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Cactodera eremica n. sp., *Afenestrata africana* (Luc et al., 1973) n. gen., n. comb., and an Emended Diagnosis of *Sarisodera* Wouts and Sher, 1971 (Heteroderidae)

J. G. Baldwin and A. H. Bell[1]

Abstract: Systematic contributions to Heteroderidae include description of *Cactodera eremica* n. sp., an emended diagnosis of *Sarisodera* Wouts and Sher, 1971, and proposal of a new genus and new combination, *Afenestrata africana* (synonym *Sarisodera africana* Luc et al., 1973). *Cactodera eremica*, from the roots of shadscale in Utah, most closely resembles *Cactodera thornei* (Golden and Raski, 1977) but differs by the presence of a finely striated cuticle, a fine surface pattern on eggs, a shorter female stylet, distance of the DGO from the stylet, vulval slit, and smaller diameter of circumfenestra, as well as a shorter tail in second-stage juveniles. The response of the host to *C. eremica* is similar to other *Heterodera* sensu lato including a large syncytium with wall ingrowths. The diagnosis of *Sarisodera* is emended to exclude cysts, which do not form in the type species, *S. hydrophila*. *Afenestrata africana* differs from *S. hydrophila* by the formation of cysts, the dorsal position of the anus in females, the shorter stylet, and a pore-like phasmid opening in second-stage juveniles. In addition, the lip pattern of males and juveniles is characterized by a greater degree of fusion of lip parts, the host response is a syncytium (versus a single uninucleate giant cell in *S. hydrophila*), and the cuticle is thinner and lacks a D layer. Unlike *Heterodera*, the cyst of *Afenestrata* lacks fenestrae.

Key words: comparative morphology, cyst nematodes, giant cell, *Heterodera*, histopathology, host response, scanning electron microscopy, taxonomy.

Cactodera Krall and Krall, 1978 and *Sarisodera* Wouts and Sher, 1971 were originally described as cyst-forming nematodes of Heteroderidae. *Cactodera* is included among four genera of *Heterodera* sensu lato which some investigators consider to comprise the subfamily, Heteroderinae. A number of systematists consider *Sarisodera* sufficiently distinctive from other cyst nematodes to place it in a separate subfamily, Sarisoderinae (8,19).

Presently we are investigating phylogenetic relationships among these and other Heteroderidae. These studies involve evaluation of classical characters as well as a search for new characters, and include comparative detailed morphology of lip patterns and other surface structures (15,16), fine structure of phasmids (2), layering of the female cuticle (1,6) and host responses (11–14).

Among species included in these phylogenetic studies is an undescribed *Cactodera* from roots of *Atriplex confertifolia* (Torr. and Frem.) Wats. (shadscale) collected from a desert habitat in Utah. The species is described herein as *Cactodera eremica* n. sp. (eremos, Gr. = desert, wilderness). Ongoing investigations also include the two species which comprise *Sarisodera*, *S. hydrophila* Wouts and Sher, 1971 (20) and *S. africana* Luc et al., 1973 (9). Contrary to the original description, we have found that females of the type species, *S. hydrophila*, do not develop into cysts. On this basis, we emend the diagnosis of *Sarisodera* to accommodate *S. hydrophila* alone and propose *Afenestrata* n. gen. (a, Gr. = without; fenestra, L. = window) to accommodate *Afenestrata africana* (= *Sarisodera africana* Luc et al., 1973).

Materials and Methods

Females, cysts, males, second-stage juveniles, and eggs of *C. eremica* were obtained from the type locality in Utah, fixed in 5% formalin, and infiltrated with glycerin for light microscope (LM) examination. Additional specimens were cultured on shadscale at 20–30 C in the greenhouse. Paratypes of *Cactodera thornei* (Golden and Raski, 1977) Mulvey and Golden, 1983[2]

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[2] Mulvey and Golden (10) first published the combination *Cactodera thornei* (synonym *Heterodera thornei* Golden and Raski, 1977) but attributed the combination to Krall and Krall, 1978 (8). However, Krall and Krall (8) apparently were unaware of this species and did not include it in their study.

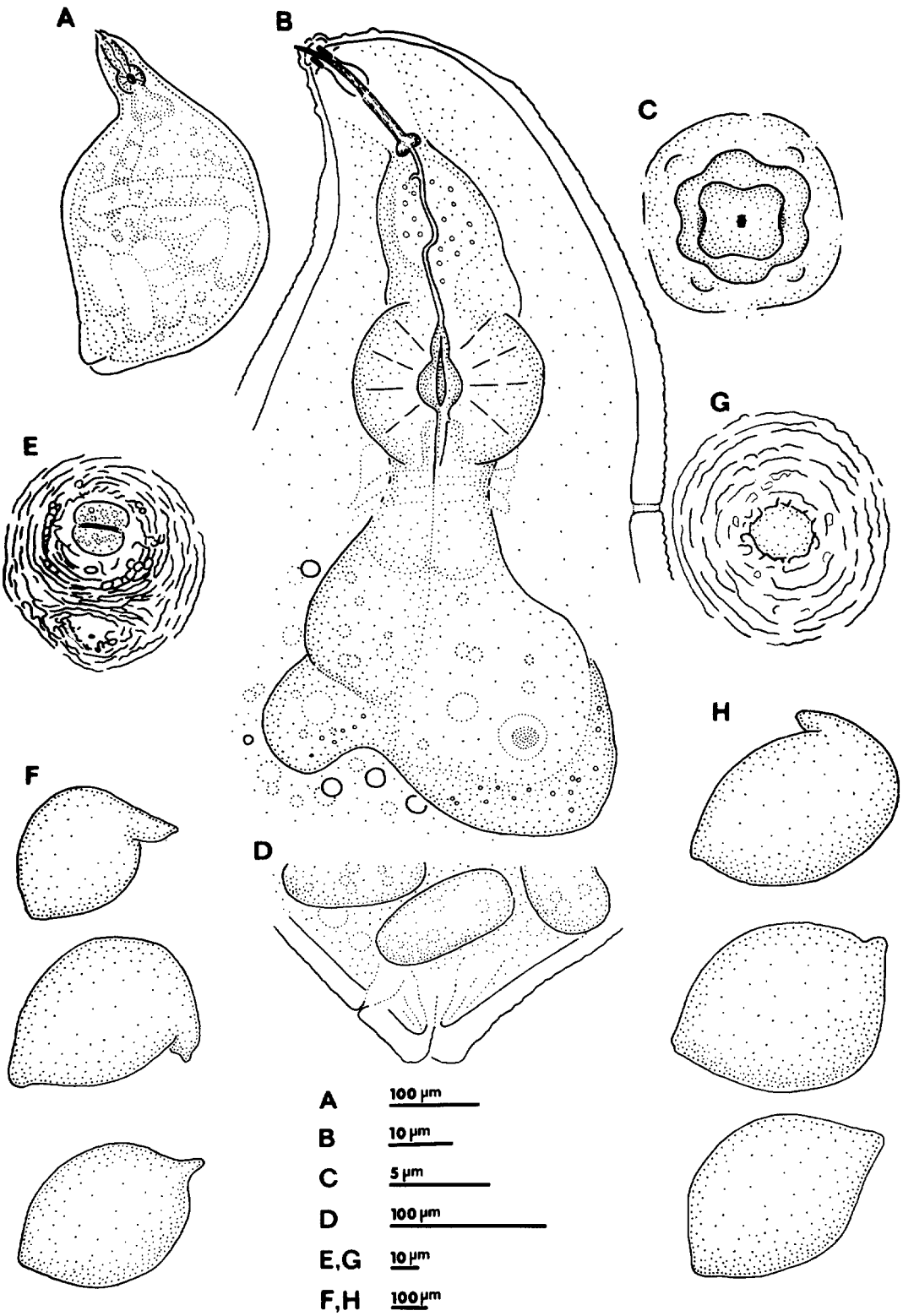


FIG. 1. Drawing of females of *Cactodera eremica* n. sp. A) Entire specimen (lateral). B) Anterior portion (lateral). C) Face view as observed with SEM. D) Terminal protuberance showing position of anus and vulva. E) End view of cone region of mature female. F) Outline of females. G) End view of cone region of cysts. H) Outline of cysts.

were borrowed for LM comparison. Although the type habitat apparently has been destroyed by construction and fresh topotypes of *C. thornei* are not available, a few unmounted specimens were provided for scanning electron microscopy (SEM) from the UCDNC mass collection, Davis, California. Paratypes of *S. hydrophila* and *A. africana* were obtained for LM comparisons. In addition, freshly collected topotypes of both species were processed as for *C. eremica*.

Specimens including females, cysts, males, juveniles, and eggs were fixed and infiltrated with glycerin for LM and SEM as previously described (4). Specimens for SEM were sputter-coated with 20 nm gold palladium and examined with a JEOL JSM-35C electron microscope at 5 kV.

Root pieces of shadscale infected with *C. eremica* were processed for LM examination of host responses as previously reported (11). Roots were fixed in 3% glutaraldehyde, dehydrated in acetone, embedded in Spurr's epoxy, sectioned (2 μm), and stained with toluidine blue. In the case of the type host of *A. africana*, Guinea grass (*Panicum maximum* Jacq.), only infected roots fixed in lactophenol were available. Lactophenol was gradually replaced with 5% aqueous formalin solution during a 170-hour period. Dehydration, embedding, sectioning, and staining were as for shadscale.

Systematics

Cactodera eremica n. sp.
(Figs. 1–18)

Female

Measurements (20 paratypes): L (including "neck") = 373–676 μm (mean 546.3 μm, 95% confidence interval ± 36.3); width = 233–495 μm (352 μm ± 36.9); neck length = 70.0–132.8 μm (101.61 μm ± 7.28); stylet (n = 13) = 23.7–27.4 μm (25.53 μm ± 0.82); DGO (n = 10) = 3.0–4.8 μm (3.90 μm ± 0.41); median bulb length (n = 10) = 25.9–33.3 μm (29.78 μm ± 1.97); median bulb width (n = 10) = 22.2–33.3 μm (29.03 μm ± 2.44); vulva–anus distance (lateral view) (n = 18) = 43.2–63.0 μm (51.17 μm ± 3.01); thickness of cuticle = 3.7–11.8 μm (7.58 μm ± 1.10); a = 1.2–2.8 (1.61 ± 0.15); o (n = 10) = 5.4–7.9 (6.69 ± 0.604); vulva length (10 cones) = 14.0–19.0 μm (15.81 μm ± 1.32).

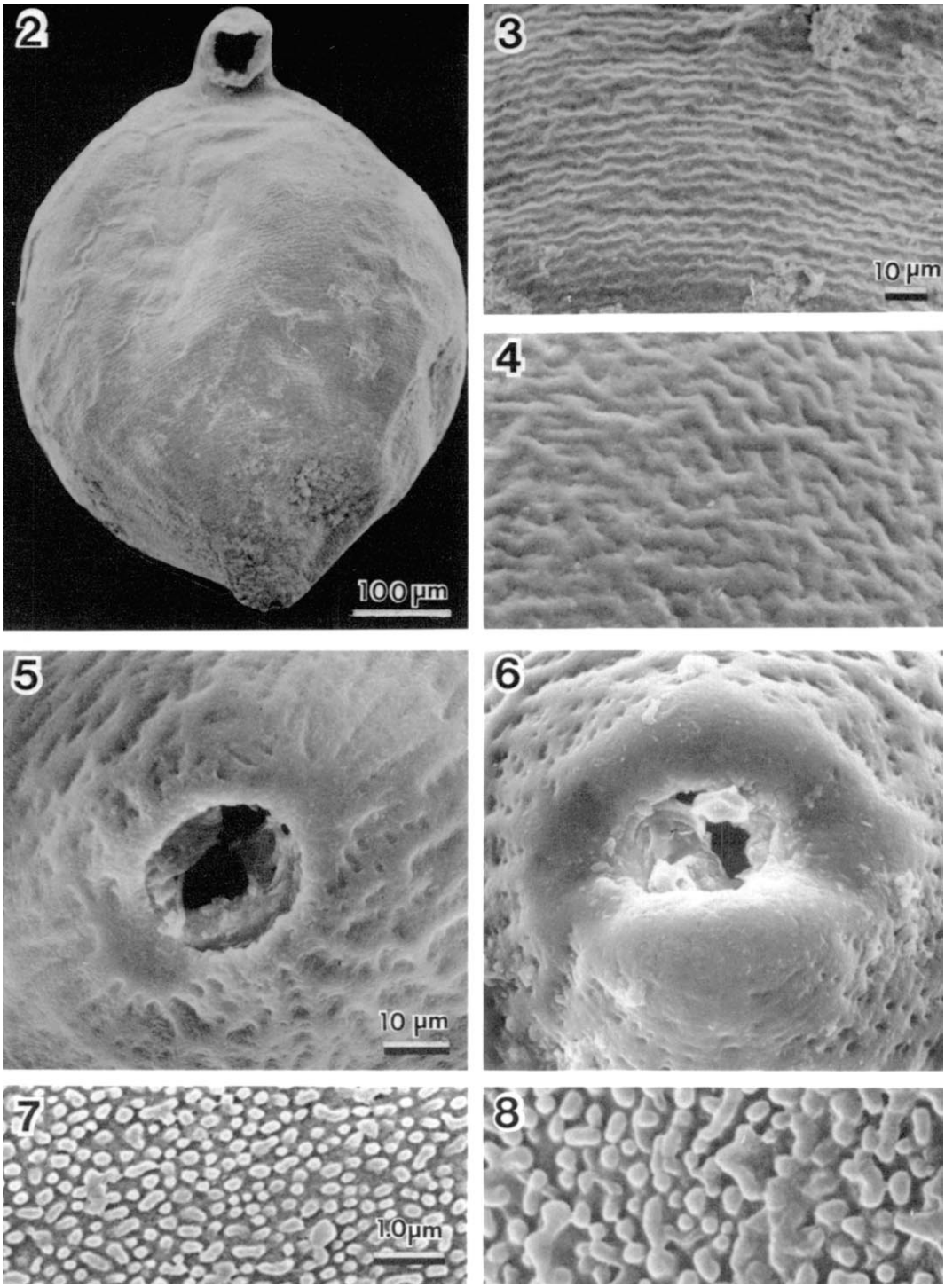
Description: Body contour varying from lemon shaped or nearly spherical in large specimens, to asymmetric with strong dorsal curvature in smaller individuals. Small terminal protuberance. Neck usually clearly offset and reflexed either dorsally or ventrally. Freshly collected specimens pearly white becoming tan after fixation in formalin. Cuticle thin with subsurface punctations; surface generally with wavy transverse striations, but head region relatively smooth without pronounced striations. A cement-like material encapsulates head and neck region, generally obscuring excretory pore which occurs at level posterior to median bulb. Head region with elevated labial disc and four submedial lobes. Anteriormost lip annule with six fused lobes. Stylet generally slightly curved dorsally. Ovaries paired. Anus small but conspicuous with LM, near base of protuberance. Surface of perineal region pitted with coarse broken striae, thin somewhat transparent ovals on each (dorsal and ventral) side of narrow vulva slit.

Holotype: L (including neck) = 380 μm; width = 250 μm; neck length = 49.2 μm; stylet = 23.0 μm; DGO = 3.3 μm; median bulb length = 33.3 μm; median bulb width = 26.6 μm; excretory pore from anterior end = 106.5 μm; vulva–anus distance = 49.6 μm; cuticle thickness = 7.4 μm; median bulb length/median bulb width = 1.25; excretory pore % = 2.63. Small, apparently young female as in general description. Body lemon shaped but with prominent dorsal curvature, light tan color. Neck region with little cement-like material, and laterally oriented showing distinct excretory pore.

Cyst

Measurements (n = 10): L, including neck = 530–810 μm (620.0 μm ± 70.1); width = 290–590 μm (434.0 μm ± 78.7); a = 1.2–1.9 (1.5 ± 0.23); cuticle thickness = 3.3–5.6 μm (4.36 μm ± 0.51); circumfenestra diameter (nine cones) = 14.4–25.2 μm (20.6 μm ± 3.2).

Description: Cysts brown, typically lemon shaped; cement-like material usually persistent in neck region. Cyst striated with striae becoming broken and somewhat



FIGS. 2–8. SEM micrographs of *Cactodera* spp. 2) Cyst of *C. eremica* n. sp. 3) Cuticle pattern of *C. eremica* n. sp. showing striations. 4) Cuticle pattern of *C. thornei* showing wavy, somewhat zig-zag pattern. Scale same as Figure 3. 5) Circumfenestra of newly formed cyst of *C. eremica* n. sp. 6) Circumfenestra of newly formed cyst of *C. thornei.* Scale same as Figure 5. 7) Pattern of surface of egg of *C. eremica* n. sp. 8) Pattern on surface of egg of *C. thornei.* Scale same as Figure 7.

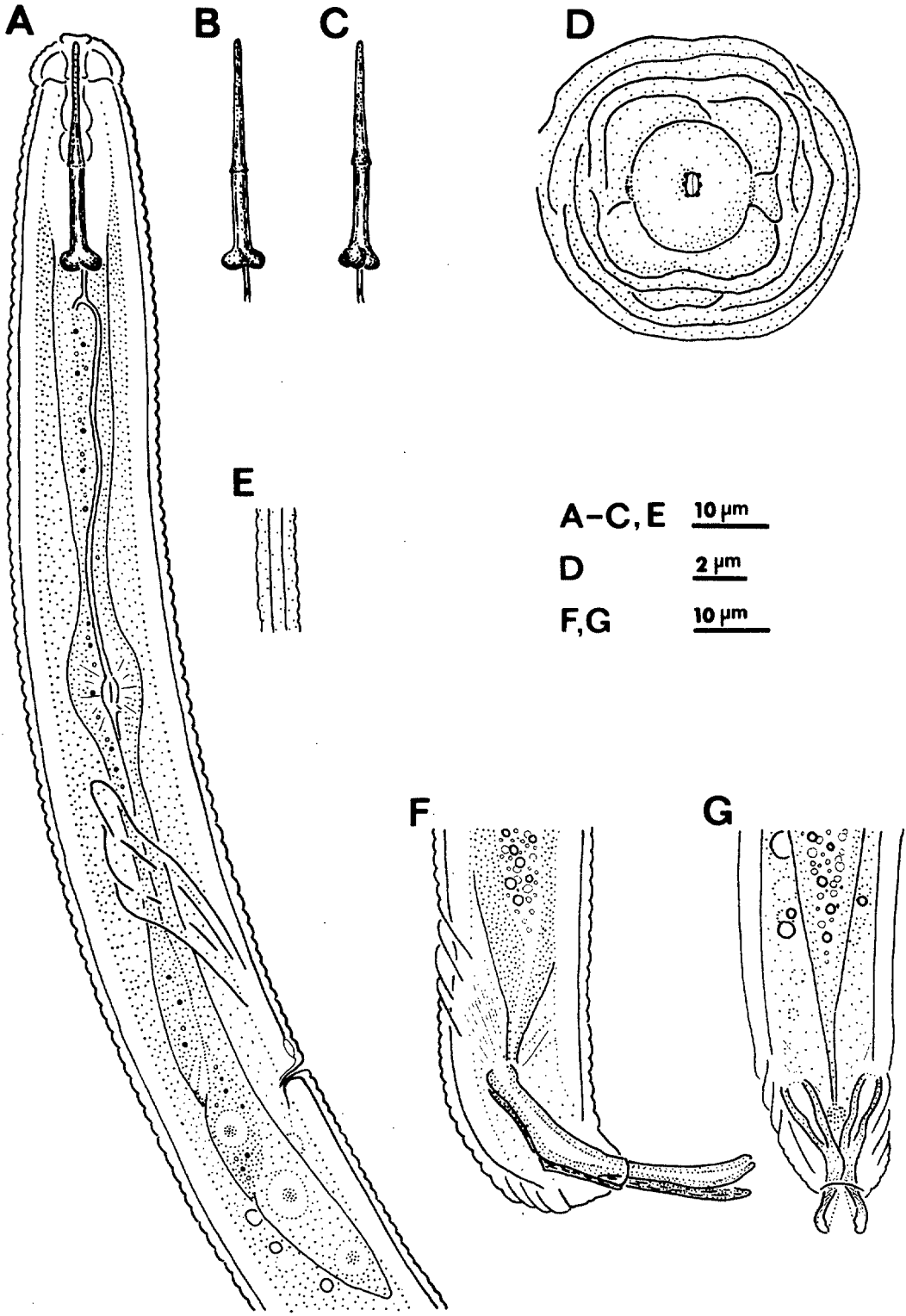


FIG. 9. Drawing of males of *Cactodera eremica* n. sp. A) Anterior portion (lateral). B) Stylet (dorsal). C) Stylet (ventral). D) Face view as observed with SEM. E) Lateral field. F) Tail (lateral). G) Tail (ventral).

wavy posteriorly. Cone region circumfenestrate (about 25 μm d) and abullate. Denticles not observed; anus inconspicuous.

Male

Measurements (15 paratypes): L = 950–1,320 μm (1,170.0 μm ± 73.0); width = 22.0–29.0 μm (26.63 μm ± 1.57); stylet = 25.5–30.5 μm (28.53 μm ± 0.82); stylet shaft and knobs = 13.0–16.0 μm (14.37 μm ± 0.45); DGO = 3.0–4.5 μm (3.40 μm ± 0.35); esophagus length = 165.0–205.0 μm (183.33 μm ± 7.88); excretory pore from anterior end = 125.0–155.0 μm (142.67 μm ± 6.77); testis length = 605.7–757.1 μm (745.49 μm ± 37.87); spicule length = 33.0–42.0 μm (38.23 μm ± 1.48); gubernaculum length = 9.5–13.5 μm (10.60 μm ± 0.73); a = 39.29–48.89 (43.39 ± 1.31); b = 6.36–9.81 (7.62 ± 0.52); b′ = 5.28–10.00 (6.68 ± 0.64); m = 0.48–0.53 (0.50 ± 0.01); O = 8.62–15.79 (11.94 ± 1.09); T % = 57.40–68.80 (63.76 ± 2.04); excretory pore % = 10.00–15.26 (12.30 ± 0.94).

Description: Body cylindrical, tapering anteriorly; posterior half of heat-killed specimens twisted about 90°. Head region slightly offset. Lip region consisting of round labial disc, surrounded by squarish first lip annule and 7–9 discontinuous head annulations. First lip annule is only rarely separated into full complement of four large submedial lips (sectors) and a pair of small lateral lips. In most males, first annule is continuous (not separated into lips); in other individuals, various intermediate degrees of fusion and separation occur. Each amphid opening, a very small lateral slit at the periphery of the labial disc. Lateral field with four incisures, center ridge not areolated; outer ridges often areolated anteriorly and posteriorly. Cephalids not observed. Hemizonid about 1½ annules long; typically immediately anterior to excretory pore. Subventral stylet knobs sloping posteriorly; dorsal knob large, flattened anteriorly. Median bulb narrow and elongate, gland lobe small and narrow, esophago-intestinal junction occurs dorsally. Testis highly variable in length filled with large irregularly shaped sperm. Bifid spicules emerge terminally or nearly so; tail very short or absent. Short spicule sheath distinctive by absence of annulation. Phasmid openings not observed.

Second-stage juvenile

Measurements (20 paratypes): See Table 1.

Description: Body cylindrical and tapered, especially posteriorly. Head region nearly continuous with body contour, having about five annules. En face pattern consistent among individuals, including a dorso-ventrally elongate labial disc surrounded by six lips of first lip annule. Lateral lips greatly reduced. Four lateral lines, outer two ridges partially areolated, particularly anteriorly and posteriorly. Cephalids and caudalid not observed; hemizonid about ½ annule anterior to excretory pore. Stylet knobs robust, rounded. Esophageal gland lobe distinct dorsally; subventral region elongate but inconspicuous; esophago-intestinal junction ventral and typically just posterior to level of excretory pore. Phasmid opening pore-like.

Egg

Measurements (n = 15): L = 99–115 μm (104.5 μm ± 1.5), width = 48–54 μm (50.3 μm ± 0.5), L/W ratio = 1.9–2.4 (2.08 ± 0.62).

Description: Surface of egg with very fine punctations visible with LM; punctations resolved as minute tubercles (about 0.2 × 0.5 μm) with SEM (Fig. 7).

Diagnosis and relationships

Cactodera eremica most nearly resembles *C. thornei,* but there are a number of distinguishing characters. The cuticle pattern of females of *C. eremica* consists of fine striations, whereas that of *C. thornei* is coarser and approaches a more wavy zig-zag pattern (Figs. 3, 4). The female stylet is slightly

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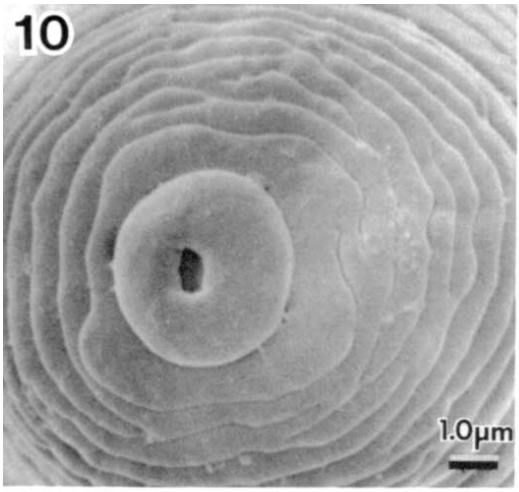
FIGS. 10–15. SEM micrographs of *Cactodera eremica* n. sp. 10) Face view of most common male lip pattern in which six lips are fused. 11) Face view of aberrant male lip pattern in which only one pair of submedial lips is fused. Scale same as Figure 10. 12) Face view of aberrant male lip pattern in which no lips are fused. Scale same as Figure 10. 13) Lateral view of male shown in Figure 11. 14) Ventrolateral view of male tail region showing protracted spicules. 15) Face view of second-stage juvenile. Scale same as Figure 10.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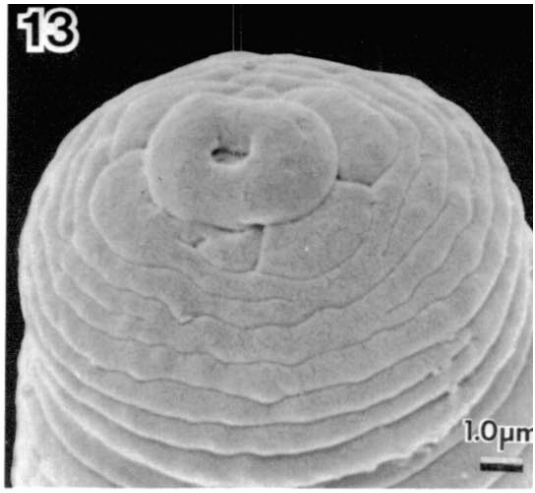
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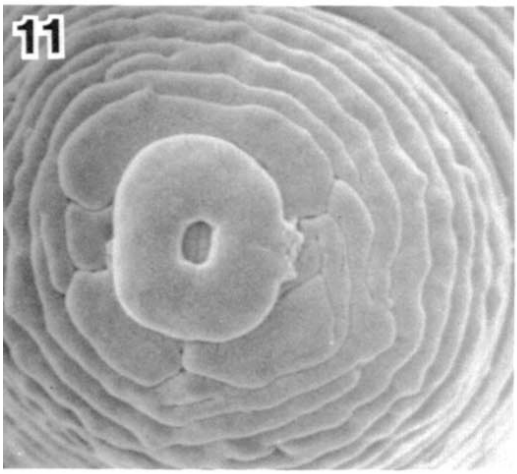
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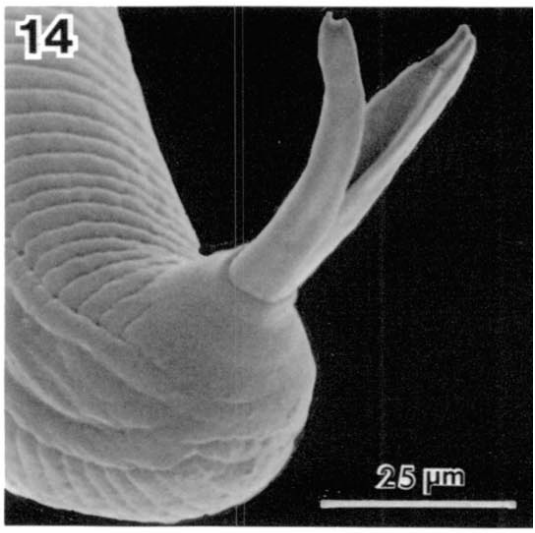
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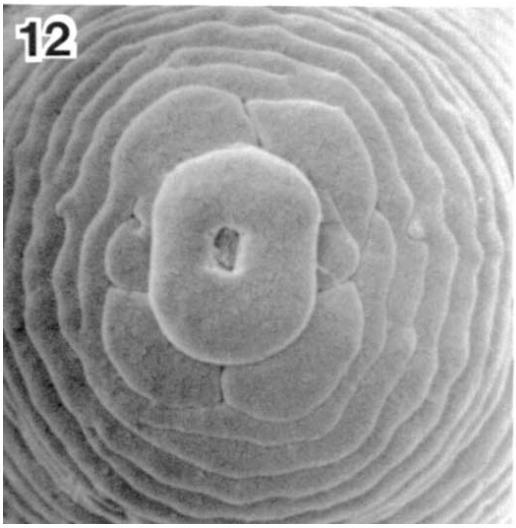
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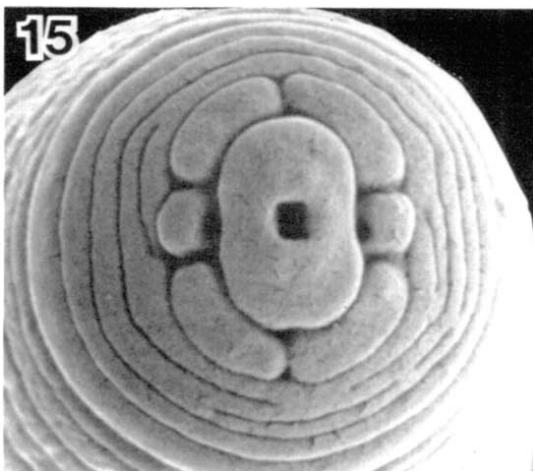
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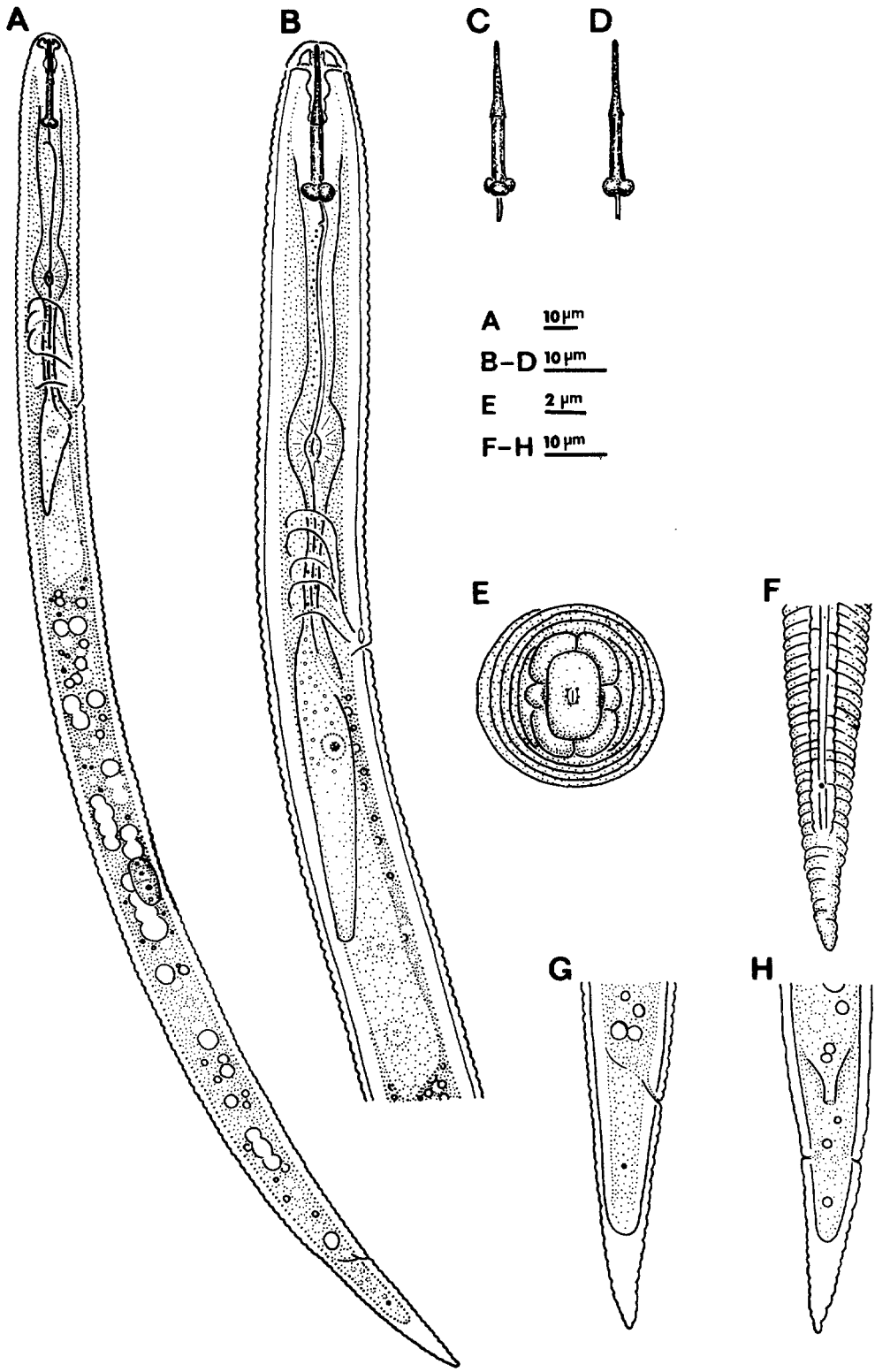


FIG. 16. Drawings of second-stage juveniles of *Cactodera eremica* n. sp. A) Entire specimen (lateral). B) Anterior portion (lateral). C) Stylet (dorsal). D) Stylet (ventral). E) Face view as observed with SEM. F) Tail surface with lateral field (lateral). G) Tail (lateral). H) Tail (ventral).

TABLE 1. Measurements of second-stage juveniles of *Cactodera eremica* (n = 20).

Character	Range	Mean	Confidence interval 95%		Confidence interval 99%		Standard deviation
Linear (μm)							
Body length	440.0–510.0	480.00	±	0.01	±	0.02	0.023
Body width	18.5–22.5	20.85	±	0.53	±	0.80	1.125
Stylet length	25.0–28.0	26.53	±	0.35	±	0.53	0.752
Stylet shaft and knobs	12.5–14.5	13.58	±	0.28	±	0.42	0.591
DGO	3.5–6.0	4.43	±	0.32	±	0.49	0.693
Esophagus length	155.0–205.0	175.80	±	4.98	±	7.56	10.650
Excretory pore to anterior end	95.0–115.0	103.75	±	2.62	±	3.97	5.590
Tail length	36.5–47.5	40.43	±	1.34	±	2.02	2.853
Tail terminus length (hyaline region)	17.0–23.5	18.13	±	0.89	±	1.34	1.891
Phasmid below anus	7.0–18.0	12.35	±	1.31	±	1.98	2.791
Genital primordium to anterior end	260.0–320.0	295.55	±	7.57	±	11.49	16.185
Ratios							
a	20.9–23.8	23.05	±	0.44	±	0.66	0.929
b	2.5–3.1	2.74	±	0.09	±	0.14	0.193
b′	2.6–3.7	3.23	±	0.12	±	0.18	0.254
c	10.1–12.5	11.91	±	0.36	±	0.54	0.764
c′	2.8–3.6	3.25	±	0.08	±	0.13	0.180
Percentages							
m	46.3–52.9	50.81	±	0.92	±	1.39	1.963
O	12.7–22.6	16.71	±	1.30	±	1.97	2.773
Excretory pore	20.9–23.0	21.55	±	0.44	±	0.67	0.944
Genital primordium	54.0–63.5	58.80	±	5.91	±	8.97	12.630

shorter in *C. eremica* (24–27 vs. 28–31 μm), distance of the DGO from stylet knobs is less (3.0–4.8 vs. 5.2–6.0 μm); the vulva slit is shorter (14–16 vs. 16–19 μm), and the diameter of the circumfenestra in cysts is 14–25 vs. 31–36 μm. Males are usually smaller in *C. eremica* (950–1,320 vs. 1,315–1,708 μm), and the DGO is less (3.0–4.5 vs. 5.5–8.0 μm). Second-stage juveniles of *C. eremica* have a shorter tail (36–47 vs. 49–64 μm) and shorter hyaline region (17–24 vs. 23–28 μm). The surface of eggs in both species is covered with minute tubercles. However, when eggs of both species are prepared under identical conditions (e.g., glycerin infiltration) the patterns are finer and tubercles smaller (about 0.2 × 0.5 μm) in *C. eremica* than in *C. thornei* (about 0.3 × 1.2 μm) (Figs. 7, 8).

Type specimens

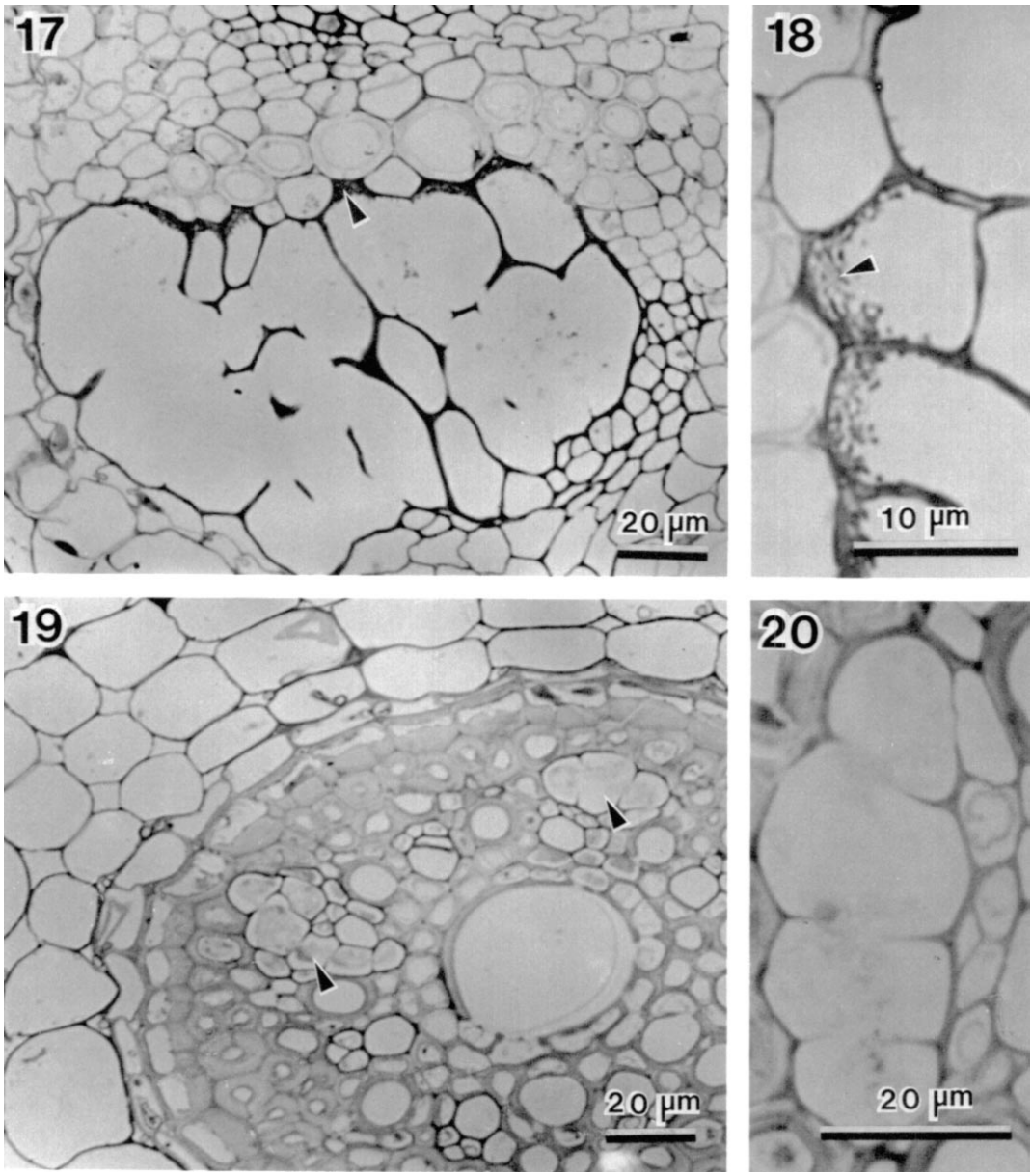
Collected by A. H. Bell on 7 June 1983. Holotype female (catalog number 55) UCRNC, Department of Nematology, University of California, Riverside. Paratypes (66 females, 82 males, 44 second-stage juveniles, 45 cysts) distributed in type collections as follows: six females, three males, eight juveniles, UCDNC, Division of Nematology, University of California, Davis; five females, five males, seven juveniles, six cysts, USDANC Nematology Investigations, Beltsville, Maryland; four females, three males, seven juveniles, six cysts, Rothamsted Experimental Station, Harpenden, England; five females, six males, seven juveniles, Museum national d'Histoire naturelle, Laboratoire des Vers, Paris, France; remaining type material (46 females, 65 males, 15 juveniles, 33 cysts) in the UCRNC, Department of Nematology, University of California, Riverside.

Type habitat, host, and locality

Roots and surrounding soil of shadscale (*Atriplex confertifolia*) near Fairfield, Cedar Valley, Utah.

Host response

Cactodera eremica induces large syncytia on shadscale similar to those associated with other *Heterodera* sensu lato (7) (Fig. 17). The syncytium generally disrupts most of the vascular cylinder, and distinct wall in-



FIGS. 17–20. LM cross sections. 17) Syncytium induced by *Cactodera eremica* n. sp. in *Atriplex confertifolia*. Arrow indicates position of wall ingrowths. 18) Wall ingrowths (arrow) in syncytium induced by *C. eremica* n. sp. in *A. confertifolia*. 19) Syncytia (arrows) induced by *Afenestrata africana* n. gen., n. comb. in *Panicum maximum*. 20) Syncytium induced by *A. africana* n. gen., n. comb. in *P. maximum*. Note absence of wall ingrowths.

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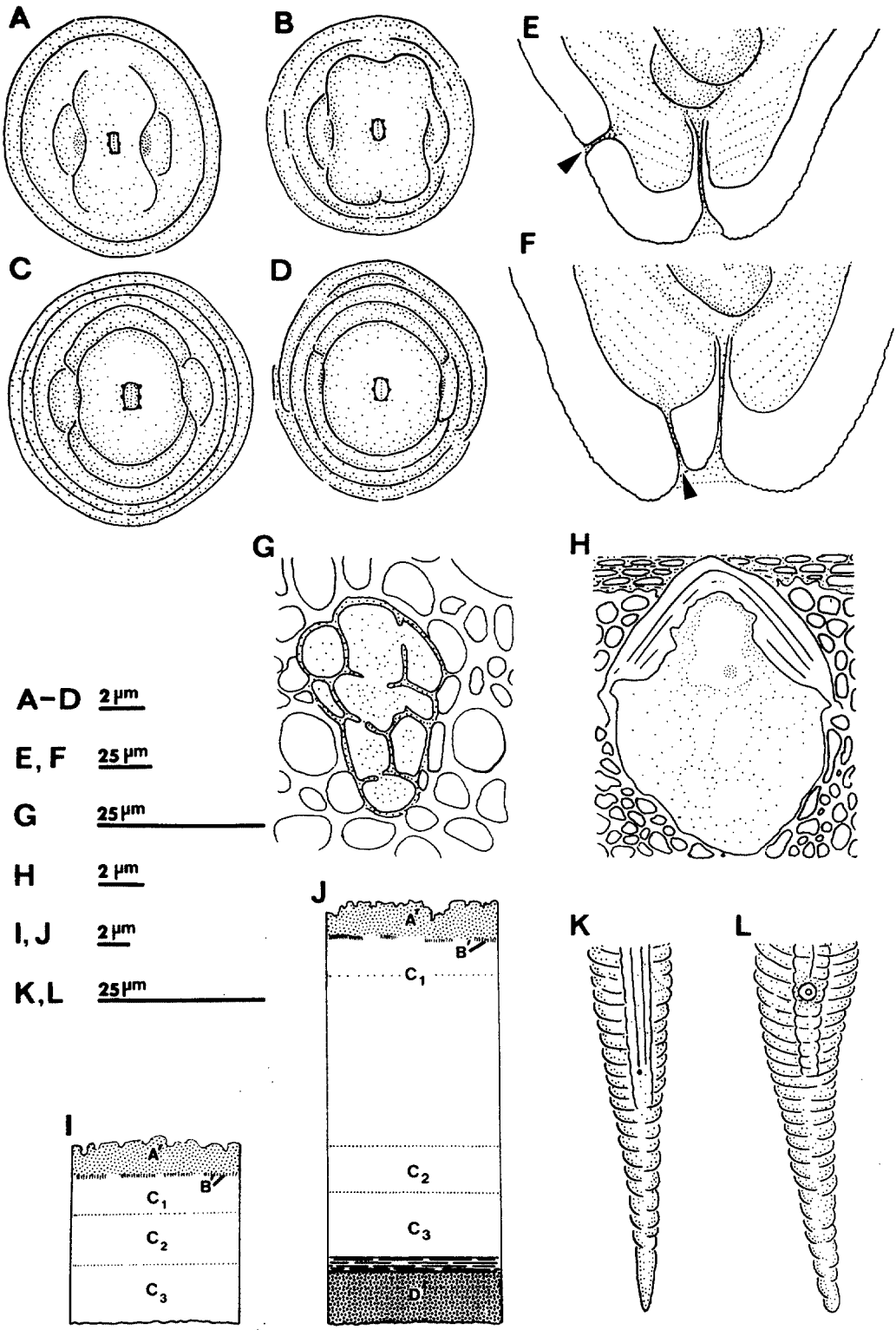
FIG. 21. Diagram comparing certain characters of *Afenestrata africana* n. gen., n. comb. and *Sarisodera hydrophila* Wouts and Sher, 1971. A) Lip pattern of second-stage juvenile of *A. africana*. B) SEM of lip pattern of male of *A. africana*. C) SEM of lip pattern of second-stage juvenile of *S. hydrophila*. D) SEM of lip pattern of male of *S. hydrophila*. E) Lateral view of cone area of *A. africana*. Arrow indicates position of anus. F) Lateral view of cone area of *S. hydrophila*. Arrow indicates position of anus. G) Syncytium induced by *A. africana*. H) Single uninucleate giant cell induced by *S. hydrophila*. I) Layering of body wall cuticle in midregion of female of *A. africana* lacking a D layer. J) Layering of body wall cuticle in midregion of female of *S. hydrophila* including a D layer. K) Lateral view of tail region of second-stage juvenile of *A. africana* including pore-like



phasmid. L) Lateral view of tail region of second-stage juvenile of *S. hydrophila* including lens-like phasmid. Drawings A–D prepared from Othman and Baldwin (16), H from Mundo and Baldwin (12), and I, J from Cliff and Baldwin (6) and Baldwin (1).

growths occur primarily in walls adjacent to xylem vessels (Fig. 18). This is in contrast to the syncytium induced by *Atalodera* spp. in which ingrowths are absent (11). The presence of ingrowths in *Cactodera* spp. strengthens the hypothesis of homoplasy between syncytia of *Atalodera* and *Heterodera* sensu lato (14).

Characterization of *Saridodera hydrophila*, Emendation of *Sarisodera*, and *Afenestrata africana* n. gen., n. comb.

Sarisodera hydrophila Wouts and Sher, 1971

Our measurements of paratypes and topotypes of *S. hydrophila* generally conform to those of Wouts and Sher (20). The most important discrepancy concerns the original description of *S. hydrophila* as possessing a "yellow to reddish brown cyst" which does not develop fenestrae around the vulva (20). However, Wouts and Sher (20) do not include a detailed description of the "cysts," and no paratype slides are designated as cysts. During the past 6 years, the type locality of *S. hydrophila*, as well as populations at additional sites, have been sampled numerous times using standard cyst collection techniques. Although frequently large numbers of females, males, and juveniles are present, cysts or persistent cuticles retaining eggs have never been recovered (1). Misinterpretation of a mature or moribund female as a cyst might occur because the female's body wall cuticle is often more than twice the thickness of most other heteroderids (1,17) (Fig. 21J). This impression may be enhanced in paratypes of moribund females which were fixed in dark-staining acid fuchsin–lactophenol and thus might appear tanned.

On the basis of these observations we emend the diagnosis of *Sarisodera* to exclude the presence of a cyst.

Sarisodera

Wouts and Sher, 1971 (20); Luc et al., 1973; Mulvey and Golden, 1983; subfamily Heteroderinae Skarbilovich, 1947; Wouts and Sher, 1971.

Diagnosis emended

Females: Cuticle with lace-like pattern. Vulva sunken into terminal vulva cone. Anus on upper inside of dorsal vulva lip. After death, cysts are not formed and there is no fenestration around vulva.

Male: Length, 1.5 mm or less. Region immediately behind lips not constricted. No longitudinal striation on basal lip annule. Tail absent. Spicule length more than 30 μm.

Second-stage juvenile: Stylet more than 38 μm. Esophageal glands fill body width. Phasmid duct with lenslike ampulla.

Discussion

Additional characteristics of *S. hydrophila* not included in the original description may prove useful in comparison with other heteroderids. For example, the lip region of second-stage juveniles of *S. hydrophila*, as observed with SEM, is slightly modified from the primitive hexaradiate pattern (3) by fusion of adjacent submedial lips, and males are further modified by fusion of all six lips forming a continuous annule around the labial disc (16) (Fig. 21 C, D). The labial disc of males is not elevated and was originally considered to be absent (20). SEM confirms the observation of Wouts and Sher (20) that no longitudinal striations occur on the basal lip annule of males.

We have shown previously that the layering of the female body wall cuticle in *S. hydrophila* is unique among Heteroderidae (3), and this is confirmed by additional comparisons with species of *Rhizonema, Verutus, Thecavermiculatus, Cactodera,* and *A. africana* (6) (Fig. 21I, J).

The host response of *S. hydrophila* has been shown to be a single uninucleate giant cell, regardless of host species (12). This response is similar to certain heteroderids which do not form cysts, but is not known to occur among genera which form cysts (Figs. 17, 19, 21G, H).

Afenestrata africana n. gen., n. comb. = *Sarisodera africana* (Luc, Germani, and Netscher, 1973) (Figs. 19–21)

Diagnosis

Genus *Afenestrata* n. gen., subfamily Heteroderinae Skarbilovich, 1947; Wouts and Sher, 1971.

Female: Cuticle with lace-like pattern of ridges. Tan to brown cyst formed from female after death. Vulva sunken into ter-

minal cone, lacking fenestration or bullae; anus dorsal to vulval lip.

Male: Spicules terminal, enclosed by sheath; tail absent.

Second-stage juvenile: Stylet less than 38 μm long; pore-like phasmid opening.

Type and only species: Afenestrata africana (Luc, Germani, and Netscher, 1973) n. comb. (synonym: *Sarisodera africana* Luc, Germani, and Netscher, 1973).

Measurements

Our measurements and light microscope observations of paratypes and topotypes of *A. africana* conform to those of Luc et al. (9) and Taylor and Luc (18). Measurements after Luc et al., 1973 (9).

Cysts (n = 40): L = 0.60 mm (0.44–0.84); l = 366 μm (260–510); L/l = 1.68 (1.18–2.00).

Males (n = 24): L = 0.885 mm (0.68–0.97); a = 28.2 (24.2–35.2); b = 7.9 (6.2–10.1); b′ = 4.7 (3.6–6.0); stylet = 26.5 μm (24.5–28); m = 53.5 (52–61); O = 14.7 (12.0–16.0); diameter (at midbody) = 30.5 μm (25–35); spicules = 40 μm (38–44); gubernaculum = 11 μm (9.5–13).

Juveniles (second stage) (n = 30): L = 0.375 mm (0.33–0.42); a = 20.3 (18.3–23.5); b = 4.4 (3.9–4.9); b′ = 2.2 (1.9–2.5); c = 6.9 (6.2–7.5); c′ = 4.6 (4.3–5.5); stylet = 21 μm (19–22.5); m = 45.2 (44.1–46.6); O = 14.3 (12.5–18.3); diameter (at midbody) = 18.7 μm (16–20).

Eggs (n = 50): L = 105 μm (92–110); l = 40.5 μm (38–46); L/l = 2.6 (2.1–2.91).

Holotype (cyst): L = 0.74 mm; l = 0.49 μm; L/l = 1.5.

Allotype (male): L = 0.840 mm; a = 25.5; b = 72; b′ = 4.8; stylet = 26 μm; m = 54; diameter (at midbody) = 33 μm; spicules = 39 μm; gubernaculum = 13 μm.

Discussion

This species cannot be accommodated within the genus *Sarisodera* as defined by our emended diagnosis. Among species with a cyst (e.g., *Heterodera, Cactodera, Globodera, Punctodera, Ephippiodera,* and *Dolichodera*), *A. africana* is most similar to *Heterodera* spp. with respect to overall shape of females. However, *Heterodera* is diagnosed as having a vulval cone which is "bifenestrate, circumfenestrate, or ambifenestrate" (10), whereas *A. africana* lacks fenestrae. We believe that species lacking fenestrae are best accommodated in a separate genus because they lack a significant derived character that is shared among every other cyst-forming genus. On this basis, and in light of additional unique characters discussed below, we propose *Afenestrata* n. gen.

Afenestrata africana produces a deeply tanned lemon-shaped, egg-filled cyst similar to that of *Heterodera.* However, the cone area is distinct from *Heterodera* in that the cuticle in this region is unusually thick and does not break to form fenestrae (9). Contrary to *S. hydrophila,* the anus of *A. africana* is not situated within the vulval depression but occurs dorsal to the lips (e.g., vulval–anal distance = 68 μm) (9) (Fig. 21E, F).

Males of *A. africana* resemble those of *S. hydrophila* in that straight spicules emerge at the tail tip and are enclosed by a sheath, also termed a "cloacal tubus"; in other respects, males of *A. africana* were considered indistinguishable from those of *Heterodera* (9). It is noteworthy, however, that tail length of males of other *Heterodera* spp. may be very short (e.g., *H. graminophila* Golden and Birchfield, 1972) and SEM observations indicate that a sheath, while generally shorter than that of *A. africana,* occurs throughout Heteroderidae including non-cyst-forming genera such as *Rhizonema* (5).

Luc et al. (9) considered the juveniles of *A. africana* to be indistinguishable from *Heterodera* species. Juveniles of *A. africana* and *Heterodera* have a pore-like phasmid, whereas *S. hydrophila* has a lens-like phasmid (Fig. 21K, L). The stylet of *A. africana* juveniles is similar to *Heterodera* but is much shorter than *S. hydrophila* (21 vs. 43 μm).

SEM observations of the lip region of males and juveniles of *A. africana* indicate a pattern similar to certain *Heterodera* species; in males and juveniles, adjacent submedial lips are fused with one another as well as with the labial disc (16) (Fig. 21A, B). However, the pattern is much different in *S. hydrophila* in which lips fuse with one another but are separate from the labial disc (16) (Fig. 21C, D).

TEM examination of layering of the body wall cuticle of *A. africana* indicates the presence of A, B, and C layers similar to *Heterodera* and in contrast to the additional zones and D layer of *S. hydrophila* (1,6) (Fig. 21I, J).

Host response

The response of *P. maximum* to *A. africana* is unique among Heteroderidae thus far examined. Mature egg-filled females feed on a syncytium composed of a few interconnected chambers ("cell" units) which are only slightly larger than apparently normal adjacent cells of metaxylem (Figs. 19, 20). Each chamber retains a relatively large degree of separation from other units (Figs. 19, 20). However, chambers that appear to be completely separate in a given cross section are likely to fuse at another level; a typical syncytium is several hundred micrometers long. Walls of the syncytium of *A. africana* as observed with LM lack ingrowths (Fig. 20), and we predict that TEM will show pit fields similar to those of *Atalodera* (12).

The syncytium induced by *A. africana* contrasted with the single uninucleate giant cell associated with *S. hydrophila*, although both plant structures apparently are similar in lacking ingrowths (12) (Figs. 19, 20, 21H, G). *Afenestrata africana* and *Heterodera* sensu lato both induce syncytia, but the response is distinctive between the two (Figs. 17–20). Walls of syncytia of *Heterodera* sensu lato have ingrowths (7). In addition, syncytia of *Heterodera* are relatively large, frequently replacing most of the vascular cylinder. Individual chambers of the syncytia of *Heterodera* typically are very large relative to normal cells, and chambers are highly interconnected (Figs. 17–20). The host range of *A. africana* is narrow (Germani, pers. comm.), so that we are unable to compare responses of *A. africana* on additional hosts. However, the diagnostic significance of the unique response on *P. maximum* could be further evaluated by comparison with responses induced by *Heterodera* species on this grass.

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