Journal of Nematology 17(3):286–296. 1985.

Fine Structure of Body Wall Cuticle of Females of Eight Genera of Heteroderidae

G. M. CLIFF[1] AND J. G. BALDWIN[2]

Abstract: Body wall cuticle of adult females of eight genera within the Heteroderidae was examined by transmission electron microscopy for comparison with previously studied species within the family. Cuticle structure was used to test some current hypotheses of phylogeny of Heteroderidae and to evaluate intrageneric variability in cuticle layering. *Verutus, Rhizonema,* and *Meloidodera* possess striated cuticle surfaces and have the simplest layering, suggesting that striations have not necessarily arisen repeatedly in Heteroderidae through convergent or parallel evolution. *Atalodera* and *Thecavermiculatus* possess similar cuticles with derived characteristics, strengthening the hypothesis that the two genera are sister groups. Similarly, the cuticle of *Cactodera* resembles the specialized cuticle of *Globodera* and *Punctodera* in having a basal layer (D) and a surface layer infused with electron-dense substance. *Heterodera betulae* has a unique cuticle in which the thickest layer (C) is infiltrated with an electron-dense matrix. Little intrageneric difference was found between cuticles of two species of *Meloidodera* or between two species of *Atalodera.* However, *Atalodera ucri* has a basal layer (E) not found in other Heteroderidae. The most striking intrageneric variation in cuticle structure was observed between the thin three-layered cuticle of *Sarisodera africana* and the much thicker four-layered cuticle of *Sarisodera hydrophila*; results do not support monophyly of *Sarisodera.*

Key words: Atalodera ucri, body wall cuticle, *Cactodera* sp., comparative morphology, fine structure, *Heterodera betulae,* Heteroderidae, *Meloidodera floridensis,* phylogeny, *Rhizonema sequoiae, Sarisodera africana,* systematics, *Thecavermiculatus gracililancea, Verutus volvingentis.*

Comparative morphology of the cuticle of adult female nematodes may be useful in phylogenetic analysis of Heteroderidae (1). Although certain surface features of the female cuticle (i.e., presence of striations or modification into a rugose pattern) have been employed as diagnostic characters among genera for some time, differences in the layering of cuticle among genera may also be valuable in interpreting relationships. Shepherd et al. (10) first noted differences in layering of female body wall cuticle among members of *Heterodera* sensu lato. The cuticle of females was found to be characterized by the addition of internal layers to a basic pattern occurring in most vermiform Tylenchida, including heteroderid males and juveniles (2,10). The basic layers of the cuticle were identified, described, and designated A, B, C, D; also zones within these layers were indicated by subscripts (Table 1). Shepherd et al. (10) found consistent variation among groups of species supporting the later separation of *Heterodera* Schmidt, 1871 and *Globodera* (Skarbilovich, 1959) Behrens, 1975. Little variability was noted in cuticular layering and morphology of males and juveniles among species of *Heterodera* sensu lato.

In a subsequent detailed study of adult females, significant and consistent differences in body wall structure were found in representatives of three morphologically diverse genera within Heteroderidae: *Meloidodera, Atalodera,* and *Sarisodera* (1). The cuticle of *Meloidodera charis* was interpreted as primitive with its narrow C layer and lack of a D layer. Although both *Atalodera lonicerae* and *Sarisodera hydrophila* had a well-developed D layer, the cuticle of *S. hydrophila* was much more complex in its organization. The presence of a D layer was considered a derived character state shared by *Atalodera, Sarisodera, Globodera,* and *Punctodera* but not by *Heterodera.* Differences in layering suggested at least two hypotheses concerning phylogenetic relationships among these genera: 1) D layer is secondarily lost in *Heterodera*; 2) *Atalodera, Sarisodera,* and *Globodera* share a common ancestor not shared by *Heterodera.* Such hypotheses must be tested through phylogenetic analyses based on a more complete understanding of cuticle structure as well as additional characters including morphology revealed by light microscopy.

The value of variation in cuticle layering

Received for publication 30 August 1984.

[1] NSERC Postdoctorate, University of Toronto, Toronto, Ontario, Canada M5S 1A1.

[2] Assistant Professor, Department of Nematology, University of California, Riverside, CA 92521.

This research was supported in part by grant 84-15627 from the National Science Foundation. The authors thank the following for supplying specimens: I. Cid Del Prado-Vera (*R. sequoiae*), J. Eisenback (*M. floridensis*), D. Kaplan (*V. volvingentis*), M. Luc (*S. africana*), R. Robbins (*H. betulae*).

TABLE 1. Layers and zones of the body wall cuticle of females of Heteroderidae.*

Layer	Zone	Characteristics
A	A_1	Homogeneous, thin (≤ 0.05 μm), moderately dense.
	A_2	Fine fibers, electron lucent.
	A_3	Electron-dense chambers among fibrous strands.
B		Patches of striations; striations with a periodicity of ± 18 nm.
C	C_1	Randomly arranged fibers.
	C_2	Randomly arranged fibers embedded in an electron-dense matrix.
	C_3	Randomly arranged fine-textured fibers.
D		Clearly defined fibers arranged in a repeating helicoidal pattern.

* Modified from Shepherd et al. (10).

in phylogenetic inference is further examined here through detailed study of the morphology of additional heteroderids (Table 2). Resulting information is used to help identify intergeneric relationships and to confirm relative consistency of cuticle structure within certain genera.

MATERIALS AND METHODS

Females of eight genera of Heteroderidae were collected from type localities or greenhouse cultures (Table 2). Species were selected from genera not previously examined (*Verutus volvingentis, Rhizonema sequoiae, Thecavermiculatus gracililancea,* and a new undescribed *Cactodera* sp.) as well as from genera in which at least one other species has been studied (*Meloidodera floridensis, Sarisodera africana, Atalodera ucri,* and *Heterodera betulae*) (1). Specimens were processed for examination of the body wall cuticle by transmission electron microscopy (TEM) and light microscopy (LM) as previously described (1). All specimens were fixed in 3.5% glutaraldehyde with the exception of specimens of *S. africana* which were fixed in formalin before shipment. Fixation of nematodes in formalin did not appear to alter the appearance of the cuticle relative to those fixed in glutaraldehyde. Following fixation, all nematodes were postfixed with 1% osmium tetroxide, dehydrated in a graduated acetone series, infiltrated with Spurr's epoxy, and embedded in flat embedding plates. Sectioning was with a Porter Blum MT-2B ultramicrotome using glass knives.

Sections were usually taken from midbody region of mature females which appeared to be of similar physiological age. Those with silver to gold interference colors (thickness = 60–100 nm) were mounted on formvar and carbon-coated 150-mesh grids. Thick sections (ca. 0.2 μm) from the females were mounted on glass

TABLE 2. Species of Heteroderidae examined and their sources.

Species	Host	Locations
Verutus volvingentis Esser, 1981	buttonweed *Diodia virginiana*	Orlando, Florida (greenhouse culture)
Meloidodera floridensis Chitwood et al., 1956	loblolly pine *Pinus taeda*	Raleigh, North Carolina (greenhouse culture)
Rhizonema sequoiae Cid Del Prado et al., 1983	redwood *Sequoia sempervirens*	Lagunitas Lake, California*
Atalodera ucri Wouts and Sher, 1971	golden bush *Haplopappus palmeri*	Riverside, California*
Thecavermiculatus gracililancea Robbins, 1978	rattail fescue *Festuca myuros*	Monterey County, California
Sarisodera africana Luc et al., 1973	guinea grass *Panicum maximum*	Senegal, Africa*
Heterodera betulae Hirschmann & Riggs, 1969	river birch *Betula nigra*	Washington County, Arkansas*
Cactodera sp. (undescribed species)	shadscale *Atriplex confertifolia*	Cedar Valley, Utah*

* Type localities.

slides and stained with toluidine blue. Staining for TEM was with uranyl acetate followed by lead citrate. Thin sections from at least 12 specimens of each species were examined with a Hitachi H-600 TEM at 75 kV.

Results

All of the eight species examined possessed layers A, B, and C, but there was variation in thickness and morphology of layers and in number of sublayers (zones) (Fig. 1). In some species additional layers were found. Although basic layers were generally resolved in thick sections with LM, the following descriptions are based on more detailed TEM observations.

The body wall cuticle of females of *V. volvingentis, M. floridensis,* and *R. sequoiae* have striated surface patterns and also have the simplest layering among species examined (Fig. 1). *Verutus volvingentis* has an average mid-body cuticle thickness of 3.5 μm (Fig. 2). The A layer (0.7 μm) is composed of a thin (0.05 μm), electron-dense, homogeneous A_1 zone and a granular A_2 zone (0.65 μm) (Fig. 3). The B layer (0.8 μm) is unusual. In some cases it can be resolved into four distinct zones: B_1 (0.2 μm) and B_3 (0.2 μm) are striated, whereas B_2 (0.3 μm) and B_4 (0.1 μm) are densely granular. Striations in the B layer are not seen in some cases (Fig. 3). Zones were not distinguished in the C layer (2.0 μm), which is relatively homogeneous with fine fibers oriented parallel to the cuticle surface and interspersed with granules (Fig. 2).

The cuticle of *M. floridensis* is about 8.5 μm thick, and its surface is relatively smooth in transverse section (Fig. 4). Layer A includes distinct A_1 (0.05 μm), A_2 (0.3 μm), and A_3 (1.3 μm) zones (Fig. 5). Layers A_1 and A_2 are homogeneous and granular; A_3 consists of a labyrinth of chambers filled with highly electron-dense material. The walls of the chambers appear fibrous. Layer B, usually thin (0.12 μm), occurs in periodic patches (Fig. 5). The C layer, 7.0 μm thick and consisting of two zones, has fibers oriented parallel to the surface (Fig. 4). Radial channels containing electron-dense material are present in C_1 (Fig. 4).

The thin (3.0 μm) body wall cuticle of *R. sequoiae* is simple in organization (Figs. 1, 6). Layer A (1.0 μm) is composed of a thin (0.04 μm) homogeneous A_1 zone, a granular A_2 zone (0.4 μm), and a more darkly staining, granular to flocculent A_3 zone (0.3 μm) (Figs. 6, 7). A narrow lighter area is occasionally seen between A_2 and A_3. The B layer (0.25 μm) is patchy with typical striations (Figs. 6, 7). Usually the relatively thick (2.4 μm) C layer is not separated into distinct zones but is composed of fibers oriented more or less parallel to the surface of the cuticle. In the area nearest the hypodermis, however, the fibers have a more random orientation, giving this area a swirled appearance (Fig. 6).

The body wall cuticles of females of *A. ucri* and *T. gracililancea* have a putative lace-like surface pattern and rather complex layering. The cuticle of *A. ucri* is unique with five layers—A, B, C, D, E (Fig. 8). The cuticle surface is highly convoluted, and A (1.3 μm) includes three distinct zones. Zone A_1 (0.04 μm) is relatively electron dense, A_2 (0.1 μm) and A_3 (1.2 μm) contain randomly oriented fibers, and A_3 is occasionally distinguished by large electron-dense chambers (Fig. 9). The B layer (0.15 μm) is clearly striated, and C (4.4 μm) is resolved into C_1 and C_2 (Fig. 8). The parallel fibers of C_1 occur in an electron-dense matrix, whereas C_2 is more electron lucent and in some regions the fibers tend to be randomly oriented, giving this zone a swirled appearance (Fig. 8). The D layer is unusually thick (4.5 μm) and has characteristically oriented (Table 2) coarse fibers (Figs. 8, 10). *A. ucri* has a fifth layer, designated E, basal to D. The E layer, consisting of fine fibers oriented parallel to the cuticle surface, varies in thickness (< 2 μm) (Fig. 8).

Cuticle of *T. gracililancea* has layers A, B, C, and D and averages 11.0 μm thick in the mid-body region (Figs. 1, 11). Within the A layer (2.2 μm), A_1 is thin (0.04 μm) and homogeneous. The rest of A consists of fine fibers interspersed with electron-dense granules; separate A_2 and A_3 zones are not resolved (Fig. 12). Layer B (0.2 μm) is patchy and typical in appearance (Figs. 11, 12). The C layer (4.0 μm) is composed of thick fibers oriented parallel to the surface; zones are not discernible (Fig. 11). A prominent D layer (5.0 μm), composed of thick fibers in a well-organized repeating helicoidal arrangement, forms

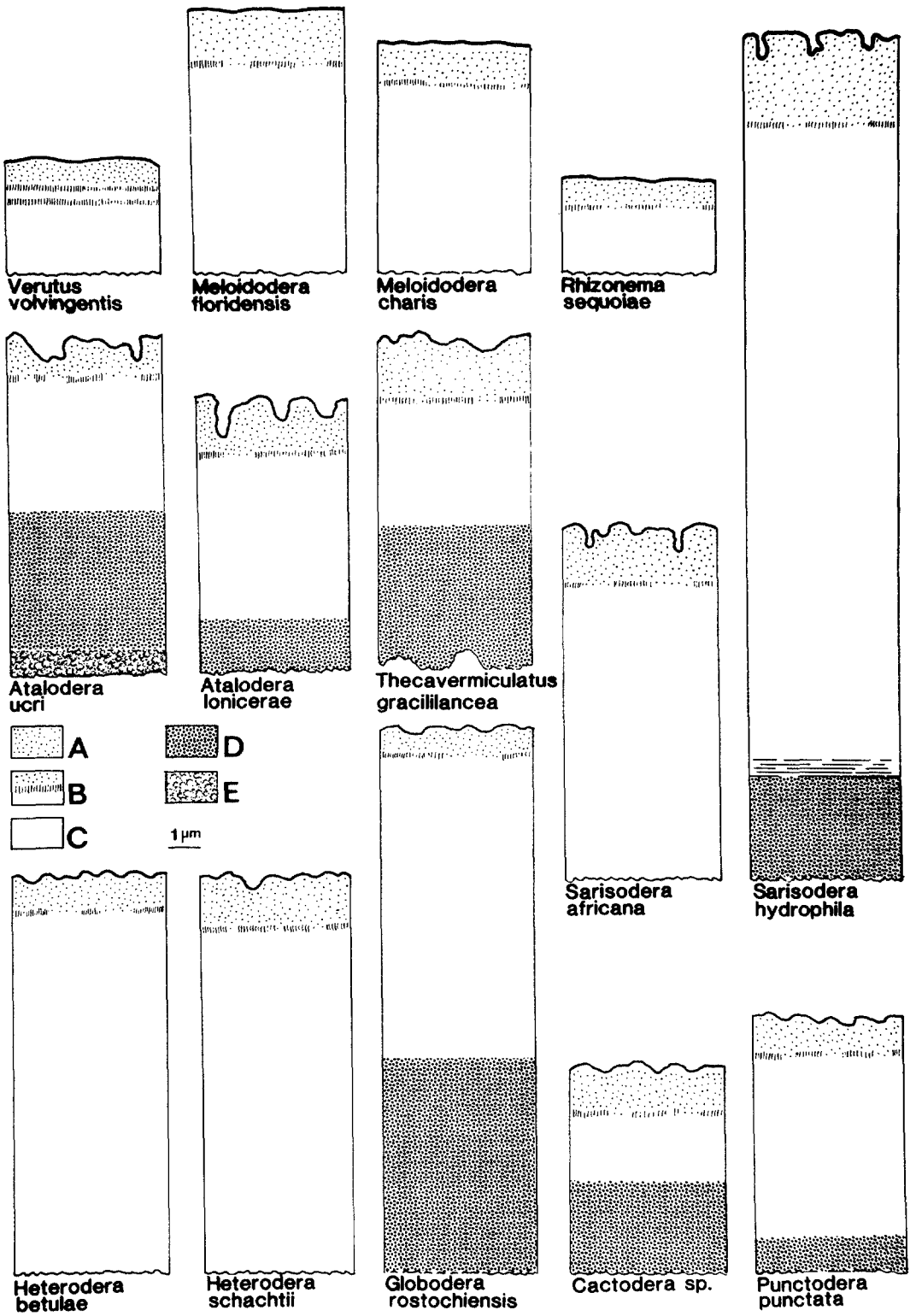
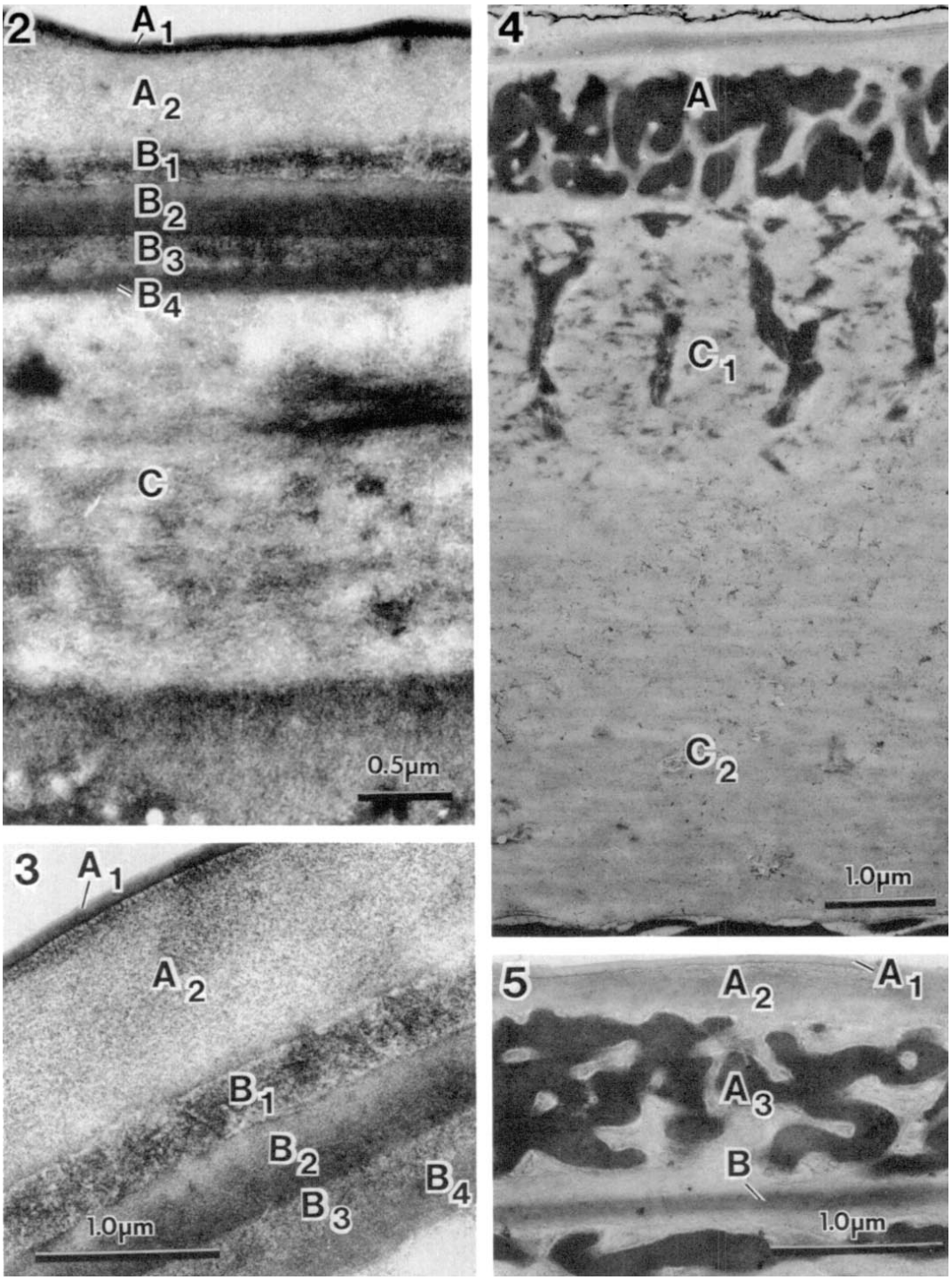


FIG. 1. Diagram illustrating layering of cuticle in midregion of mature females of 14 species of Heteroderidae. *Meloidodera charis, Atalodera lonicerae,* and *Sarisodera hydrophila* redrawn from Baldwin (1); *Globodera rostochiensis* and *Punctodera punctata* redrawn from Shepherd et al. (10).



FIGS. 2–5. TEM of transverse section of cuticle from the midregion of *Verutus volvingentis* and *Meloidodera floridensis* mature females. 2) *V. volvingentis* composed of layers A, B, and C. Layer A consists of A_1 and A_2; layer B includes B_1, B_2, B_3, and B_4. 3) Layers A (A_1 and A_2) and B (B_1, B_2, B_3, and B_4) of *V. volvingentis*. 4) *M. floridensis* showing layers A and C. Layer C is resolved into C_1 and C_2. 5) Layer A of *M. floridensis* includes zones A_1, A_2 and A_3, followed by layer B.

the innermost layer of the cuticle. Unlike other species examined, the D layer surface adjacent to the hypodermis is very irregular (Fig. 11).

Although the body wall cuticle of females of *S. africana, H. betulae,* and *Cactodera* sp., unlike the other species examined, becomes modified into a cyst following egg production, the surface pattern and cuticular layering are highly variable among these species.

The cuticle of *S. africana* is relatively thick (11.0 μm) consisting of three layers—A (2.0 μm), B (0.2 μm), and C (9.0 μm) (Figs. 13, 14). The cuticle surface is rough and irregular with narrow, deep (about 1.0 μm) invaginations. Zone A_1 is about 0.05 μm wide; the remainder of A is not resolved into additional zones (Figs. 13, 14). Layer B is patchy with typical striations, and C includes two or sometimes three zones (Figs. 13, 14). Zone C_1, consisting of fibers, oriented parallel to the surface, stains more densely than the rest of C. Zone C_2 has coarser, more randomly arranged fibers; whereas C_3 is finer textured with indistinct fibers. Channels containing dark-staining granules occur throughout C_1 but are predominant in C_2 (Fig. 13).

The cuticle of *H. betulae* is thick (13.0 μm) with an A layer (1.1 μm), a poorly defined B layer (0.3 μm), and a broad (12.5 μm) C layer (Figs. 1, 15, 16). Layer A is resolved into A_1 (0.5 μm), A_2 (0.1 μm), and A_3 (0.5 μm) (Fig. 16). Zones C_1 and C_2 are heavily infiltrated with an electron-dense matrix and are not resolved into distinct regions, but C_3 is electron lucent and composed of typical fine fibers in random arrangements (Fig. 15).

The cuticle of *Cactodera* sp., thinner (6.5 μm) than in *H. betulae,* includes layers A, B, C, and D (Figs. 1, 17). The A layer (1.0 μm) is composed of a thin (0.05 μm) dark-staining homogenous A_1 zone and a combined A_2 and A_3 sublayer (1.5 μm) consisting of fibers in a random arrangement interspersed with fine granules and large dark-staining bodies of variable size and irregular outline. A striated B layer is located basal to the A layer (Figs. 17, 18). Layer C is thick (2.0 μm), homogeneous, and composed of fibers oriented parallel to the surface as well as electron-dense granules (Fig. 17). A thick well-organized D layer (3.0 μm), made up of coarse fibers oriented in a repeating helicoidal pattern, is present adjacent to the hypodermis (Fig. 17).

Discussion

Differences in body wall cuticle layering of female Heteroderidae appear to be useful for evaluating taxonomic relationships within the family. Representative species of 10 of the 14 genera have now been examined; only *Cryphodera, Hylonema, Dolichodera,* and *Ephippiodera* remain to be studied. Certain features, such as the presence or absence of a D or E layer or electron-dense deposits in the A_3 zone, can be used, along with other characters, to test current hypotheses of phylogeny.

Verutus, Rhizonema, and *Meloidodera* share certain characters, including the presence of surface striations on the female cuticle. The simple cuticular layering pattern revealed for these genera during this study (i.e., presence of layers A, B, and C, with C occasionally resolved into zones only in *Meloidodera* and B into zones only in *Verutus*) may be considered primitive (plesiomorphic) because it more closely resembles the pattern present in vermiform Tylenchida than the more complex, specialized pattern present in other heteroderid females. Occurrence of a common primitive cuticle among these genera suggests that striations have not necessarily arisen repeatedly through convergent or parallel evolution. However, a separate evolution of cuticular striations might be suggested for *Rhizonema* because of incongruence in the distribution of other characters. For example, the vulval cone, position of the anus on the dorsal lip, and cloacal tubus in the male of *Rhizonema* resemble *Sarisodera* (3), yet the simple *Meloidodera*-like cuticle is in sharp contrast to the elaborately layered cuticle of *Sarisodera hydrophila* (1). It remains to be determined whether the striated cuticle of the genus *Dolichodera* also has simple layering, as in *Rhizonema,* or if it has a more complex cuticle similar to that of *Globodera,* with which it shares several other characters (7).

Atalodera and *Thecavermiculatus* have been proposed as sister groups on the basis of several shared derived characters (synapomorphies) (4). During our study it was noted that the cuticle of *T. gracililancea* also

resembles that of *Atalodera* in possessing a D layer (a derived character). This additional synapomorphy strengthens the case for the proposed monophyly of these two genera.

The detailed structure of *S. africana* does not support monophyly with *S. hydrophila*. The cuticle of *S. africana* is relatively thick (11.0 μm) with A, B, and C layers and is most similar to *Heterodera* spp. (10). Conversely, *S. hydrophila* has a thick (14.0–30.0 μm) complex cuticle characterized by a well-organized D layer and an electron-dense substance infused into layers near the surface (1). The monophyly of *Sarisodera* is placed further in question by the formation of cysts in *S. africana* (6) and the apparent absence of cyst formation in *S. hydrophila* (1).

The cuticle of female *Cactodera* sp. is identical to *Globodera* and *Punctodera* (10). The cuticle in these three genera includes a D layer; they also include an A layer infused with an electron-dense substance. We have suggested that these two characters are derived, and their occurrence in *Cactodera, Globodera,* and *Punctodera* supports the hypothesis that these genera form a monophyletic group. These synapomorphies in the cuticle suggest that *Heterodera* sensu Mulvey and Stone is not a monophyletic group and support separation of *Cactodera* Krall and Krall from *Heterodera* (5,8).

The taxonomic position of *H. betulae* is controversial. It has been included in *Cactodera* by Krall and Krall (5) and considered ". . . apart from all described *Heterodera*" by Mulvey and Golden (8). Cuticle structure supports the conclusion of Mulvey and Golden. Unlike *Cactodera,* the cuticle of *H. betulae* lacks a D layer, and although A, B, and C layers are delineated, they are embedded in an electron-dense material (absent only in C_3) which is not confined to channels; in this respect the cuticle is distinct from any other Heteroderidae female examined.

Detailed studies of the cuticle of Heteroderidae generally support existing hypotheses of phylogeny (4). As previously noted (1), however, the occurrence of the derived state (i.e., D layer present) in *Atalodera lonicerae, Globodera,* and *Punctodera* but not in *Heterodera* is incongruent with the proposed phylogeny (1). The significance of this incongruence is strengthened by new findings of a D layer in an additional species of *Atalodera* (*A. ucri*) as well as *Thecavermiculatus* and *Cactodera.* The best explanation for the distribution of D may be that this layer is secondarily lost in *Heterodera.* This hypothesis must be further tested with new characters, including, for example, recent observations of comparative host responses (9).

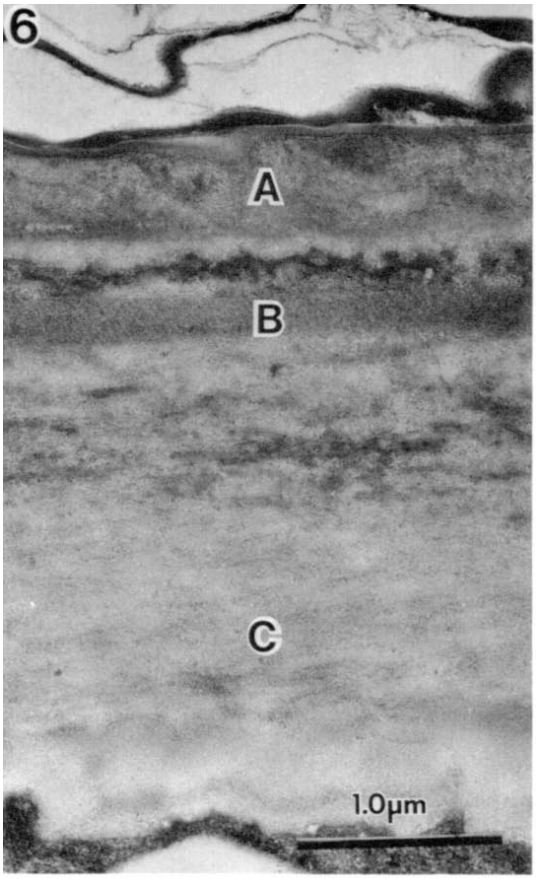
Intrageneric variation in cuticle structure was investigated in *Meloidodera* and *Atalodera.* Little variation was noted between cuticles of *M. floridensis* and *M. charis,* although the cuticle of *M. floridensis* is slightly thicker (10.0 vs. 8.0 μm) and the C layer is occasionally resolved into two zones in *M. floridensis* and three zones in *M. charis* (1). The cuticle of *A. ucri* resembles that of *A. lonicerae* in the presence of A, B, C, and D layers and in the highly convoluted surface revealed in transverse section. *Atalodera ucri,* however, is distinguished by a much thicker D layer (4.5 vs. 1.5 μm) and the presence of a fifth layer, E. This is the first report of a fifth cuticle layer in Het-

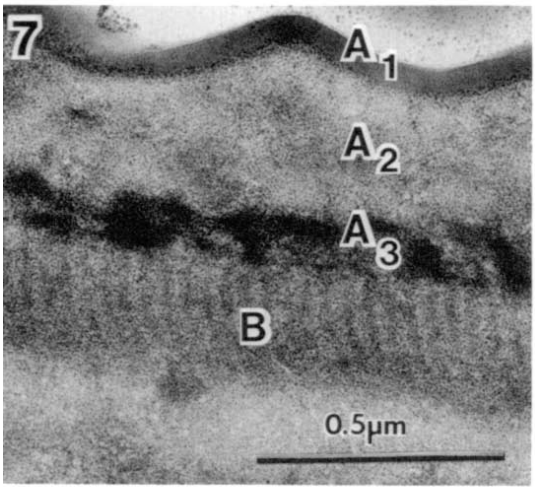
→

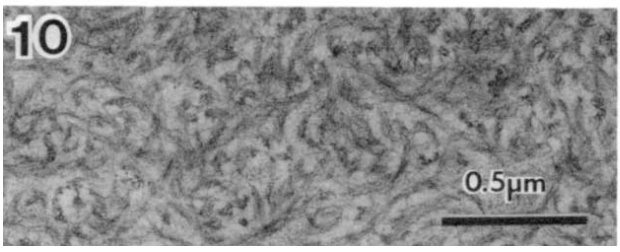
FIGS. 6–10. TEM of transverse section of cuticles from the midregions of *Rhizonema sequoiae* and *Atalodera ucri* mature females. 6) *R. sequoiae* composed of layers A, B, and C. 7) Zones A_1, A_2, and A_3 and layer B of *R. sequoiae.* 8) *A. ucri* composed of layers A, B, C, D, and E. Layer C consists of C_1 and C_2. 9) Layers A (A_1, A_2, and A_3) and B of *A. ucri.* 10) Fibers composing D layer of *A. ucri.*

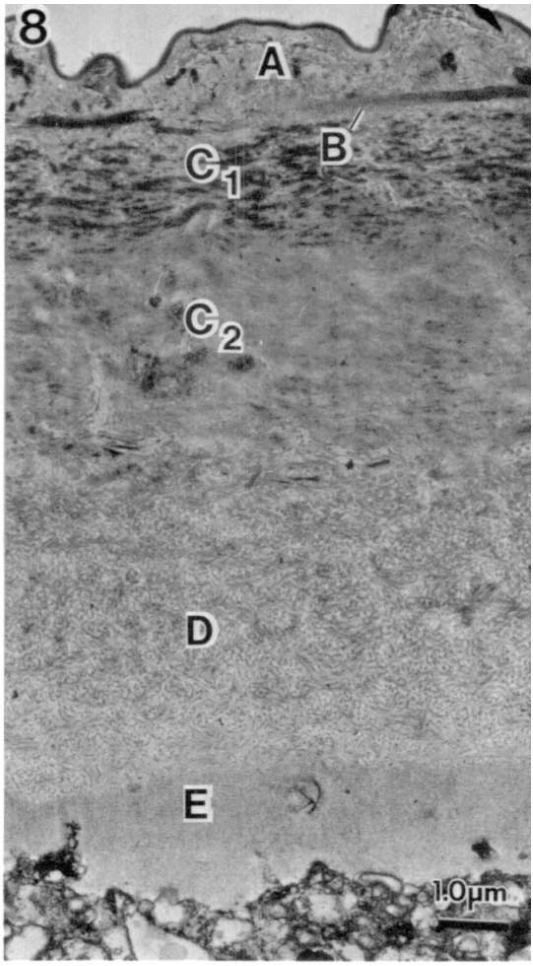
FIGS. 11–14. TEM of transverse sections of cuticles from midregion of *Thecavermiculatus gracililancea* and *Sarisodera africana* (mature females). 11) *T. gracililancea* composed of A, B, C, and D. 12) Layer A (A_1 and A_3) and B of *T. gracililancea.* 13) *S. africana* showing layers A and C (C_1, C_2, and C_3). 14) Layers A (A_1 and A_2) and B of *S. africana.*

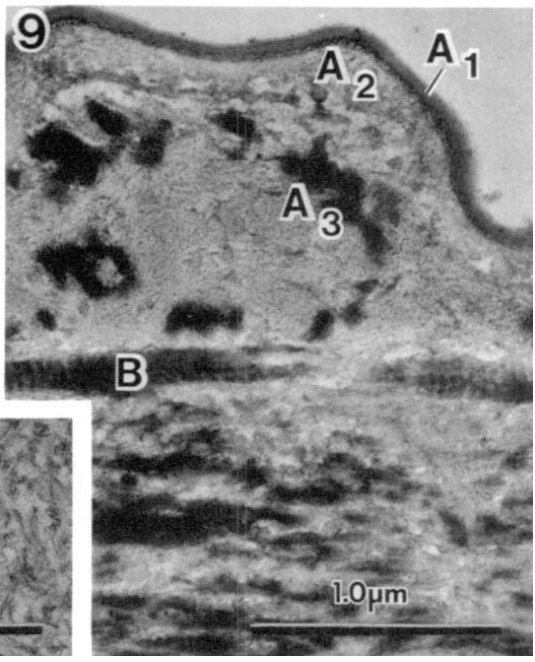
FIGS. 15–18. TEM of transverse sections of cuticles from midregion of *Heterodera betulae* and *Cactodera* sp. mature females. 15) *H. betulae* showing layers A and C (C_1, C_2, and C_3). 16) Layer A (A_1, A_2, and A_3) and a faint indication of B. 17) *Cactodera* sp. showing A (A_1 externally), C, and D. 18) Layer A (A_1 externally) and B of *Cactodera* sp.

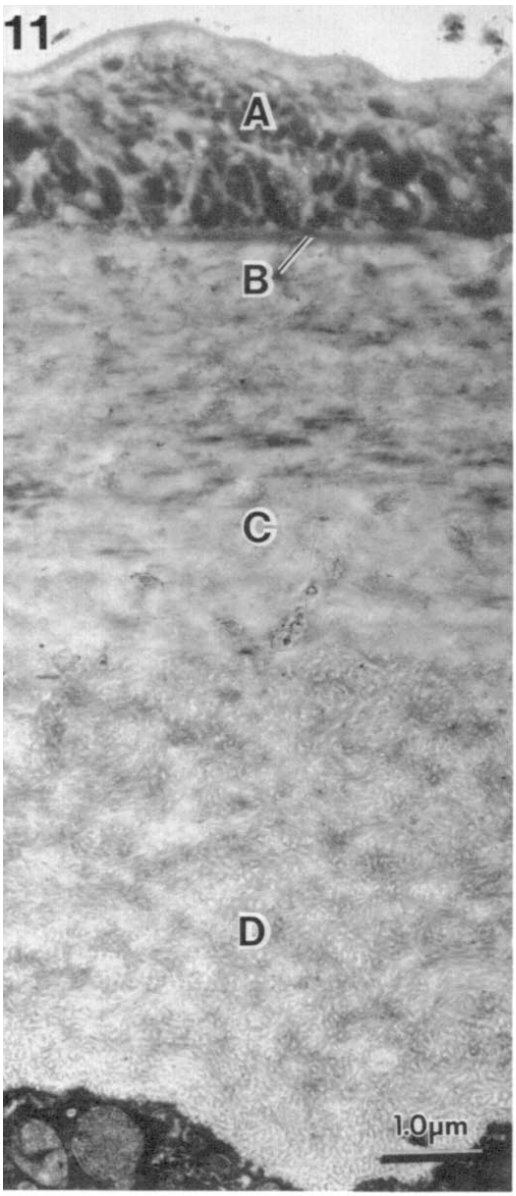

6
A
B
C
1.0μm

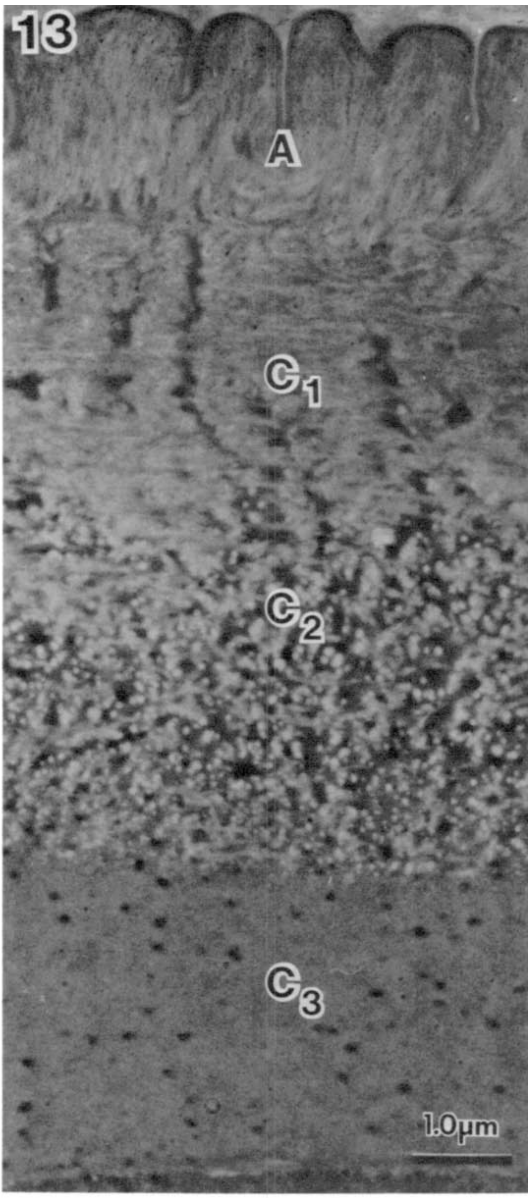

7
A1
A2
A3
B
0.5μm

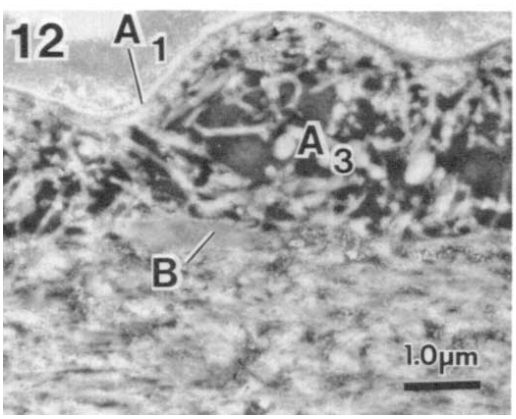

10
0.5μm

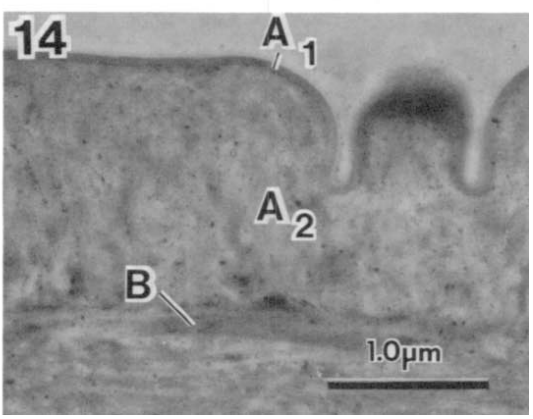

8
A
B
C1
C2
D
E
1.0μm

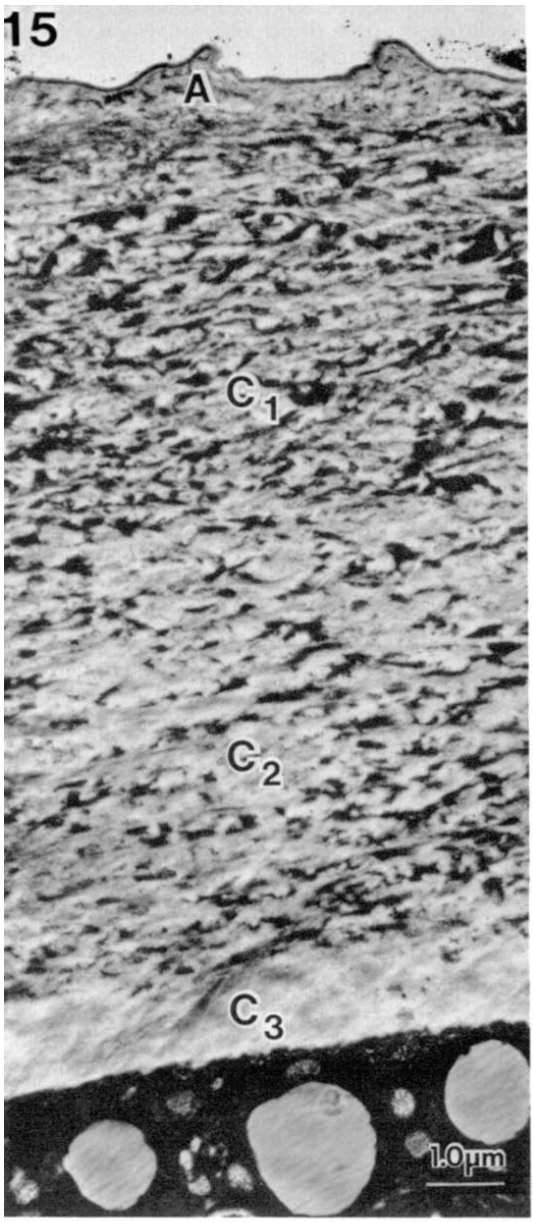

9
A1
A2
A3
B
1.0μm

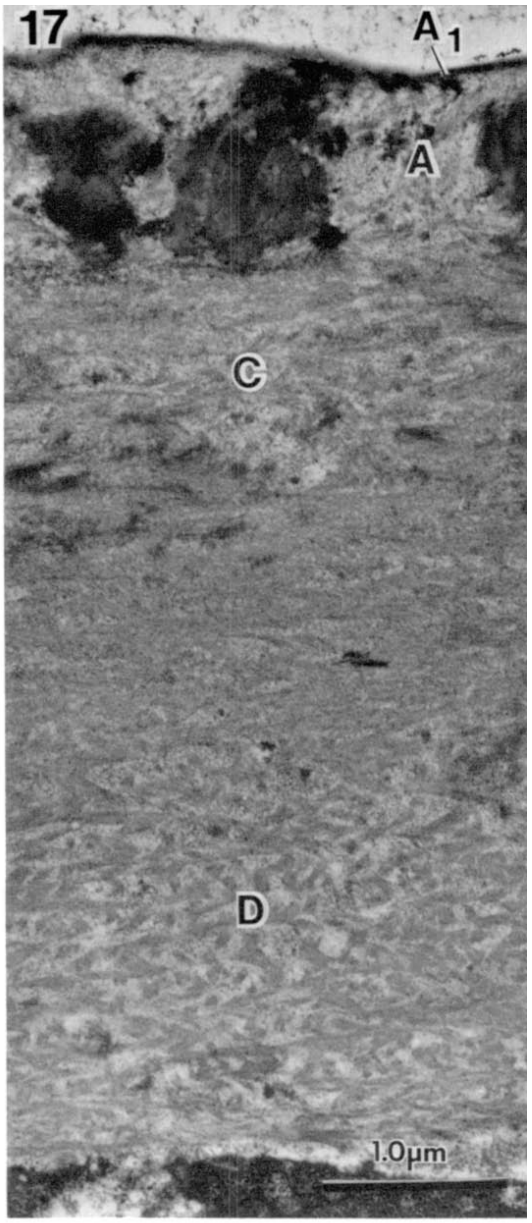

11
A
B
C
D
1.0μm

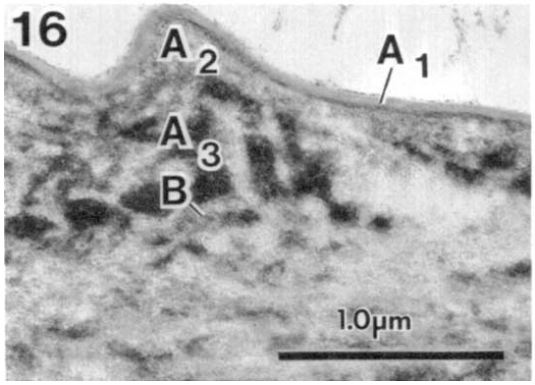

13
A
C1
C2
C3
1.0μm

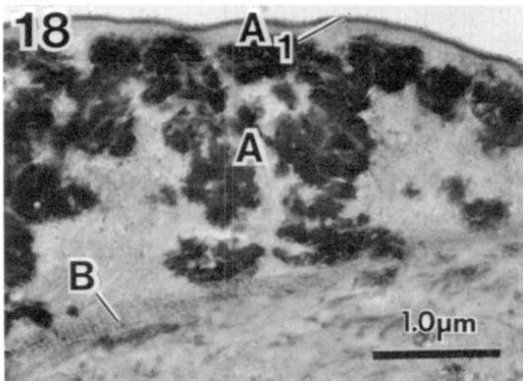

12
A1
A3
B
1.0μm


14
A1
A2
B
1.0μm


15
A
C1
C2
C3
1.0μm


17
A1
A
C
D
1.0μm


16
A2
A1
A3
B
1.0μm


18
A1
A
B
1.0μm

eroderidae. Since intrageneric differences exist, caution should be exercised in using these characters in phylogenetic interpretations when only one species in a genus has been examined. Also, the examination of several species in a genus may help indicate whether a certain species belongs in a group (e.g., identify polyphyly vs. monophyly) as in the case of *S. africana.*

Examination of female body wall cuticle in the remaining Heteroderidae genera and the study of more species within each genus may allow the development of a useful system based, in part, on cuticle structure, to aid in determining the phylogeny of Heteroderidae.

Addendum

Subsequent to acceptance of this manuscript for publication, *Sarisodera africana* was placed in a new genus *Afenestrata africana* (Luc et al., 1973) Baldwin and Bell, 1985, and the undescribed species of *Cactodera* was described as *Cactodera eremica* Baldwin and Bell, 1985 (Journal of Nematology 17:187–201).

Literature Cited

1. Baldwin, J. G. 1983. Fine structure of body wall cuticle of females of *Meloidodera charis, Atalodera lonicerae,* and *Sarisodera hydrophila* (Heteroderidae). Journal of Nematology 15:370–381.

2. Baldwin, J. G., and H. Hirschmann. 1975. Body wall fine structure of the anterior region of *Meloidogyne incognita* and *Heterodera glycines* males. Journal of Nematology 7:175–193.

3. Cid Del Prado Vera, I., B. F. Lownsbery, and A. R. Maggenti. 1983. *Rhizonema sequoiae* n. gen. n. sp. from coast redwood *Sequoia sempervirens* (P. Don) Endl. Journal of Nematology 15:460–467.

4. Ferris, V. R. 1979. Cladistic approaches in the study of soil and plant parasitic nematodes. American Zoologist 19:1195–1215.

5. Krall, E. L., and H. A. Krall. 1978. Systematic changes of phytonematodes of the family Heteroderidae based on trophic specialization of those parasites and their evolutionary connection with agricultural plants. Fitogel; mintologicheskie issledovanikla, Akademikila nauk S.S.S.R. Vsesokiluznoe obschchestvo. Moskva Pp. 39–56 (in Russian).

6. Luc, M., G. Germani, and C. Netscher. 1973. Description de *Sarisodera africana* n. sp. et considerations sur les relations entre les genres *Sarisodera* Wouts and Sher, 1971 et *Heterodera* A. Schmidt, 1871 (Nematoda: Tylenchida). Cahiers O.R.S.T.O.M. Serie Biologie 21:35–43.

7. Mulvey, R. H., and B. A. Ebsary. 1980. *Dolichodera fluvialis* n. gen. n. sp. (Nematoda: Heteroderidae) from Quebec, Canada. Canadian Journal of Zoology 58:1697–1702.

8. Mulvey, R. H., and A. M. Golden. 1983. An illustrated key to the cyst-forming genera and species of Heteroderidae in the Western Hemisphere with species morphometrics and distribution. Journal of Nematology 15:1–59.

9. Mundo-Ocampo, M., and J. G. Baldwin. 1984. Comparison of host response of *Cryphodera utahensis* with other Heteroderidae and a discussion of phylogeny. Proceedings of the Helminthological Society of Washington 51:25–31.

10. Shepherd, A. M., S. A. Clark, and P. J. Dart. 1972. Cuticle structure in the genus *Heterodera.* Nematologica 18:1–17.