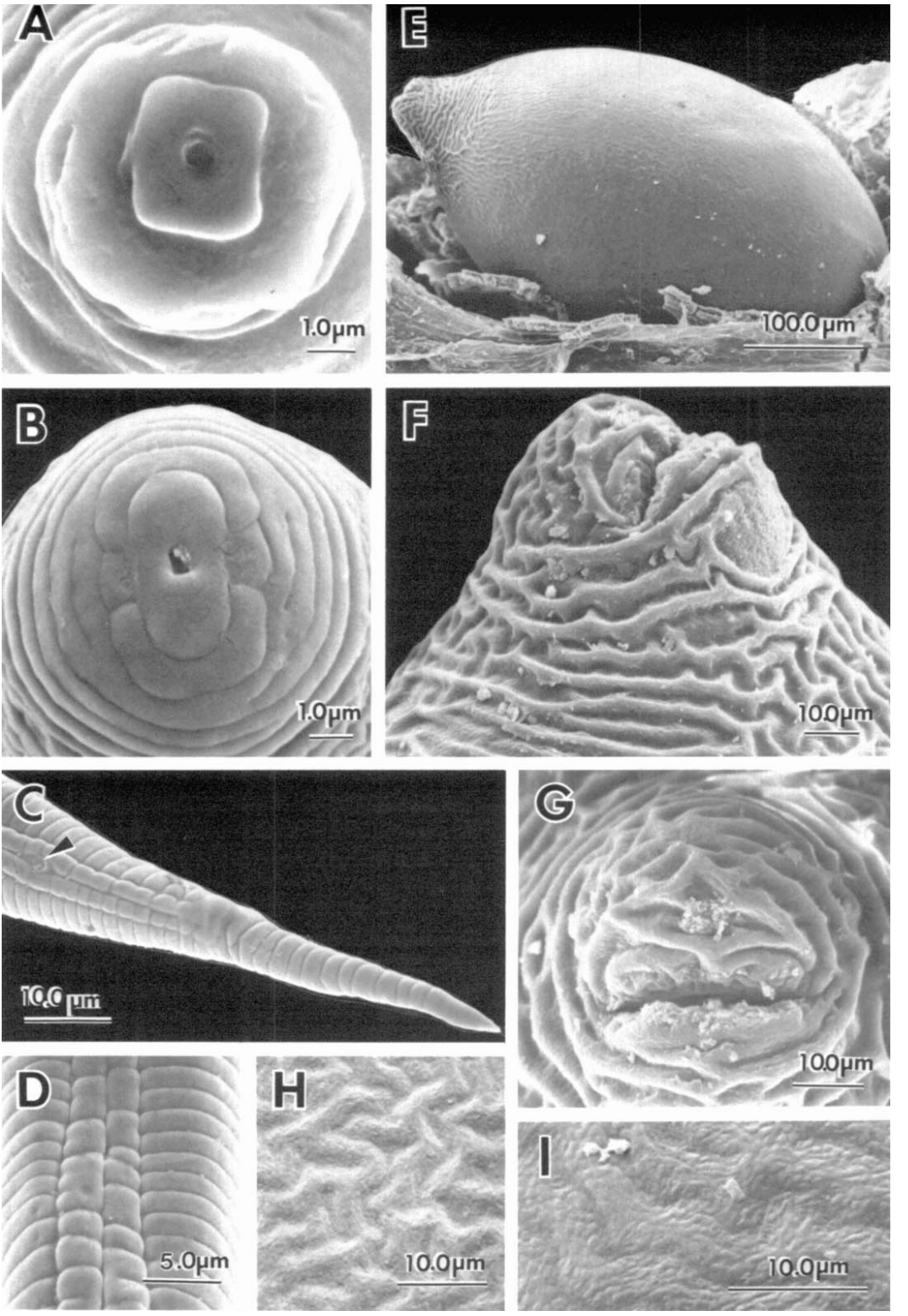


FIG. 6. SEM of *Atalodera trilineata* n. sp. A) *En face* view of female. B) *En face* view of second-stage juvenile (J2). C) J2 tail; arrowhead indicates position of phasmid opening. D) Lateral field of J2 at midbody. E) Female embedded in host root (latero-ventral). F) Vulval region (lateral). G) Vulval region (end view). H) Overview of female cuticular pattern at midbody. I) Detail of female cuticular pattern at midbody.

excretory pore from anterior end = 102.5–120.4 (112.0 ± 7.2); vulva–anus distance (lateral view) 14.4–25.0 (19.1 ± 2.0); vulva length (n = 6) = 28.7–32.6 (29.8 ± 4.1); cuticle thickness 5.5–10.5 (7.4 ± 0.6); a = 1.5–2.4 (1.9 ± 0.1); m = 44.0–74.5 (56.4 ± 2.2); o = 11.1–30.3 (20.5 ± 0.8); length median bulb/width median bulb = 0.7–1.4 (1.0 ± 0.4); excretory pore % = 13.8–20.2 (16.5 ± 2.3).

Lemon-shaped with distinct terminal prominence; neck region set-off, straight or reflexed ventrally, less often dorsally or laterally. Fresh specimens cream colored, becoming slightly darker after fixation in formalin. Cuticle surface finely pebbled, superimposed on a faint, longitudinally oriented wavy pattern, becoming deeper, more zig-zag and transverse posteriorly. Subcrystalline layer heavy, especially prominent posteriorly. Head region with squarish elevated labial disc. Lips six, fused forming a single round plate. Stylet with slight dorsal curvature; knobs typically broad, anteriorly flattened. Esophagus with short, broad procorpus containing large dorsal gland ampulla. Isthmus short, gland lobe with long ventral extension containing subventral gland nuclei. Excretory pore near level of dorsal gland nucleus. Vulva with prominent ventral lip on distinct terminal prominence; anus slightly dorsal to vulva.

Holotype (female): L = 699; width = 344; neck length = 130; stylet length = 26.5; DGO = 5.6; median bulb (length) = 29.4; median bulb (width) = 28.9; esophagus length = 129.0; excretory pore from anterior end = 104.5; vulva–anus distance (lateral view); = 13.7; vulval length (unlike paratypes, calculated from foreshortened lateral view) = 28.5–32.6 (29.8 ± 4.1); thickness of cuticle = 9.3; a = 20.3; m = 42.0; o = 21.4; length median bulb/width median bulb = 1.0; excretory pore % = 15.0. Female as in general description; large, lemon-shaped with distinct cone, eggs numerous. Anus distinct, on large dorsal lip. Cuticular surface relatively smooth except at cone, covered with subcrystalline material.

Male: Not found.

Second-stage juvenile: Measurements are in Table 3. Body large, cylindrical and tapering, especially posteriorly. Head region slightly offset, having about six annules. Labial disc oval surrounded by fused adjacent submedial lips, lateral lips partially fused with labial disc. Stylet knobs usually indented anteriorly. Lateral lines three, areolation primarily anteriorly and posteriorly. Cephalids typically near second and eighth annules; hemizonid immediately anterior to excretory pore, at level of esophageal isthmus. Esophagointestinal junction near base of isthmus. Esophageal gland lobe long, narrow. Dorsal gland anterior, texture coarse, nucleus very large with one or two nucleoli; subventral glands texture smooth, gland nuclei in tandem. Phasmid opening conspicuous, ampulla lens-like.

Type designations: Collected by A. H. Bell on 6 June 1985. Holotype (female), slide number 59 deposited in UCRNC. Paratypes (71 females, 67 J2) distributed as follows: 3 females, 5 J2, UCDNC; 3 females, 6 J2, USDANC, Beltsville, Maryland; 3 females, 5 J2, Nematode Collection of the Entomology and Nematology Department, Rothamsted Experimental Station, Harpenden, England; remaining types (62 females, 51 J2) in the UCRNC.

Type habitat, host, and locality: Roots and surrounding soil of *Lupinus bicolor* Lindl. on the north side of the driveway of the U.S. San Joaquin Experimental Range, Madera County, California.

Diagnosis and relationships: Atalodera trilineata n. sp. resembles *Atalodera ucri* by the absence of a cyst and distinct vulval cone with anus on the dorsal lip. Females of both species have a large dorsal gland ampulla which swells the procorpus with granules. Second-stage juveniles of the two species are similar in that adjacent submedial lips are fused and lateral lips are partially fused with the labial disc; in addition, J2 of both species have a narrow esophageal gland lobe typical of ataloderines. *Atalodera trilineata* is distinct from *A. ucri* by the more subtle cuticular pattern on females in the

TABLE 3. Measurements of second-stage juveniles of *Atalodera trilineata* n. sp. (n = 23).

Character	Range	Confidence interval 95%	Confidence interval 99%	Standard deviation
Linear (μm)				
Body length	560.0–760.0	672.2 ± 16.00	± 21.80	37.00
Body width	17.0–21.5	19.9 ± 0.47	± 0.64	1.09
Stylet length	27.5–31.0	28.6 ± 0.44	± 0.60	1.02
DGO	5.5–9.0	7.4 ± 0.43	± 0.58	7.37
Esophagus length	215.0–315.0	275.5 ± 8.91	± 12.11	20.61
Excretory pore to anterior end	100.0–125.0	116.4 ± 3.31	± 4.50	7.65
Tail length	57.0–72.5	66.0 ± 1.94	± 2.63	4.48
Tail terminus length (hyaline)	37.0–47.0	40.9 ± 1.40	± 1.90	3.25
Phasmid to tail tip	51.5–65.0	58.2 ± 8.56	± 11.70	4.09
Genital primordium to tail tip	250.0–330.0	293.4 ± 12.59	± 17.18	29.80
Ratios				
a	31.0–37.0	33.9 ± 0.74	± 1.00	1.70
b	4.2–5.5	5.0 ± 0.14	± 0.19	0.32
b′	2.1–2.8	2.5 ± 0.07	± 0.10	0.16
c	9.0–11.2	10.2 ± 0.25	± 0.34	0.58
c′	3.3–4.8	4.3 ± 0.19	± 0.26	0.44
Percentages				
m	45.0–50.0	47.3 ± 0.70	± 0.95	1.61
o	19.0–32.0	25.9 ± 1.46	± 1.98	3.38
Excretory pore	15.4–19.1	17.3 ± 0.41	± 0.56	0.96
Genital primordium	52.0–62.0	56.9 ± 1.08	± 1.48	2.38

former. Juveniles of *A. trilineata* are longer (672 [560–760]) than those of *A. ucri* (503 [450–555]) and their tails are much longer, 66 (57–73) versus 39 (29–42). Second-stage juveniles of *A. trilineata* are distinct by having three lateral lines, versus four in other species. Juveniles of *A. trilineata* have fused submedial lips as do *A. ucri*, but in *A. ucri* the separate lips are marked by an indentation not present in *A. trilineata*.

Atalodera festucae n. sp.
(Figs. 7, 8)

Female (n = 19): L (including neck) = 440–680 (mean 516, 95% confidence interval ± 33); width = 145–380 (234 ± 34); neck length = 62–124 (104 ± 43); stylet length 24.0–27.5 (25.5 ± 2.7); DGO = 3.5–6.5 (3.9 ± 0.6); median bulb (length) = 23.5–35.0 (27.9 ± 1.5); median bulb (width) = 21.5–30.5 (24.7 ± 2.6); esophagus length = 115.0–155.0 (137.5 ± 10.4); excretory pore from anterior end = 74.5–125.0 (97.5 ± 16.7); vulva–anus distance (lateral view) = 10.0–17.5 (14.5 ± 2.9); vulva length (n = 8) = 29.5–44.5 (37.4 ± 14.3); thickness of cuticle = 4.0–10.5 (7.2 ± 0.8); a = 1.5–3.2 (2.3 ± 1.3); m (n = 10) = 48.0–50.5 (49.5 ± 0.2); o = 2.5–6.5 (3.9 ± 0.6); length median bulb/width median bulb = 1.0–1.6 (1.1 ± 0.3); excretory pore % = 18.3–23.4 (20.4 ± 0.6).

Body small and saccate or lemon-shaped in young individuals to large and spherical with distinct protuberance in mature specimens. Neck usually clearly offset, rarely reflexed. Freshly collected specimens cream colored, becoming slightly darker after fixation in formalin. Cuticle with shallow zig-zag pattern, coarser posteriorly; subsurface punctate. Subcrystalline layer moderately thick, forming reticulate pattern anteriorly. Head region with elevated square labial disc; lips generally fused, but sometimes one or both lateral lips demarcated. Stylet generally curved dorsally, knobs rounded. Esophagus with long procorpus, gland lobes often clavate, ventral lobe with subventral gland nuclei. Excretory pore near level of dorsal gland nucleus. Second-stage juveniles persistent in moribund females or possibly escaping

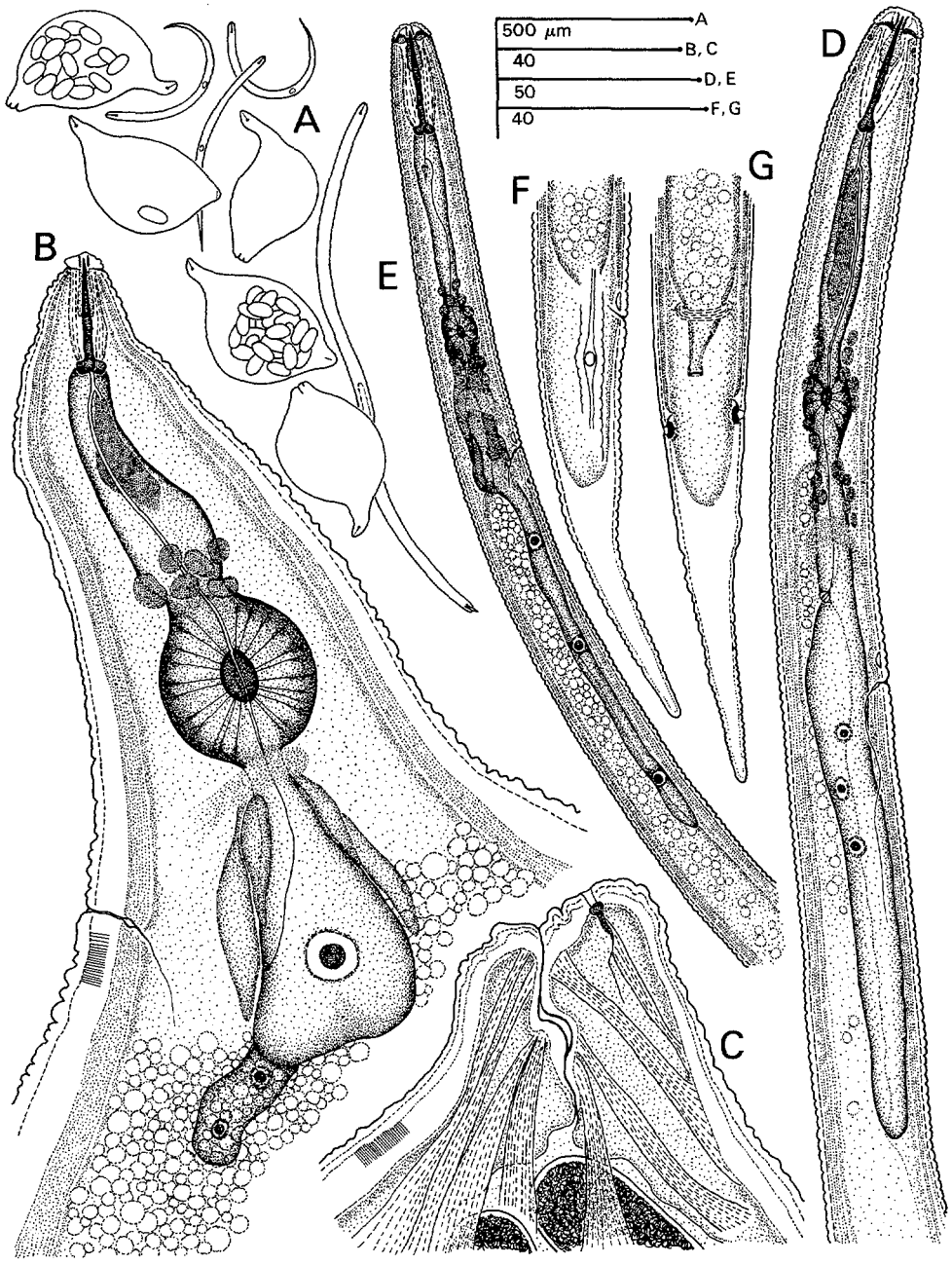


FIG. 7. Line drawings of *Atalodera festucae* n. sp. A) Overall shape of females, male, second-stage juveniles (J2). B) Anterior end, esophageal region of female (lateral). C) Vulval-anal region (lateral). D) Anterior end, esophageal region of male (lateral). E) Anterior end, esophageal region of J2 (lateral). F) J2 tail (lateral). G) J2 tail (ventral).

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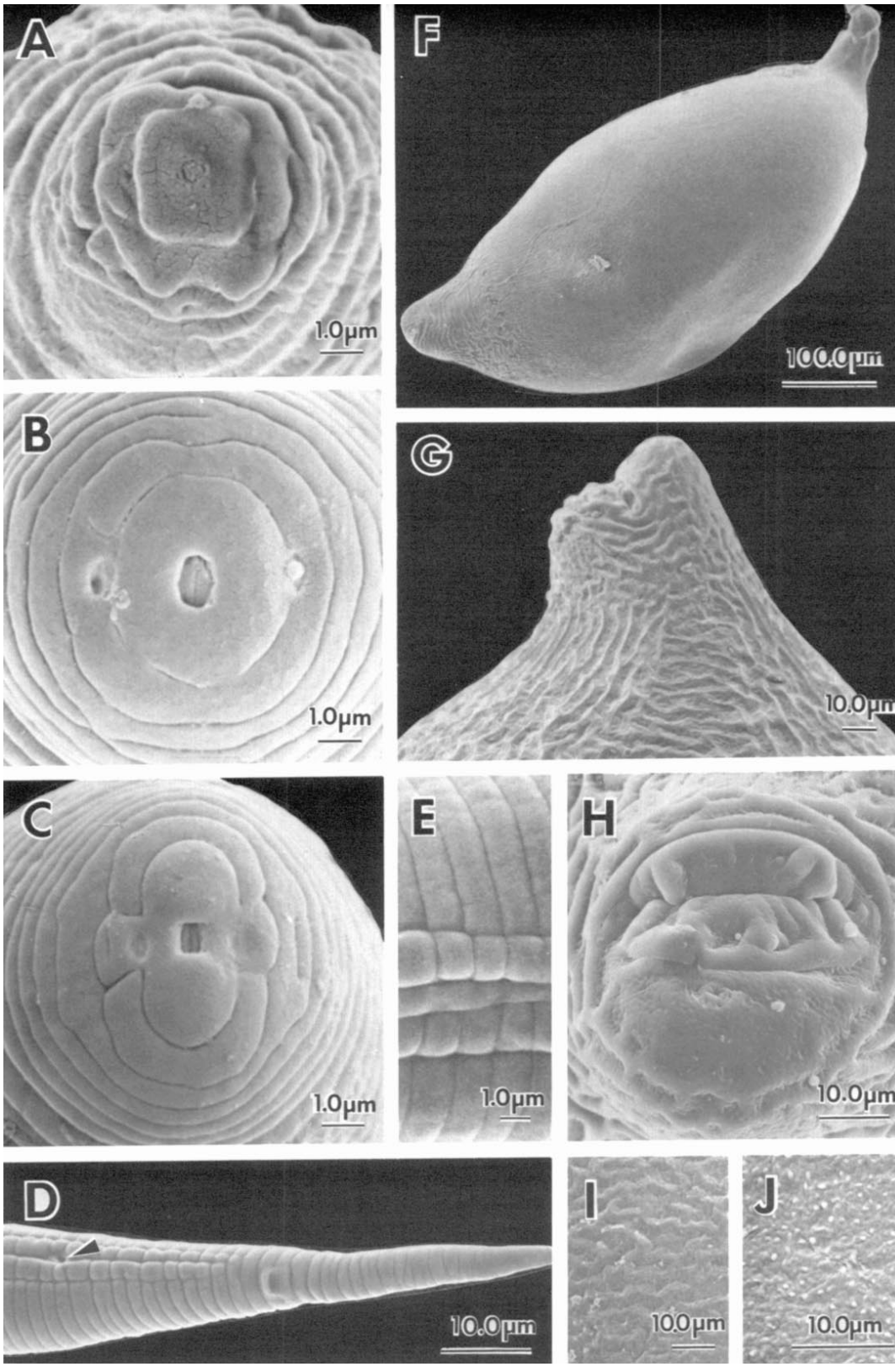
FIG. 8. SEM of *Atalodera festucae* n. sp. A) *En face* view of female. B) *En face* view of male. C) *En face* view of second-stage juvenile (J2). D) J2 tail; arrowhead indicates phasmid opening (lateral). E) Lateral field of J2. F) Female (dorso-ventral). G) Vulval region (lateral). H) Vulval region (end view). I) Overview of female cuticular pattern at midbody. J) Detail of female cuticular pattern at midbody.


A
1.0µm
F
100.0µm
B
1.0µm
G
10.0µm
C
1.0µm
E
1.0µm
H
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D
10.0µm
I
10.0µm
J
10.0µm

TABLE 4. Measurements of second-stage juveniles of *Atalodera festucae* n. sp. (n = 23).

Character	Range	Confidence interval 95%	Confidence interval 99%	Standard deviation
Linear (μm)				
Body length	470.0–580.0	530.0 ± 10.00	± 19.80	30.80
Body width	18.0–22.0	19.9 ± 0.42	± 0.58	0.98
Stylet length	24.0–27.0	25.6 ± 1.60	± 2.19	0.77
DGO	3.0–7.0	5.2 ± 0.42	± 0.57	0.96
Esophagus length	150.0–215.0	176.1 ± 10.51	± 14.29	24.31
Excretory pore to anterior end	100.0–120.0	107.6 ± 2.25	± 3.05	5.19
Tail length	57.0–71.5	65.0 ± 1.46	± 2.98	3.37
Tail terminus length (hyaline)	39.5–48.0	41.0 ± 3.70	± 5.03	8.56
Phasmid to tail tip	49.5–64.0	57.4 ± 6.52	± 8.92	3.11
Genital primordium to tail tip	255.0–305.0	291.1 ± 10.46	± 14.25	15.16
Ratios				
a	22.0–28.0	26.5 ± 0.62	± 0.85	1.44
b	3.8–5.0	4.4 ± 0.13	± 0.18	0.30
b′	2.4–3.7	3.0 ± 0.17	± 0.23	0.39
c	7.2–9.0	8.1 ± 0.16	± 0.22	0.37
c′	3.2–4.8	4.2 ± 0.14	± 0.19	0.32
Percentages				
m	39.0–47.0	42.8 ± 0.94	± 1.27	2.27
o	12.0–26.0	20.4 ± 1.58	± 2.15	3.66
Excretory pore	18.0–23.0	20.4 ± 0.60	± 0.81	1.38
Genital primordium	50.0–64.0	57.2 ± 3.07	± 4.47	3.99

through deteriorating head region. Vulva on terminal prominence with dorsal lip particularly elevated; anus on prominence adjacent to dorsal lip.

Holotype (female): L = 442; width = 193; neck length = 119; stylet length = 25.3; DGO = 6.6; median bulb (length) = 23.5; median bulb (width) = 22.4; excretory pore from anterior end = 90.8; vulva–anus distance = 11.2; thickness of cuticle = 6.0; a = 2.3; m = 44; length median bulb/width median bulb = 1.1; excretory pore % = 20.5. Female as in general description; most eggs not yet mature. Body lemon-shaped, head latero-ventral, posterior region lateral. Head region with distinct stylet and esophagus, excretory pore near posterior level of median bulb. Neck partially constricted at level of procorpus by ring of cement. Position of anus on dorsal lip clearly visible in lateral view. Cuticular pattern zigzag, very coarse posteriorly, subsurface punctations prominent.

Male (n = 1): L = 1,513, width = 32, stylet length = 30.6, DGO = 7.5, esophagus length = 313.1, excretory pore to anterior end = 166.3, tail length = 5.0, testes length = 743.4, spicule length = 34.6, gubernaculum length not visible, a = 47.8, b = 5.4, b′ = 4.8; c = 302.5; c′ = 3.56; m = 48.0; o = 24.8; T = 58.0, excretory pore % = 10.9.

Body cylindrical, tapering anteriorly; posterior half of heat-killed specimen slightly twisted. Head region slightly offset, with 5–7 annulations, labial disc round. Lips fused with one another, except lateral lips faintly marked, fused with labial disc. Lateral field with four incisures, areolated anteriorly and posteriorly. Cephalids distinct on third and eighth annules. Hemizonid about one-half annule anterior to excretory pore. Stylet knobs rounded. Esophago-intestinal junction dorsal, at base of isthmus. Spicules nearly terminal, spicule sheath short. Phasmid openings not observed.

Second-stage juveniles: Measurements are in Table 4. Body cylindrical and tapered, especially posteriorly. Head region nearly continuous with body contour, having about five annulations. Labial disc elon-

gate, adjacent submedial lips fused, lateral lips separate or nearly separate from adjacent lips, fused with labial disc. Lateral lines four, areolated anteriorly and posteriorly. Cephalids not observed; hemizonid immediately anterior to excretory pore. Stylet knobs large, rounded, indented anteriorly. Esophago-intestinal junction at base of isthmus, gland lobe very narrow, long. Phasmid opening with lens-like ampulla.

Type designations: Collected by A. H. Bell in February 1985 and 1986. Holotype (female), slide number 60 deposited in UCRNC. Paratypes (58 females, 1 male, 321 J2) distributed in collections as follows: 4 females, 7 J2, UCDNC; 3 females, 7 juveniles, USDANC, Beltsville, Maryland; 3 females, 7 J2, Nematode Collection of the Entomology and Nematology Department, Rothamsted Experimental Station, Harpenden, England; remaining type material (48 females, 1 male, 274 J2) in the UCRNC.

Type habitat, host, and locality: Roots and surrounding soil of *Festuca megalura* Nutt. on the north side of the driveway of the U.S. San Joaquin Experimental Range, Madera County, California. Type locality same as for *A. trilineata* n. sp.

Diagnosis and relationships: Atalodera festucae n. sp. resembles other ataloderines with respect to absence of a cyst, general shape of vulval cone, position of anus, lip pattern of J2 and males, and narrow esophageal gland lobe of J2. Females of *A. festucae* consistently retain J2, as described for the ataloderine *Thecavermiculatus* spp. Like *A. ucri* Wouts and Sher, 1971, females are smaller than *A. trilineata* (length 530 [470–580] versus 672 [560–720]). The esophagus of females of *A. festucae* tends to be shorter than that of other species. The dorsal vulval lip of *A. festucae* protrudes much more than in other species, including *A. ucri.* The body wall pattern of *A. festucae* is subtle and more like *A. trilineata* than *A. ucri.* Second-stage juveniles of *A. festucae* are generally similar to those of *A. ucri.* They have four lateral lines, but the tail is much longer than in *A. ucri* (65 [57–72] versus 39 [29–42]). Lip pattern of J2 resembles that of *A. trilineata* with completely fused adjacent submedial lips; the male lip pattern is similar to that of *A. ucri* in which all lips are fused forming a continuous annule; however, *A. ucri* has only three head annules, whereas *A. festucae* has about seven.

Discussion

Unique features of *Ekphymatodera* offer the potential for new insights into phylogenetic relationships of Heteroderidae. We have noted the morphological similarity of *Ekphymatodera* to *Hylonema*; yet the new genus has not yet been incorporated in a phylogenetic analysis of Heteroderidae, and it is uncertain if a parsimonious scheme will support a hypothesis of the two genera as sister groups. Some preliminary hypotheses of phylogeny generated by computer using the PAUP algorithm (Fink [6] compares various software for phylogenetic analysis) suggest *Hylonema* as a monophyletic group with *Sarisodera, Rhizonema,* and *Bellodera* (sarisoderines) (Baldwin and Schouest, unpubl.). These four genera share uniquely narrow submedial lips in J2 but lack the syncytial host response of ataloderines (*Atalodera, Sherodera, Thecavermiculatus*) and heteroderines (*Heterodera, Afenestrata, Cactodera, Globodera, Punctodera, Dolichodera*). The vulva–anus distance is highly variable among sarisoderines, with *Bellodera* and *Ekphymatodera* retaining wide separation similar to *Cryphodera*; by contrast, *Sarisodera* has closer separation similar to *Hylonema.* While it is tempting to consider *Ekphymatodera* a sister group of *Hylonema,* supported by the shared character of narrow submedial lips fused with the labial disc, the scheme would require independent evolution of the syncytium in the new genus. Parsimonious phylogenetic analyses may therefore indicate *Ekphymatodera* was derived from an ancestor intermediate between sarisoderines and ataloderines. An alternative hypothesis is that *Ekphymatodera* and *Hylonema* are monophyletic with *Afenestrata* and *Heterodera.* These genera all have fusion of submedial lips with the labial disc, bifid spicules, and pore-

like phasmid openings. The submedial lips may not be homologous, however, because they are narrower than in *Heterodera* and *Afenestrata*; in addition, the bifid spicules also occur in an undescribed *Sarisodera*-like nematode from Brazil (Hirschmann, pers. comm.) and *V. californicus*. Similarly, the small phasmids of *Ekphymatodera* and *Hylonema* may not be homologous with those of *Heterodera* and *Afenestrata*, since with light microscopy the openings are relatively large and have a heavy cuticular lining as in *Meloidodera charis*. As in *M. charis*, fine structural examination may support homology of the diminutive phasmids of *Ekphymatodera* and *Hylonema* with lens-like phasmids rather than with the pore phasmids of cyst-forming genera (1). Common ancestry of *Ekphymatodera* and *Hylonema* with *Afenestrata* and *Heterodera* is also confounded by apparent absence of cysts in *Ekphymatodera* and *Hylonema* and a single uninucleate giant cell induced by *Hylonema*. Competing hypotheses of the phylogenetic relationship of these two genera with each other and other Heteroderidae must be tested with investigations of additional characters.

Verutus, while sharing the primitive character of a subequatorial vulva with *Meloidodera*, has a number of genus-specific derived characters including highly specialized lip patterns. Unlike *Meloidodera*, *Verutus* induces a diminutive syncytium in the host (4). The phasmid of *Verutus* also is diminutive relative to other Heteroderidae. In his description of the type species, *V. volvingentis*, Esser (5) noted that juveniles ". . . differ from all other larvae in the Heteroderidae in lacking a detectable phasmid." Subsequently the phasmid opening was shown with SEM in infective juveniles of *V. volvingentis* (11), but preliminary TEM examination suggests that internal structures of the phasmid are reduced or absent (Carta and Baldwin, unpubl.). Minagawa (8) described the phasmid of *V. mesoangustus* J2 as minute. In *V. californicus* phasmids are more evident with the light microscope than in *V. volvingentis*. In adults of *Verutus*, phasmid openings are not apparent (10). The distribution of *Verutus* may also support its monophyly. Both *Verutus volvingentis* and *V. californicus* occur in similar marshy habitats, and the grass host, *Miscanthus sinensis* Anderss., might indicate a similar habitat for *V. mesoangustus*. The occurrence of species in California as well as Florida (5), Japan (8), and Germany (Sturhan, pers. comm.) suggests wide distribution indicative of an ancient ancestor, perhaps evolved when these regions shared a common land mass. Computer-generated phylogenetic analyses of Heteroderidae typically place *Verutus*, with its many unique characters, as an outgroup of all other Heteroderidae.

Monophyly of the ataloderines, *Atalodera*, *Sherodera*, and *Thecavermiculatus*, is strongly supported by a number of characters shared with the new species *A. festucae* and *A. trilineata*. The ataloderines have a unique narrow esophageal gland lobe in the J2 (5), and this may be further reflected in the attenuated subventral glands described in females of *A. festucae* and *A. trilineata*. Ataloderines also are united by consistent features of the lip patterns, they induce syncytia without wall ingrowths (9), and females have a D-layer without infusion of external layers of the cuticle with a dense material (3). Hatching and retention of J2 in females are characteristic of *Thecavermiculatus* (12), and our observations suggest that similar retention may be characteristic, to some extent, of all ataloderines; such retention is particularly characteristic of *A. festucae*. The new species of *Atalodera* extend the range of variation of surface cuticular patterns of females. Previously, SEM patterns indicated broad zigzags in *Atalodera ucri* which are less pronounced in *Thecavermiculatus carolynae* Robbins, 1986 (= *Thecavermiculatus* sp. [11]) and *Sherodera lonicerae* Wouts, 1973 (11). The patterns are particularly shallow and fine textured in *Thecavermiculatus crassicrustatus* Bernard, 1981, in an undescribed species from Alaska collected by E. Bernard, and particularly in *Thecavermiculatus andinus* Golden et al., 1983 (7). In these respects, *A. trilineata* and *A. fes-*

tucae resemble these *Thecavermiculatus* species, although phylogenetic significance of this character is uncertain since patterns of females of Heteroderidae are mosaic in distribution in many groups (e.g., sarisoderines, heteroderines).

The terminal region of ataloderines is variable, having either distinct vulval lips with a pronounced vulval slit and a nearby anus or vulva and anus widely separated and reduced slit and lips. Distinct lips have been shown by SEM to occur in *A. ucri, S. lonicerae, A. trilineata, A. festucae,* and, to a lesser degree, in *T. carolynae* (11) and *T. gracililancea* (12). The elevation of the anus on a terminus above the vulva in *A. festucae* may represent an extreme in a broad transformation series within ataloderines, with *Thecavermiculatus andinus* representing the contrasting extreme. This feature combined with other characters incongruent with ataloderines prompted Wouts to place *T. andinus* in *Dolichodera* (15); conversely, our phylogenetic analysis using PAUP indicates *T. andinus* as a sister group of all other ataloderines with the broad vulva–anus distance considered a primitive condition as in *Cryphodera.* The broad vulva–anus distance is not only conserved in *T. andinus* but in many sarisoderines. We agree witih Wouts that additional investigation of *T. andinus* is needed to test hypotheses of its phylogenetic relationships.

Lip patterns of *A. festucae* and *A. trilineata* include an elongate labial disc and fusion of lateral lips with the labial disc, patterns typical of ataloderines, including *T. andinus.* Whereas some ataloderines are highly variable within populations with respect to fusion or lack of fusion between adjacent submedial lips (11), patterns of the new species are relatively consistent. Lip patterns of males of *A. festucae* resemble those of *A. ucri,* with fusion of all lips and with few or no blocks on the head region. This is in contrast to blocks on males of other ataloderines including *Sherodera lonicerae, Thecavermiculatus gracililancea,* and *T. carolynae* (11,13; Baldwin, unpubl.), which we interpret as a primitive state. Blocks on male heads are also present in certain species of *Meloidodera, Cryphodera, Bellodera,* and genera of the outgroup Hoplolaimidae (2,10).

Since *A. trilineata* and *A. festucae* are similar and came from adjacent type localities, attempts were made to propagate each on the type host of the other. While we were successful in obtaining greenhouse cultures on type hosts, neither species developed on the host of the other, and greenhouse cultures remained pure.

Different heteroderids often occur in close proximity. The two species of *Ataloderа* have the same type locality, *Verutus* and *Ekphymatodera* both occur in Yosemite Valley, and type localities of *Sherodera lonicerae* and *Sarisodera hydrophila* are in close proximity. This curious distribution probably cannot wholly be attributed to patterns of collecting. In California, many sites of heteroderids are at points where runoff may concentrate soil and debris from higher elevations, and persistent moisture in such regions may sustain diverse hosts and their parasites during relatively dry periods. Other more specific requirements common to heteroderids may not be recognized.

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