The Genera of the Subfamily Heteroderinae
(Nematoda: Tylenchoidea) with a Description of Two New Genera

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Abstract: The family Heteroderidae, its two subfamilies Heteroderinae and Meloidogyninae and the nominal genera of Heteroderinae (Heterodera Schmidt, 1871; Meloidodera Chitwood, Hannon & Esser, 1956; and Cryptodera Colbran, 1966) are rediagnosed. Meloidoderita Pogosyan, 1966 is considered a genus inquirenda. Two new genera from southern California are described in the subfamily Heteroderinae. A key to the genera, illustrations and a phylogeny of the Heteroderinae are proposed. Key Words: Heteroderidae, Heteroderinae, Meloidogyninae, Heterodera, Meloidodera, Cryptodera, Meloidoderita, Sarisodera n. gen., Atalodera n. gen., Taxonomy, Phylogeny, Key.

The subfamily Heteroderinae Filipjev and Schuurmans Stekhoven, 1941 (16) was introduced for the genera Heterodera Schmidt, 1871 (35), Paratylenchus Micoletzky, 1922 and Tylenchulus Cobb, 1913. In 1947 Skarbilovich (38), on the basis of sexual dimorphism (swollen females), proposed the family Heteroderidae for Heteroderinae and the new subfamily Tylrenchulinia. In 1949 Thorne (43), independently, also proposed Heteroderidae. Basing it on the shape of the female body, the short rounded male tail and the absence of caudal alae, he included only the subfamily Heteroderinae. Chitwood and Chitwood (7) included Hoplolaiminae Filipjev, 1934 and the new subfamily Nacobbinia in this family and Skarbilovich (39) added Sphaeronematinae Raski and Sher, 1952 and the new subfamily Meloidogyninae. Paramonov (30) included only two subfamilies, Heteroderinae and Meloidogyninae.

It was Thorne's 1949 classification of the family Heteroderidae that became generally accepted (1, 21, 24, 34).

Thorne (43) included in the subfamily Heteroderinae the genera Heterodera and Meloidogyne Goeldi, 1892 (18), thereby accepting the genus Meloidogyne for the root-knot nematodes, as proposed by Chitwood (6) that same year.

The genus Meloidodera Chitwood, Hannon and Esser, 1956 (8) was described with juveniles similar to Heterodera but with annulated females and no cyst formation. It was, therefore, considered the link between Heterodera and Meloidogyne. Skarbilovich (39) placed Meloidodera in the subfamily Heteroderinae, most other workers (1, 8, 21), however, did not recognize this subfamily and placed Meloidodera in Heteroderidae.

Since 1956 the genera Cryptodera Colbran, 1966 (11), from Australia; Meloidoderita Pogosyan, 1966 (32), from Russia; and Hypsoperine Sledge & Golden, 1964 (40) from the U.S.A. have been described. Hypsoperine was synonymized with Meloidogyne by Whitehead (47).

A survey of the nematode collection of the University of California, Riverside, revealed

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4 Baker's (4) assignation of this subfamily is considered correct.

5 The name Meloidogyne was not published until 1892 and this date is considered correct.
many specimens closely related to *Heterodera*, *Meloidodera*, *Cryphodera* and *Meloidoderita* which seemed to form a natural group (Heteroderinae) within the family Heteroderidae. Although many new forms (genera and species) were recognized after a comparative study, only two new species representing two new genera are being described in this study because of insufficient and/or poorly preserved material for the remaining new forms.

**Materials and Methods**

This study was primarily based on preserved specimens in the nematode collection of the Department of Nematology, University of California, at Riverside. Additional preserved specimens were obtained from the nematode collections of the University of California, Davis; the USDA Plant Industry Station, Beltsville, Maryland; the Queensland Department of Primary Industries, Brisbane, Australia; and the California State Department of Agriculture, Sacramento. Fresh specimens of the proposed new genera were collected from soil and root samples from their type localities; from the University of California, Berkeley; and from Santa Cruz Island, off the coast of southern California. Over 1400 females and cysts, 600 males and 2600 juveniles, representing three nominal genera, 23 nominal species, two new genera and species, two undescribed genera and 12 undescribed species in the subfamily Heteroderinae were examined during this study.

Material was isolated from soil by a modified combination of Cobb's (2, 9) sifting method and sugar flotation (5, 14). The stages attached to roots were obtained by boiling infected roots for 30 sec in acid–fuchsin–lactophenol, clearing overnight in lactophenol and dissecting the roots for nematodes (23). Males were extracted from soil or from infected roots in a mist chamber (41). All stages extracted from soil and roots were fixed by adding 5 ml of boiling 4% formalin to approximately 5 ml of an aqueous nematode suspension. After at least four days in this fixative they were processed to glycerine, either through the “Baker rapid method” (3) or a modified “slow glycerin method” (44) in which the cuticles were punctured with a fine needle to allow the glycerin to enter. The nematodes were mounted in dehydrated glycerin between cover glasses held in aluminum slides.

The anterior end of the female specimen was studied after it had been severed with a surgical blade under the dissecting microscope and mounted as described above. When structures to be measured and studied required a particular orientation, specimens were mounted in glycerin jelly (20).

**Systematics**

Family Heteroderidae (Filipjev & Schuurmans Stekhoven, 1941) Skarbilovich, 1947


Diagnosis Emended: Superfamily Tylenchoidea (Filipjev, 1934) Chitwood and Chitwood, 1937. Female.—Swollen to subspherical, sedentary, didelphic. Excretory pore in anterior part of body. Tail absent. Anus located terminally or dorsally. Procorpus and median bulb not amalgamated. Median bulb ovate to spherical, with well developed musculature and crescentic valve plates. Esophageal glands overlap the intestine ventrally. Second-stage juvenile.—Vermiform; infective, migratory stage. Third-stage juvenile.—Swollen with short, blunt tail. Fourth-stage juvenile.—Swollen with terminal anus. Male.—Vermiform, migratory. Body twisted as much as half a turn (180°) in passing from head to tail. Tail very short or absent. Caudal alae ab-
sent. Stylet and cephalic framework well developed.

**TYPE GENUS:** *Heterodera* Schmidt, 1871

*Syn. Heterobulbus* Railliet, 1896
*(Heterodera)* Skarbilovich, 1959
*(Globodera)* Skarbilovich, 1959

Nominal subfamilies included: Heteroderinae Filipjev & Schuurmans Stekhoven, 1941.
Meloidogyninae Skarbilovich, 1959.

The family Heteroderidae can be distinguished from the other families in the Tylenchoidea by the swollen to subspherical didelphic female without a tail; the swollen third- and fourth-stage juvenile; the twisted body of the male with very short or absent tail lacking the caudal alae.

**Subfamily Meloidogyninae**

Skarbilovich, 1959


**DIAGNOSIS EME NDED:** Family Heteroderidae. *Female.*—No irregular body annules around perineum. Excretory pore posterior to median bulb. Lip region with two lateral lips narrower than four sublateral. Stylet more than 20 μ. *Second-stage juvenile.*—Lips of labial region similar to female with well developed framework. Stylet robust, more than 20 μ. *Third- and fourth-stage juvenile.*—Stylet well developed, more than 20 μ. *Male.*—Lips and labial region similar to female. Testis single, with blunt anterior end.

*TYPE GENUS:* *Meloidogyne* Goeldi, 1892

*Syn. Caconema* Cobb, 1924
*Heterodera* in part of Müller, 1884 and Goodey, 1932
*Hypsoperine* Sledge and Golden, 1964

**DI FFERENTIAL DIAGNOSIS:** The subfamily Meloidogyninae can be recognized by the anterior position of the excretory pore and the irregular perineal pattern of the body annulation of the female; the large lateral lips of the lip region; the weakly developed labial framework and short, moderately developed stylet in the second-stage juvenile (under 20 μ); and the cap cell terminus of the testis in the male.

**Subfamily Heteroderinae**

Filipjev & Schuurmans Stekhoven, 1941


**DIAGNOSIS EME NDED:** Family Heteroderidae. *Female.*—No irregular body annules around perineum. Excretory pore posterior to median bulb; the swollen third- and fourth-stage juvenile; the twisted body of the male with very short or absent tail lacking the caudal alae.

**TYPE GENUS:** *Heterodera* Schmidt, 1871

*Syn. Heterobulbus* Railliet, 1896
*(Heterodera)* Skarbilovich, 1959
*(Globodera)* Skarbilovich, 1959

Nominal genera included: *Meloidodera* Chitwood, Hannon and Esser, 1956
*Cryphodera* Colbran, 1966
*Atalodera,* new genus
*Sarisodera,* new genus

*Genus inquirenda:* *Meloidoderita* Pogosyan, 1966

The genus *Meloidoderita* was described with a short stylet and large phasmids in the female in common with the Meloidogyninae. It also has the excretory pore posterior to the median bulb and the marking around the vulva as in the Heteroderinae. Therefore it does not appear to fit in either subfamily. The illustrations and the description indicate that it is closest to *Cryphodera.* Since type material or specimens were not available to confirm this, and the original description and illustrations are not considered adequate, *Meloidoderita* is placed in genus inquirenda.
DIFFERENTIAL DIAGNOSIS: The subfamily Heteroderinae can be distinguished from the subfamily Meloidogyninae by the more posterior position of the excretory pore and the absence of irregular body annules around the perineum of the female; the small lateral lips of the lip region, well developed labial framework and the longer (over 20 μ) robust stylet of the second-stage juvenile; the presence of a stylet in the third- and fourth-stage juvenile; and the absence of a cap cell terminus in the testis.

Genus *Heterodera* Schmidt, 1871
(Fig. 3 P–W)


TYPE SPECIES: *Heterodera schachtii* Schmidt, 1871

Syn. *Tylenchus schachtii* (Schmidt, 1871) Oerly, 1880

*Heterodera schachtii minor* O. Schmidt, 1930

Over 40 species have been described in this genus. Twenty nominal species and at least six species which appear to be undescribed from the nematode collection of the University of California, Riverside, were examined for this study.

The genus *Heterodera* can be identified by the cyst stage, the dorsal anus and fenestration around the vulva in the female; and the absence of a lens-like structure under the phasmids of the juveniles.

Genus *Meloidodera* Chitwood, Hannon and Esser, 1956
(Fig. 3 A–G)


Nominal species included: *M. charis* Hopper, 1960.

Species inquirendae:

*M. armeniaca* Pogosyan, 1960
*M. tadshikistanica* Kirjanova and Ivanova, 1966

*M. armeniaca* is based on one female (31) of which the head is missing. *M. tadshikistanica* has characters typical for the subfamily Meloidogyninae (26), but was placed in the genus *Meloidodera* because of the equatorial position of the vulva. Both of these species are considered inadequately described and, as material was not available for study, they are considered species inquirendae.

DIFFERENTIAL DIAGNOSIS: The genus *Meloidodera* can be distinguished from the genus *Heterodera* by the absence of a cyst
stage, the subequatorial position of the vulva and the annulated cuticle of the female; the lens-like structure under the phasmids of the juvenile; and the small male (under 1 mm), with distinct labial disc and short spicules (less than 30 μ).

Specimens of both nominal species were available for study and in addition at least one undescribed species was examined.

**Genus Cryphodera** Colbran, 1966

*Fig. 3 H-I*

**Cryphodera** Colbran, 1966: 41–47.


**Type Species:** *Cryphodera eucalypti* Colbran, 1966.

**Differential Diagnosis:** The genus *Cryphodera* is most closely related to the genus *Meloidodera* from which it differs only in the subterminal position of the vulva.

The type and only named species in the genus was available for study. In addition, at least two undescribed species were examined, one from Australia and one intercepted in a sample from Oregon, U.S.A.

**Genus Atalodera** new genus

*(Fig. 1 and Fig. 3 J-O)*

**Diagnosis:** Subfamily Heteroderinae. Female.—No cyst stage. Cuticle with lace-like pattern. Anus and vulva terminal, on prominence. No fenestration around vulva. **Second-stage juvenile.** —Labial disc absent. Stylet less than 30 μ. Esophageal glands do not fill body width. Phasmids with lens-like structure in muscle layer. **Male.** —To 1.5 mm. Region immediately behind lip region not constricted. Labial disc prominent. No longitudinal striations on basal lip annule. Tail present. Spicules more than 30 μ.

**Type Species:** *Atalodera ucri* new species.

**Differential Diagnosis:** The genus *Atalodera* is closest to the genera *Heterodera* and *Cryphodera*. It can be distinguished from *Heterodera* by the absence of a cyst and the terminal anus of the female; the lens-like structure associated with the phasmids and the narrow esophageal glands of the juvenile; and the prominent labial disc of the male. It differs from the genus *Cryphodera* in that the cuticle of the adult female is not annulated, and the vulva and anus are terminal; the narrow esophageal glands in the juvenile; and the larger males with longer spicules.

The name *Atalodera* is derived from the Greek *atalos* = “tender” and *deros* = “skin,” as modified into a Latin feminine by Schmidt (35) for *Heterodera*.

Juveniles identified as *Atalodera* have been collected from soil or roots from the following habitats and localities in southern California: *Haplopappus palmari* Gray, University of California campus, Riverside; *Adenostoma fasciculatum* Hooker and Arnott, from a hill east of the University of California, Riverside campus; *Salvia* sp., *Arabis pulchra* Jones, *Eriodictyon trichocalyx* Heller and *Haplopappus cooperi* (Gray) Hall from several localities in the Mojave Desert south of Victorville; *Salvia* sp. one mile northwest of Gilman Hot Springs, Riverside County; oak (*Quercus* sp.) and *Salvia* sp. from Bishop Ranch, Santa Barbara County; and *Styrax officinalis* L. var. *californica* (Torr.) Rehd. from...
Fig. 1. *Atulodera ucni* n. gen., n. sp. (A–E, juvenile) A. Face view; B. Anterior end; C. Esophagus; D. Posterior end, lateral; E. Posterior end, dorso-ventral; (F–I, male) F. Face view; G. Anterior end; H. Posterior end, lateral; I. Posterior end, dorso-ventral; (J–L, female) J. Face view; K. Anterior end; L. Female, entire; M. Male, entire.
Mount Palomar, San Diego County. Some of these juveniles appear to represent the same species, but they differ from the type species.

*Atalodera ucri* n. sp.

(Fig. 1 and Fig. 3 J–O)

**Measurements** (20♀ ♂ paratypes): L = 501 μ (360–680); width = 354 μ (275–439); a = 1.5 (1.0–2.2); stylet = 29 μ (26–32); length stylet knobs (11) = 2.4 μ (2.0–2.8); width stylet knobs (11) = 4.9 μ (4.1–5.5); O = 22 (13–30); length median bulb = 28 μ (26–36); width median bulb = 29 μ (24–36); length/width ratio median bulb = 0.97 (0.9–1.2); length valve in median bulb = 8.5 μ (7.2–10.0); width valve in median bulb = 6.7 μ (5.0–7.5); height vulva cone (10) = 70 μ (56–85); width cone base (10) = 92 μ (83–110); vulva-anus distance (9) = 17.7 μ (12–24); length vulva slit (11) = 34 μ (28–39); anus-Phasmid distance (7) = 17 μ (12–21).

(20♂ ♂ paratypes): L = 1296 μ (1036–1420); a = 53 (47–63); b = 10.5 (9.4–12.8); b’ = 5.4 (4.2–7.0); c (6) = 280 (276–468); stylet = 27 μ (24–29); length stylet knobs = 2.3 μ (2.0–2.6); width stylet knobs = 4.7 μ (4.0–5.5); O = 24 (15–34); hemizonid from anterior end (14) = 142 μ (123–178); gubernaculum = 11 μ (10–13); spicules = 35 μ (34–37).

(25 second-stage juvenile paratypes): L = 503 μ (450–555); a = 29 (25–34); b = 5.3 (4.7–5.7); b’ = 2.3 (2.0–2.6); c = 13.4 (12.3–15.5); stylet = 24 μ (23–25); length stylet knobs = 1.7 μ (1.5–2.0); width stylet knobs = 4.1 μ (3.5–5.0); O = 27 (21–33); hemizonid from anterior end = 103 μ (98–116); tail = 39 μ (29–42); H = 21 μ (15–24); phasmid from tail terminus = 31 μ (25–36).

(♀ holotype): L = 490 μ; width = 215 μ; a = 2.3; stylet = 27 μ; length stylet knobs = 2 μ; width stylet knobs = 4.5 μ; 0 = 20; length median bulb = 23 μ; width median bulb = 23 μ; length valve in median bulb = 8.5 μ; width valve in median bulb = 6.5 μ; excretory pore from anterior end = 102 μ (21 μ posterior to median bulb); vulva-anus distance = 22.5 μ; height vulva cone = 67 μ; width cone at base = 82 μ; cuticle thickness at mid-body = 10 μ. Female, young. Body asymmetrically swollen, contains approximately 30 eggs; egg size (6) 29 to 33 × 70 to 83 μ. Cuticle of head annulated from anterior end to middle of stylet, rest of cuticle with lace-like pattern. Lip region with distinct labial disc; first lip annule prominently set off. Stylet well developed, knobs rounded. Median bulb, spherical. Dorsal esophageal gland along ventral side of body; ventral glands looped laterally below dorsal gland.

(♂ paratypes): Young females elongate, ovaries do not fill body, increase gradually in size to a fully swollen, spherical, old female filled with eggs. Maximum number of eggs observed per female approximately 300. Vulva cone distinct, flattened posteriorly. Body pearly white, covered with distinct sub-crystalline layer. Neck bends dorsally, ventrally or laterally. Labial disc in *en face* view tetraradiate, narrow lateral lips difficult to see. Dorsal gland in fully swollen females greatly expanded with large vacuole below nucleus. Ventral glands appear as small appendix below the dorsal gland.

(♂ allotype): L = 1220 μ; a = 50.1; b = 11.0; b’ = 5.5; stylet = 28 μ; length stylet knobs = 2.5 μ; width stylet knobs = 5 μ; O = 16; hemizonid from anterior end = 111 μ; excretory pore—hemizonid = 9.0 μ; gubernaculum = 11 μ; spicules = 35 μ. Lip region with pronounced labial disc, four lip annules. Stylet knobs sloping. Median bulb 16 μ long, 9 μ wide; valve obscure. Esophageal glands overlap five times body width, fill ventral half of body; nuclei obscure. Lateral field with four incisures, approxi-

(♂ paratypes): Lip region with 3–6 annules. Excretory pore anterior, posterior or at position of hemizonid. Esophageal glands narrow, middle of overlap usually fills ventral half of body. All males were isolated from soil.

Second-stage juveniles (paratypes): Lip region with 4 annules, basal annule slightly wider than anterior ones. Anterior cephalid two annules below the lip region, posterior cephalid at middle of stylet. Stylet knobs round or anteriorly flattened. Procorpus constricted immediately anterior to median bulb. Median bulb ovate. Esophageal glands fill about the ventral half of the body; nucleus of dorsal gland larger than nuclei of ventral glands. Hemizonid at position of or one annule anterior to excretory pore. Lateral field with three incisures; outer incisures smooth; near phasmids crenate. Phasmids with asymmetrical lens-like structure immediately under muscle layer.

Holotype: Female collected by W. M. Wouts, April 14, 1969, catalog number 16 University of California Nematode Collection, Riverside, California.

Allootype: Male, same data except collected March 26, 1969, catalog number 17.

Paratypes: 133 ♀♂, 76 ♂♂, 136 juvenile paratypes from same locality as holotype, distributed as follows: 56 ♀♀, 17 ♂♂, 41 juveniles, Department of Nematology, University of California, Riverside; 34 ♀♀, 9 ♂♂, 23 juveniles, Department of Nematology, University of California, Davis, catalog numbers UCNC 175–177; 10 ♀♀, 16 ♂♂, 23 juveniles, Nematode Collection Entomology Division, DSIR, Nelson, New Zealand; 8 ♀♀, 7 ♂♂, 9 juveniles, USDA Nematode Collection, Nematology Investigations, Beltsville, Maryland; 5 ♀♀, 9 ♂♂, 13 juveniles, Nematology Department, Rothamsted Experimental Station, Harpenden, England; 6 ♀♀, 6 ♂♂, 10 juveniles, Nematode Collection Agricultural University, Wageningen, the Netherlands; 4 ♀♀, 6 ♂♂, 8 juveniles, Nematode Collection, Entomology Research Institute, Central Experimental Farm, Ottawa, Canada; and 10 ♀♀, 6 ♂♂, 10 juveniles, Entomology Laboratory, Department of Primary Industries, Brisbane, Queensland, Australia.

Type habitat and locality: Soil and roots of *Haplopappus palmari* Gray in the uncultivated eastern part of University of California campus, Riverside, California.

Diagnosis: Atalodera ucri can be distinguished from the two undescribed species examined by the well-developed stylet and the large vacuole in the dorsal esophageal gland of the fully developed female; also the low dorsal esophageal gland opening, the three lateral incisures, the asymmetrical lens-like structure under the phasmid, and relatively short tail of the second-stage juvenile.

Specimens of *Atalodera ucri* have been collected only from the type locality. All stages were collected only during April, males during March and April and juveniles were obtainable all year.

Genus Sarisodera new genus

(Fig. 2 and Fig. 3 X-AA)

Fig. 2. Sarisodera hydrophila n. gen., n. sp. (A–E, juvenile) A. Face view; B. Anterior end; C. Esophagus; D. Posterior end; E. Tail near phasmids, ventral view: (F–I, male) F. Anterior end; G. Esophagus; H. Posterior end, lateral; I. Posterior end, dorso-ventral: (J–L, female) J. Face view; K. Anterior end; L. Outline.
Fig. 3. Subfamily Heteroderinae. (A–B) Meloidodera floridensis, juvenile. A. Face view; B. Phasmids, dorso-ventral: M. charis. C. Phasmids, dorso-ventral, juvenile: (D–F, male) D. Posterior end; E. Anterior end; F. Face view: Meloidodera sp. G. Outline female: (H–J) Cryptodera sp. H. Anterior end, juvenile; I. Outline female: (J–O) Atalodera ucri n. gen., n. sp. J. Esophageal glands, juvenile; K. Phasmids, dorso-ventral, juvenile; L. Posterior end, male; M. Anterior end,
TYPE SPECIES: Sarisodera hydrophila
new species

DIFFERENTIAL DIAGNOSIS: The genus Sarisodera is closest to the genus Heterodera with which it shares the ability to form a cyst. It can be distinguished from all the genera in the subfamily Heteroderae by the vulva sunken into the vulva cone, the anus located on the upper inside of the dorsal vulva lip, the long stylet and the absence of the male tail. It can further be distinguished from Heterodera by the lens-like structure associated with the phasmids in the juvenile.

The name Sarisodera is derived from the Greek sarisa = "long Macedonian pike" and deros = "skin," as modified into a Latin feminine by Schmidt (35) for Heterodera.

Specimens of the genus Sarisodera have been collected from soil or roots from the following habitats and localities in California: willow (Salix lasiolepis Benth.), 12 miles east of Temecula, Riverside County; fern and Laurel sp., University of California, Berkeley; fern, Humboldt County; Lyono-thamnus floribundus Gray, Santa Cruz Island; Pinus sp., Monterey; and Quercus sp., Santa Barbara. Specimens reported as Heterodera sp. by Nickle (28) from white pine (Pinus monticola Dougl.) in Idaho have been identified as belonging to the genus Sarisodera. These collections appear to represent at least five species. Sufficient specimens of only the following species were available for an adequate description.

Sarisodera hydrophila n. sp.

MEASUREMENTS: (19♀♂ paratypes) L = 565 μ (359-688); width = 385 μ (238-481); a = 1.5 (1.2-1.8); stylet = 51 μ (45-56); length stylet knobs = 3.3 μ (2.6-4.1); width stylet knobs = 7.3 μ (6.0-9.0); O (6) = 9.0 (6.5-12.3); length median bulb = 28 μ (23-35); width median bulb = 25 μ (19-32); length/width ratio median bulb = 1.1 (0.9-1.4); length valve in median bulb = 6.4 μ (5.1-8.5); width valve in median bulb = 4.9 μ (4.4-9.8); length vulva slit = 72 μ (62-85).

(20♂♂ paratypes): L = 1053 μ (597-1405); a = 46 (33-55); b = 7.3 (5.0-9.4); b' = 5.3 (4.0-6.5); stylet = 43 μ (38-46); length stylet knobs = 2.7 μ (2.3-3.6); width stylet knobs = 6.5 μ (5.0-7.0); o = 9.6 (7.0-12.6); hemizonid from anterior end (15) = 155 μ (112-203); gubernaculum (10) = 14 μ (12-18); spicules (10) = 39 μ (33-46).

(25 second-stage juvenile paratypes): L = 579 μ (466-558); a = 26 (24-28); b = 3.6 (3.3-3.9); b' = 2.2 (1.9-2.4); c = 9.7 (9.0-10.6); stylet = 40 μ (39-43); length stylet knobs = 3.4 μ (3.0-3.8); width stylet knobs = 7.4 μ (6.9-8.0); o = 11 (8-14); hemizonid from anterior end = 122 μ (113-131); tail = 54 μ (44-61); H = 31 μ (26-36); phasmid from tail terminus = 46 μ (37-50).

(♀ holotype): L = 610 μ; width = 385 μ; a = 1.6; stylet = 50 μ; length median bulb = 35 μ; width median bulb = 29 μ; length valve in the median bulb = 7.7 μ; width valve in median bulb = 4.5 μ; excretory pore from the anterior end = 162 μ; thickness of cuticle at mid-body = 19 μ. Body fully swollen, head asymmetrically placed. Cuticle with lace-like pattern. Stylet distinctly visible. Median bulb oval, valve distinct. Dorsal esophageal gland approximately size of...
median bulb, ventral glands obscure. Body with approximately 70 eggs, size of eggs (3) 38 to 42 x 110 μ. Vulva lips broadly rounded, anus on ventral side of dorsal vulva lip.

(♀ paratypes): Young females oval, ovaries do not fill body, increase in size during development to old female. Fully swollen females longer than wide. Maximum number of eggs per female approximately 400. Posterior end characterized by distinct vulva lips without distinct cone. Cyst yellow to reddish-brown. Lip region with distinct labial disc and prominently set off first lip annule. Body cuticle at anterior end annulated, annulation not extending posterior to middle of stylet. Median bulb usually distinctly longer than wide.

(allotype) L = 1240 μ; a = 51.7; b = 8.5; b' = 6.0; stylet = 44 μ; length stylet knobs = 3.5 μ; width stylet knobs = 7.5 μ; O = 16; length median bulb = 19 μ, width median bulb = 10 μ; length valve = 4 μ, width valve = 2 μ; hemizonid from anterior end = 161 μ; excretory pore from anterior end = 177 μ; gubernaculum = 16.5 μ; spicules = 45 μ. Lip region slightly set off, 6 lip annules. Stylet knobs slightly sloping. Lateral field with 4 incisures, approximately ½ of body width wide, outer incisures crenate. Excretory pore 5 annules posterior to the hemizonid. Hemizonid almost 2 annules long. Esophageal glands overlap intestine ventrally two times body width; anterior half fills body width, posterior half fills ½ of body width; esophageal nuclei distinct, of equal size, two located in anterior half, one in posterior half of overlap. Tail absent. Spicules almost straight, protruding from ventral side of body terminus in a conical extension of the cuticle (spicular sheath); spicular sheath opening with fine, dorsal and ventral micro-spines. Gubernaculum slightly curved, anterior half wider than posterior half.

(♂ paratypes): Lip region with 5–8 annules. Stylet knobs sloping. Excretory pore 1–7 annules posterior to hemizonid. Esophageal glands usually fill body width. Males were extracted primarily from the roots in a mist chamber.

SECOND-STAGE JUVENILES: (paratypes) Lip region with 4 annules. Stylet knobs flattened. Procorms constricted immediately anterior to median bulb. Median bulb oval. Esophageal glands fill the body width, overlap intestine ventrally and laterally; nucleus of dorsal gland larger than nuclei of ventral glands. Lateral field with 4 incisures. Phasmids with symmetrical lens-like structure immediately under the muscle layer.

HOLOTYPE: Female collected by W. M. Wouts, July 19, 1969, catalog number 18 University of California Nematode Collection, Riverside, California.

ALLOTYPE: Male same data except collected June 26, 1969, catalog number 19.

PARATYPES: 187 ♀ ♀, 152 ♂ ♂, 153 juveniles distributed as follows: 98 ♀ ♀, 55 ♂ ♂, 63 juveniles, Department of Nematology, University of California, Riverside; 34 ♂ ♀, 12 ♂ ♂, 12 juveniles, Department of Nematology, University of California, Davis, catalog numbers UCNC 178–181; 29 ♀ ♀, 29 ♂ ♂, 15 juveniles, Nematode Collection, Entomology Division, DSIR, Nelson, New Zealand; 3 ♀ ♂, 6 ♂ ♂, 15 juveniles, USDA Nematode Collection, Nematology Investigations, Beltsville, Maryland; 8 ♀ ♀, 13 ♂ ♂, 11 juveniles, Nematology Department Rothamsted Experimental Station, Harpenden, England; 3 ♀ ♂, 15 ♂ ♂, 12 juveniles, Agricultural University, Wageningen, the Netherlands; 3 ♀ ♂, 13 ♂ ♂, 14 juveniles, Nematode Collection, Entomology Research Institute, Central Experimental Farm, Ottawa, Canada; and 9 ♀ ♀, 9 ♂ ♂, 11 juveniles, Entomology Laboratory, Department of Primary Industries, Brisbane, Queensland, Australia.
**TYPE HABITAT AND LOCALITY:** Soil and roots of willow (Salix lasiolepis Benth.) in Arroyo River, 12 miles east of Temecula, Riverside County, California.

**DIAGNOSIS:** Sarisodera hydrophila can be distinguished from the five undescribed species examined, by the long stylet in all stages, the lace-like pattern of the cuticle and the oval shape of the female; the four lateral incisures, the stylet with anteriorly flattened knobs and the short tail of the second-stage juvenile.

Specimens of Sarisodera hydophila have been collected only from the type locality. All stages of the life cycle could be obtained at any time of the year.

**KEY TO THE GENERA OF THE SUBFAMILY HETERODERINAE**

1. Female cuticle not annulated, juveniles without labial disc, spicules more than 30μ long .......................................................... 2

2. Female cuticle annulated, juveniles with indistinct labial disc, spicules less than 30μ long ........................................... 4

2. Females not forming a cyst, esophageal glands of the juveniles do not fill the width of the body, males with labial disc ............ Atalodera n. gen.

Females forming a cyst, esophageal glands in the juveniles fill the width of the body, males without labial disc .......................... 3

3. Vulva not sunken into a terminal cone, anus not on vulva lip, juvenile stylet less than 30μ long, males with tail .... Heterodera 

Vulva sunken into a terminal cone, anus on vulva lip, stylet juvemile more than 38μ long, males without tail - Sarisodera n. gen. 4

4. Vulva close to anus (subterminal) ..................................... 5

Vulva some distance away from anus (sub-equatorial) ............................... Meloidodera

**DISCUSSION**

Well defined morphological, biological and cytogenetic differences separate the subfamilies Heteroderinae and Meloidogyninae. These include: size of the lateral lips in the lip region; position of the excretory pore and type of cuticle in the female; length and development of stylet and labial framework in the juvenile (stylet absent in third and fourth stage Meloidogyne juveniles); testis morphology; host parasite relationships; host range; habitat; chromosome morphology, number, and composition (45); and symptoms and signs of disease. On the basis of these differences Heteroderidae is considered to contain two subdivisions as proposed by Paramonov (30).

The main features distinguishing the genera of the subfamily Heteroderinae are listed in Table 1 and illustrated in Fig. 3. The genera are first grouped on the basis of annulated and non-annulated female cuticle, then the latter are subdivided into cyst-forming and non-cyst-forming. Several characters in the female and the male separate the non-annulated and annulated forms. The annulated genera include Meloidodera and Cryphodera. They differ from each other only in the position of the vulva; thus the female is essential for separation of these genera. Within the genera with non-annulated females the differences between the females, males and juveniles of the non-cyst-forming, Atalodera, and the cyst-forming, Heterodera and Sarisodera, are very pronounced. Sarisodera is unique in having a long stylet, the sunken vulva and the anus on the inside of the dorsal vulva lip.

Within Heterodera, the largest and best known genus, many different forms are represented. Several workers have tried to combine these. Cooper (12) used the bullae and number of fenestrae in the vulva cone of the cyst; Decker (13), Skarbilovich (39), Taylor (42) and Triantaphyllou (46) used the shape of the cyst to define the groups they proposed. Intensive comparative study of all stages of Heterodera is needed for an understanding of the speciation and phylogeny within this group.

The Heteroderinae are considered to have evolved from slender didelphic plant-parasitic nematodes with annulated cuticle, short
TABLE 1. Genera-differentiating characters within subfamily Heteroderinae.

<table>
<thead>
<tr>
<th>Comparison feature</th>
<th>Females annulated</th>
<th>Females not annulated</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Meloidodera</td>
<td>Cryphodera</td>
</tr>
<tr>
<td>Adult size</td>
<td>small</td>
<td>small</td>
</tr>
<tr>
<td>Stylet</td>
<td>short</td>
<td>short</td>
</tr>
<tr>
<td>Vulva</td>
<td>subequatorial</td>
<td>subterminal</td>
</tr>
<tr>
<td>Annulation,♀ cuticle</td>
<td>present</td>
<td>present</td>
</tr>
<tr>
<td>Cyst</td>
<td>absent</td>
<td>absent</td>
</tr>
<tr>
<td>Labial disc, juvenile</td>
<td>present</td>
<td>present</td>
</tr>
<tr>
<td>Longit. ann., δ lip</td>
<td>present</td>
<td>present</td>
</tr>
<tr>
<td>Labial disc, δ</td>
<td>present</td>
<td>present</td>
</tr>
<tr>
<td>Constricted neck, δ</td>
<td>present</td>
<td>present</td>
</tr>
<tr>
<td>Spicules</td>
<td>short</td>
<td>short</td>
</tr>
<tr>
<td>Tail, δ</td>
<td>present</td>
<td>present</td>
</tr>
<tr>
<td>Esoph. gland, juvenile</td>
<td>wide</td>
<td>wide</td>
</tr>
<tr>
<td>Phasmid lens, juvenile</td>
<td>present</td>
<td>present</td>
</tr>
</tbody>
</table>

tail, large phasmds, longitudinally striated lip annules and four lateral incisures; a form equal or close to the Hoplolaiminae. Supporting this theory, Heteroderinae juveniles closely resemble the recently described second-stage juveniles of *Hoplolaimus concaudajuvencus*, Golden and Minton, 1970 (19) and juveniles and males of *Meloidodera* and *Cryphodera* have longitudinally striated lip annules as in *Hoplolaimus* (37). Since *Meloidodera* has a subequatorial vulva in common with species in Hoplolaiminae, that genus is considered most primitive. *Cryphodera* is considered to have evolved from *Meloidodera* via a shift of the vulva, to a more efficient posterior position which enables the female to lay eggs outside the roots, even when her body is still partially embedded in the root. The two genera are identical in all other characters (Fig. 3). *Atalodera* is considered to have evolved from *Cryphodera* through cuticular changes which permitted the adult to grow larger, but distorted the annulation. The considerable differences between *Atalodera* and *Cryphodera*, most probably indicate that several non-cyst forming non-annulated forms developed at this level of evolution of which three genera are probably present in southern California. From these, *Heterodera* and *Sarisodera* could have evolved by acquiring the ability to form a cyst. *Heterodera* developed a dorsal anus in the female, lost the large phasmid in the juvenile, but retained the shorter stylet and the short male tail of its ancestors. Simultaneously, *Sarisodera* retained the terminal anus and the large phasmid in the juvenile but developed a sunken vulva in the female,
a long stylet in all stages and lost the tail in the male. These changes can be best understood by assuming that Sarisodera and Heterodera evolved along two different evolutionary lines, Sarisodera from a short styled, non-annulated, non-cyst forming genus with a sunken vulva, as has been seen in an undescribed genus from southern California and Heterodera from a form with a terminal vulva close to Atalodera.

The subfamily Heteroderinae is considered to be a large well-defined group widely separated from Meloidogyninae. With the increasing number of genera it may become necessary to subdivide it into groups of genera, probably based on the annulated cuticle and the ability to form a cyst, each group of genera representing a subfamily in the family Heteroderidae. None of these, however, resemble Meloidogyninae, which would, therefore, be removed from Heteroderidae. The unique characters of Meloidogyninae make inclusion in other families of the Tylenchoidea impossible and separation of Meloidogyninae from Heteroderidae will therefore most probably result in elevation of this subfamily to family rank. At this time, however, such decisions are not justified.

**Literature Cited**

41. Small, R. H. And R. J. Minette. 1969. Mist chamber for recovery of nematodes from plant roots. Mimeograph, Nematology Department, Univ. of California, Riverside.