

## Description of *Atalodera gibbosa* n. sp. and synonymization of *Thecavermiculatus* Robbins, 1978 to *Atalodera* Wouts & Sher, 1971 (Nemata : Heteroderidae) <sup>(1)</sup>

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**Summary** – *Atalodera gibbosa* n. sp. is a parasite of the grass *Trachypogon montufoi* Nees (Poaceae) in Brazil. This new species is characterized by a large stylet, spicules, vulval slit and vulva-anus distance, profile of the vulval region varying from no or small protuberance to typical vulval cone, both eggs and hatched second-stage juveniles (J2) retained in female body, cloacal tubus present, and in J2 oesophageal glands filling body cavity, and three atypical lateral lines. Because of this nematode overlapping the previously differentiated characters, *Thecavermiculatus* Robbins, 1978 is synonymized to *Atalodera* Wouts & Sher, 1971. In the field, the nematode populations were high and fluctuated during the wet season, and low and reduced in reproduction during the dry season in which J2 in hatched form and within eggs survived inside the female body.

**Résumé** – Description d'*Atalodera gibbosa* n. sp. et synonymisation de *Thecavermiculatus* Robbins, 1978 avec *Atalodera* Wouts & Sher, 1971 (Nemata : Heteroderidae) – *Atalodera gibbosa* n. sp. est parasite de la graminée *Trachypogon montufoi* Nees (Poacées) au Brésil. Cette nouvelle espèce est caractérisée par : la grande longueur du stylet, des spicules, de la fente vulvaire et de la distance vulve-anus, ainsi que par le profil variable de la région vulvaire – continu, faible protubérance ou cône vulvaire typique – les œufs et les juvéniles de deuxième stade (J2) éclos conservés dans le corps de la femelle, la présence d'un tube cloacal, les glandes œsophagiennes remplissant la cavité du corps des J2 et enfin le champ latéral constitué de trois lignes atypiques. *Thecavermiculatus* Robbins, 1978 est synonymisé à *Atalodera* Wouts & Sher, 1971. Au champ, les populations du nématode sont élevées et fluctuantes pendant la saison humide, tandis qu'elles sont faibles et la reproduction réduite durant la saison sèche pendant laquelle les J2 survivent à l'intérieur du corps de la femelle (dans les œufs ou libres après éclosion).

**Key-words** : *Atalodera*, *Thecavermiculatus*, *Trachypogon montufoi*, taxonomy, Heteroderinae.

While studying nematode fauna in natural and cultivated "cerrados" (savanna) of central Brazil during 1988-1989 Cares and Huang (1991) found some second-stage juveniles (J2) with large stylet and lens-like phasmids, belonging to the subfamily Heteroderinae. In 1990-1991, a number of females, males and J2 of this nematode were successfully collected from the same sampling site for further characterizations (Souza, 1992). This article describes this nematode as a new species of *Atalodera* Wouts & Sher, 1971 (*A. gibbosa* n. sp.), and proposes *Thecavermiculatus* Robbins, 1978 as a junior synonym of *Atalodera*. Also, ecological studies are reported on its population.

### Materials and methods

For morphological studies, the nematodes were killed by gentle heating, fixed with Golden solution (Hooper,

1970), and mounted in glycerine, according to Seinhorst (1959), for observation under an optical microscope. Many specimens were fixed with formaldehyde/glutaraldehyde solution, dehydrated by series of acetone concentrations, dried at critical point with carbon dioxide, and coated with gold for observation under the scanning electron microscope (SEM) JEOL JSM 840 A (5 kV) (Eisenback, 1985).

For ecological studies, soil and root samples were collected twice a month from August 14, 1990 to October 11, 1991 at many random points of the area (about 400 m<sup>2</sup>) situated in the recorded location. The nematodes were extracted from 1 dm<sup>3</sup> soil of composted samples by the flotation-sedimentation-sieving techniques (Flegg & Hooper, 1970) and clarified by the centrifugal flotation technique (Jenkins, 1964), and then the numbers of J2 counted. On the other hand, ten mature females were randomly removed from the root

(1) A part of the MS thesis of the first author.

samples, and their body content released for counting numbers of eggs and juveniles. Soil water content was determined by counting the different weights before and after drying at 110 °C for 72 h. Correlation coefficients between soil water content and nematode populations were calculated.

*Atalodera gibbosa* \* *n. sp.*  
(Figs 1-4, 7)

MEASUREMENTS

See Table 1.

DESCRIPTION

*Females*: Body white, oval, no cyst formed. Neck elongate  $118 \pm 28.1$  (71-210)  $\mu\text{m}$ , laterally projecting out of body at about right angle, showing hunchbacked shape at the anterior part. Subcrystalline layer present. Anterior half or two-thirds of the neck annulated. The rest of the neck with transversal lines of tubercles. In some specimens, the anterior neck showing asymmetrical expansion. Presence of "collar" at six to fourteen annuli after the labial region, composed of one to four transverse annuli with longitudinal wrinkles. After the "collar", cuticle thickness increasing from 0.5 to 1.2  $\mu\text{m}$  and neck diameter from 1.5 to 5.0  $\mu\text{m}$ . The surface of the oval body decorated with lace-like pattern. The surface of vulval region with rough transversal annuli clearly separated from the body, with or without small tubercles. The surface of the internal vulval lips with wrinkle at dorsal-ventral direction, and the external vulval lips with irregular or lateral wrinkles. Labial disc elevated, circular, irregular, square or rectangular with raised ring in the centre; lips fused to form round or irregular cephalic plate. Anastomoses present in the annuli of head region. Amphids visible. Stylet straight or with little inclination at conus, with round knobs. Procorpus bulky, with constriction joining to metacarpus. Metacarpus globose localized at the level of body "shoulder", and its valve a little behind the centre. Cardia at the level of dorsal oesophageal gland which is  $34.8 \pm 7.3$  (23.5-47.8)  $\mu\text{m}$  long and  $23.3 \pm 4.0$  (17.5-29.6)  $\mu\text{m}$  wide, lobelike and overlapping on subventral glands. Length of three glands,  $63.9 \pm 12.8$  (48.0-85.5)  $\mu\text{m}$ . Excretory pore located at the level of dorsal gland and cardia. Profile of vulval region varied from no or small protuberance to typical vulval cone, but females with vulval cone predominated in the population. Vulva predominantly terminal, but few subterminal found. Vulval slit never sunken. Bullae, fenestra and underbridge not observed. Fourteen to sixteen vulval protractor muscles distinct. Anus located near the dorsal margin of vulval cone. Phasmids not observed. Fifty five (9-124) eggs ( $119 \times 48.7 \mu\text{m}$ ) and hatched J2 found

inside female body. Gelatinous matrix without eggs present beside some females.

*Males*: Body vermiform, curved ventrally and twisted at posterior region. Cephalic region offset from the body contour, formed by three to five transverse annuli with many longitudinal and transverse striae. En face pattern round, with labial disc oblong or round. Submedian lips fused or not, but separated from two lateral lips in which the amphids are situated. Anterior cephalids located at 8th to 11th body annule; posterior cephalids two and a half to three annuli posterior to the anterior ones. Stylet robust, and straight; guiding ring localized at posterior one-fifth part of conus; knobs anchor-like. Median bulb ellipsoidal,  $97.4 \pm 15.7$  (75.5-117)  $\mu\text{m}$  from anterior end, valve at or a little behind the centre. Hemizonid lens-like, one and a half annuli long, two to twenty annuli behind the metacarpus. Excretory pore located at seven annuli posterior to hemizonid, and seven to eight annuli anterior to hemizonid which is 0.5 annuli long. Distance from anterior end to hemizonid and to hemizonion,  $140 \pm 17.1$  (114-173)  $\mu\text{m}$  and  $180 \pm 18.4$  (152-212)  $\mu\text{m}$ , respectively. Tail smooth, round and short, but two specimens showing no tail. Cloacal tubus short, gubernaculum present, spicules curved. Lateral field with four incisures which may or may not be areolated with dots. Phasmids not observed.

*Juveniles*: Cephalic region offset from body, three transverse annuli without anastomoses. The en face pattern oblong or hexagonal, with or without indentation at one of the fused submedian lip pairs. Labial disc fused with submedian lips only, or also completely or incompletely fused with lateral lips in which amphids are localized. In some specimens, the centre of labial disc is slightly elevated. None of these en face patterns predominated in the population. Anterior cephalids located at 8th to 10th body annule, and posterior cephalids, three annuli behind. Stylet robust and straight, and its knobs anchor-like. Median bulb ellipsoidal, with valve at or a little behind the centre. Oesophageal glands filling body cavity. Hemizonid lenslike, one and a half annuli long,  $133 \pm 3.6$  (101-124)  $\mu\text{m}$  from anterior end, eight to twenty annuli posterior to metacarpus and fourteen annuli anterior to hemizonion, which is  $136 \pm 7.4$  (125-147)  $\mu\text{m}$  from anterior end. Excretory pore just below hemizonid. Genital primordium  $12.2 \pm 1.6$  (9.8-15.7)  $\mu\text{m}$  long and distance from anterior end/body length  $57 \pm 4.2$  (53.8-62.4) %. Tail tapering or conoid, and hyaline region longer than half of tail length. Phasmids lens-like, one to one and a half annuli long and three annuli posterior to anus. Lateral field with three areolated incisures - the central one distinct, deep and through whole body, and at its sides two trace-like and discontinuous incisures.

\* From the Latin adjective *gibbosus* = hunchbacked.

**Table 1.** Morphometrical characters of *Atalodera gibbosa* n. sp. (all measurements in  $\mu\text{m}$ ).

Character	FEMALE		MALE		JUVENILE		Holotype	Allotype
	n	X $\pm$ SE (min-max)	n	X $\pm$ SE (min-max)	n	X $\pm$ SE (min-max)		
L	26	806 $\pm$ 100 (623-992)	15	1286 $\pm$ 177 (930-1551)	90	528 $\pm$ 28.5 (445-646)	954	1027
L dilat. portion	81	503 $\pm$ 52.6 (395-630)					598	
Width	81	339 $\pm$ 48.4 (251-455)	13	33.2 $\pm$ 4.3 (26.9-43.3)	83	19.8 $\pm$ 1.2 (18.1-25.3)	372	27.5
a	28	2.3 $\pm$ 0.3 (1.5-2.8)	13	38.7 $\pm$ 6.4 (28.4-52.2)	83	26.6 $\pm$ 1.7 (21.6-30.7)	2.6	37.3
Lip region (height)			13	7 $\pm$ 0.6 (6.1-8.3)	51	5.3 $\pm$ 0.4 (4.4-6.6)		7.6
Lip region (width)			13	11.9 $\pm$ 0.6 (10.8-12.7)	51	11.3 $\pm$ 0.5 (10-12.1)		11.5
Stylet	25	39 $\pm$ 2.3 (34.5-42.4)	14	38.7 $\pm$ 2.3 (32.7-42.5)	71	34.8 $\pm$ 1.5 (31-39.2)	40.7	40.2
Stylet conus	23	21.2 $\pm$ 1.3 (18.9-23.5)	13	19.6 $\pm$ 0.9 (18.1-21.6)	71	17.1 $\pm$ 0.8 (14.7-18.6)	21.6	19.1
Stylet shaft	17	15.5 $\pm$ 1.3 (12.8-17.6)	14	15.9 $\pm$ 0.8 (14.1-17.3)	71	14.5 $\pm$ 1 (12.2-18.6)	16.2	16.7
M %					68	49.3 $\pm$ 2.3 (43.6-53.8)	...	...
Knobs (height)	17	2.8 $\pm$ 0.4 (2.2-3.7)	13	3.6 $\pm$ 0.3 (3.2-4.4)	71	3.2 $\pm$ 0.4 (2-4.4)	2.9	4.4
Knobs (width)	24	4.9 $\pm$ 0.8 (3.4-7.1)	13	7.3 $\pm$ 0.5 (6.4-8.1)	71	7.1 $\pm$ 0.4 (6.4-8.3)	4.9	8
DGO	15	5.6 $\pm$ 1 (3.9-6.9)	11	3.6 $\pm$ 0.6 (2.7-4.6)	71	4.9 $\pm$ 0.6 (3.9-6.4)	...	3.4
0 %					68	14.2 $\pm$ 1.9 (10.5-19.5)	...	...
Median bulb (length)	43	30.7 $\pm$ 4 (24-42)	8	16.6 $\pm$ 1.8 (14.7-20.6)	39	15.1 $\pm$ 1.1 (12.2-18.4)	29.3	14.7
Median bulb (width)	43	25.3 $\pm$ 3 (18.7-31.6)	7	10.5 $\pm$ 0.8 (9.6-11.5)	40	10.1 $\pm$ 0.8 (8.8-12.5)	26	9.6
Excr. pore-ant. end	12	163 $\pm$ 31.6 (105-225)	6	145 $\pm$ 14.4 (131-166)	30	116 $\pm$ 5.5 (105-128)	...	131
Excr. pore (%)	6	21.9 $\pm$ 4.8 (15.6-28.7)	6	11.6 $\pm$ 1.4 (10.1-14.6)	30	22.1 $\pm$ 1.1 (18.5-24.3)	...	11.6
Vulval cone (height)	50	52.2 $\pm$ 9.3 (25.1-70.8)					60.8	
Vulval cone (width)	50	137 $\pm$ 15.7 (99.4-175)					160	
Vulva-anus distance (lat. view)	50	35.5 $\pm$ 4.9 (25-55.6)					38.6	
Vulval slit length	22	53.3 $\pm$ 6.1 (39.2-65.5)					...	

Table 1. Continued

Character	FEMALE		MALE		JUVENILE		Holotype	Allotype
	n	X ± SE (min-max)	n	X ± SE (min-max)	n	X ± SE (min-max)		
Spicules			9	39.2 ± 3 (34.8-44.1)				...
Gubernaculum			5	13.3 ± 1.4 (10.8-14.7)				...
Tail			9	3.9 ± 1.2 (2-5.6)	54	65.4 ± 5 (51.3-75.5)		5.6
Hyaline region					74	42 ± 4.3 (29.5-51)		

## DIAGNOSIS AND RELATIONSHIPS

*Atalodera gibbosa* n. sp. is characterized by the following combination of characters: great variability in the profile of vulva-anus region, great spicule length, great length of stylet in female, J2 and male, and three lateral incisures, three lip annuli and oesophageal glands filling the body cavity in J2.

*A. gibbosa* n. sp. is close to *A. trilineata* Baldwin, Bernard & Mundo-Ocampo, 1989 and *A. festucae* Baldwin, Bernard & Mundo-Ocampo, 1989, and can be distinguished by profile of vulval region (see Table 2) and vulva-anus distance ( $35.5 \pm 4.9$  vs  $19.1 \pm 2.0$  and  $14.5 \pm 2.9$   $\mu\text{m}$ , respectively) in female, and width of oesophageal glands (filling vs half and less than half body cavity, respectively) and en face pattern (fused vs defined labial disc) in J2. *A. gibbosa* n. sp. can be also distinguished from *A. festucae* by longer stylet of female ( $39 \pm 2.3$  vs  $25.5 \pm 2.7$   $\mu\text{m}$ ) and male ( $38.7 \pm 2.3$  vs  $30.6$   $\mu\text{m}$ ), longer spicules ( $39.2 \pm 3.0$  vs  $34.6$   $\mu\text{m}$ ), en face pattern of male (see Figure 6), and discontinuity and number of J2 incisures (three vs four).

## TYPE HOST AND LOCALITY

*Atalodera gibbosa* n. sp. was collected from rhizosphere and roots of the grass *Trachypogon montuformi* Nees (Poaceae), growing beside the highway Belém-Brasília, about 20 km from Planaltina (DF), Brazil.

## TYPE SPECIMENS

Holotype female, allotype male and paratypes were deposited in the Nematode Collection of Departamento de Fitopatologia, Universidade de Brasília, Brasília, Brazil.

Paratypes with five females and ten J2 also deposited at Muséum National d'Histoire Naturelle, Paris, France, and Department of Nematology, University of California, Riverside, California, USA.

***Atalodera* Wout & Sher, 1971**  
**= *Thecavermiculatus* Robbins, 1978, n. syn.**

## DIAGNOSIS AMENDED

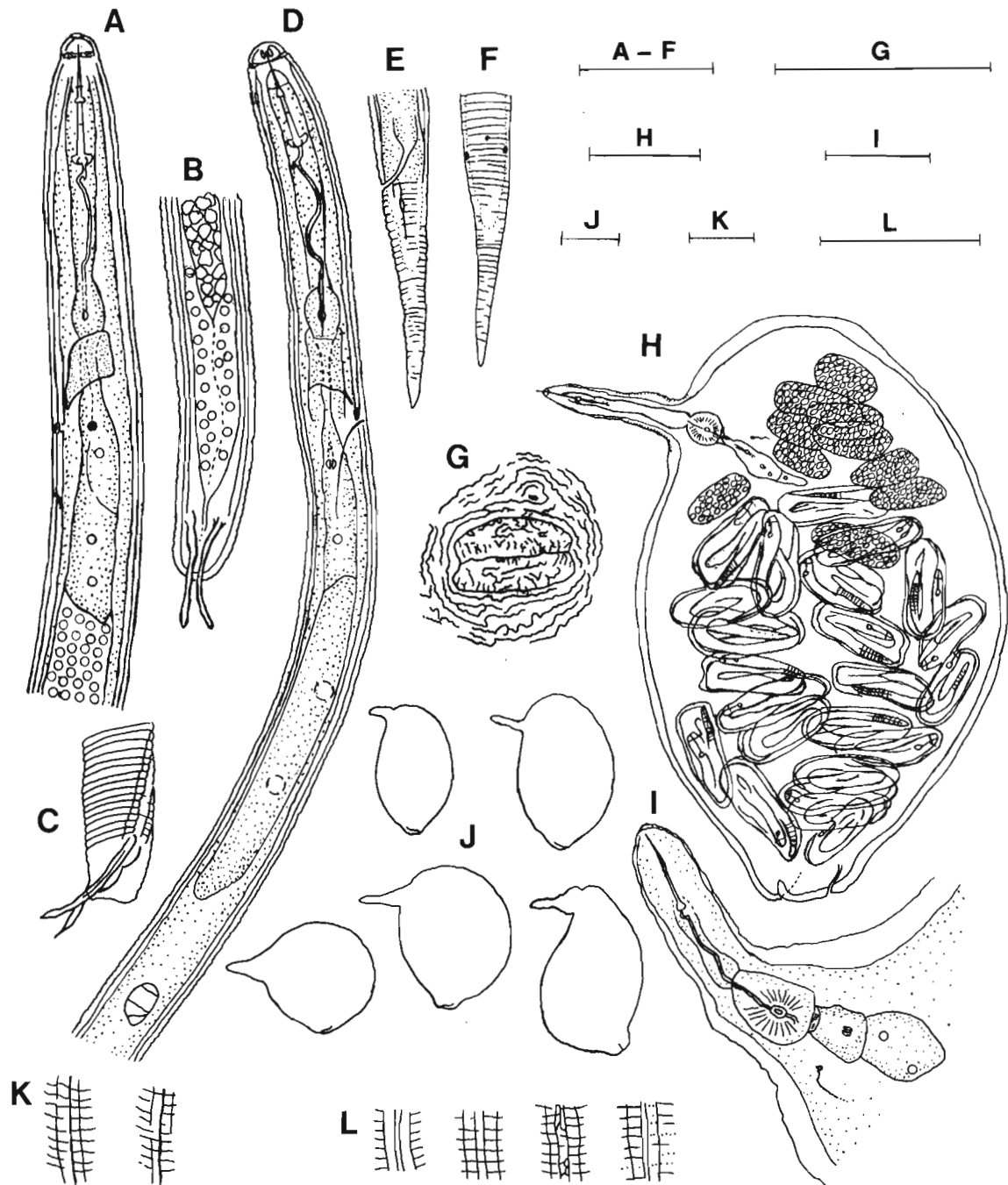
Heteroderinae. *Female*: No cyst stage. Body globose with projecting neck. Cuticle thick, annulated in the major part of neck, and with lace-like pattern on the dilated body. D-layer present. Vulva terminal or sub-terminal. Anus near to or at some distance from vulva. With or without vulval cone. Eggs retained in female body, in some cases, together with hatched J2. *Male*: Body twisted. Lateral field with four lines. Spicules slightly curved, tail and cloacal tubus short or absent. No phasmids. *Second stage juvenile*: Lateral field with three or four incisures. Width of oesophageal glands varying from less than half, half to filling body cavity. Tail conical or tapering with hyaline part, at least half of total length. Phasmids lens-like.

## TYPE SPECIES

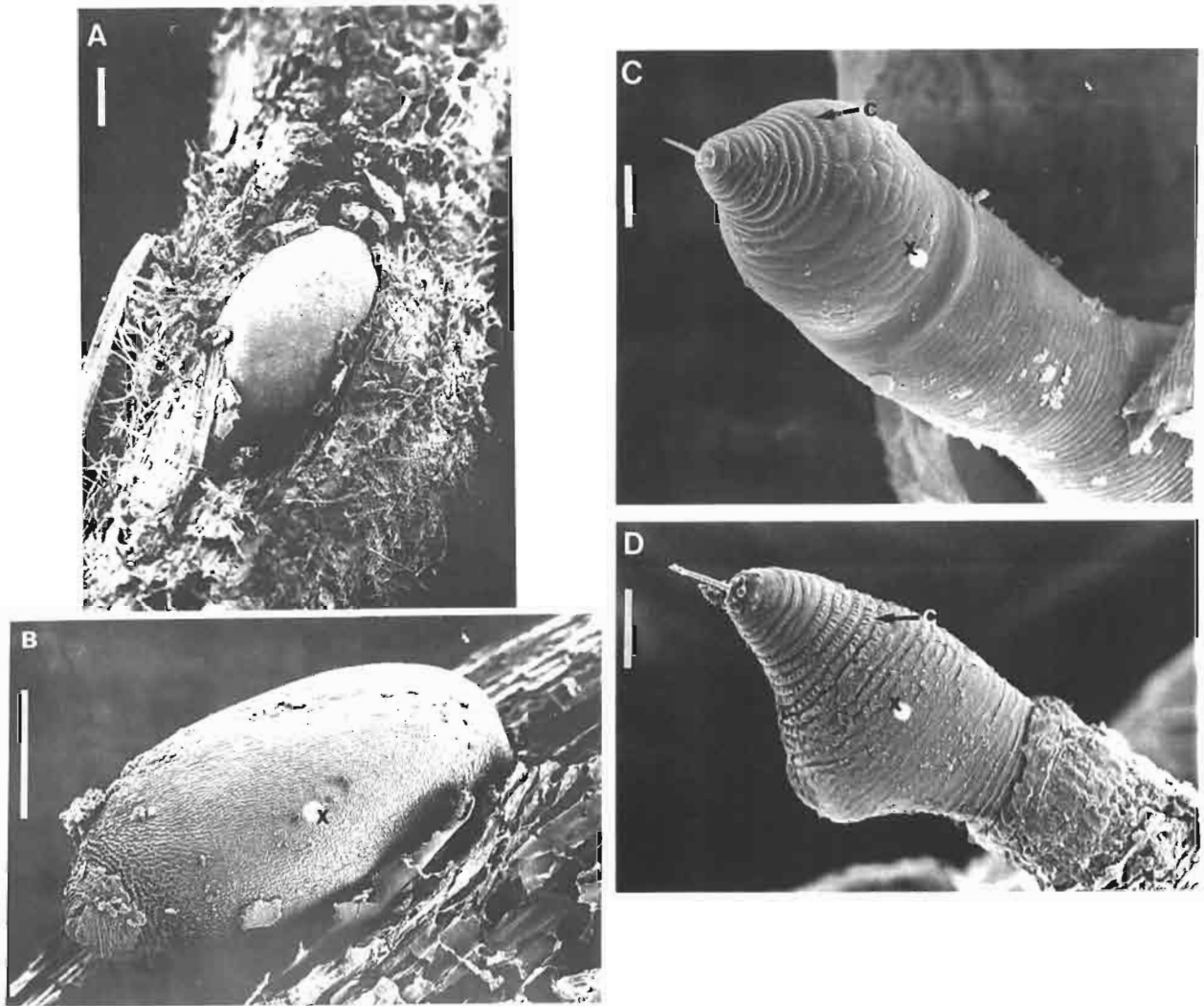
*A. ucrici* Wouts & Sher, 1971.

## OTHER SPECIES

- A. loniceriae* (Wouts, 1973) Luc, Taylor & Cadet, 1978  
= *Sherodera loniceriae* Wouts, 1973
- A. gracililancea* (Robbins, 1978) n. comb.  
= *Thecavermiculatus gracililancea* Robbins, 1978
- A. crassicrustata* (Bernard, 1981) n. comb.  
= *T. crassicrustata* Bernard, 1981
- A. andina* (Golden, Franco, Jatala & Astogaza, 1983) n. comb.  
= *T. andinus* Golden, Franco, Jatala & Astogaza, 1983
- A. carolynae* (Robbins, 1986) n. comb.  
= *T. carolynae* Robbins, 1986
- A. trilineata* Baldwin, Bernard & Mundo-Ocampo, 1989
- A. festucae* Baldwin, Bernard & Mundo-Ocampo, 1989
- A. gibbosa* n. sp.



**Fig. 1.** *Atalodera gibbosa* n. sp. Male : A : Anterior region; B, C : Posterior region; L : Lateral field. - ♀2 : D : Anterior region; E, F : Posterior region; K : Lateral field. - Female : G : Vulval region; H : Whole body; I : Anterior region; J : Body shapes. (Bar equivalent : A-F, I, L = 40 μm; G, H = 100 μm; J = 200 μm; K = 10 μm.)



**Fig. 2.** *Atalodera gibbosa* n. sp. Female: A, B: Mature female parasitizing root surface of *Trachypogon montufori* (A) and cylindrical center (B); C, D: Anterior region of female (c = collar of neck; x = film spot). (Bar equivalent: A, B = 100  $\mu$ m; C = 3  $\mu$ m; D = 6  $\mu$ m.)

#### RELATIONSHIPS

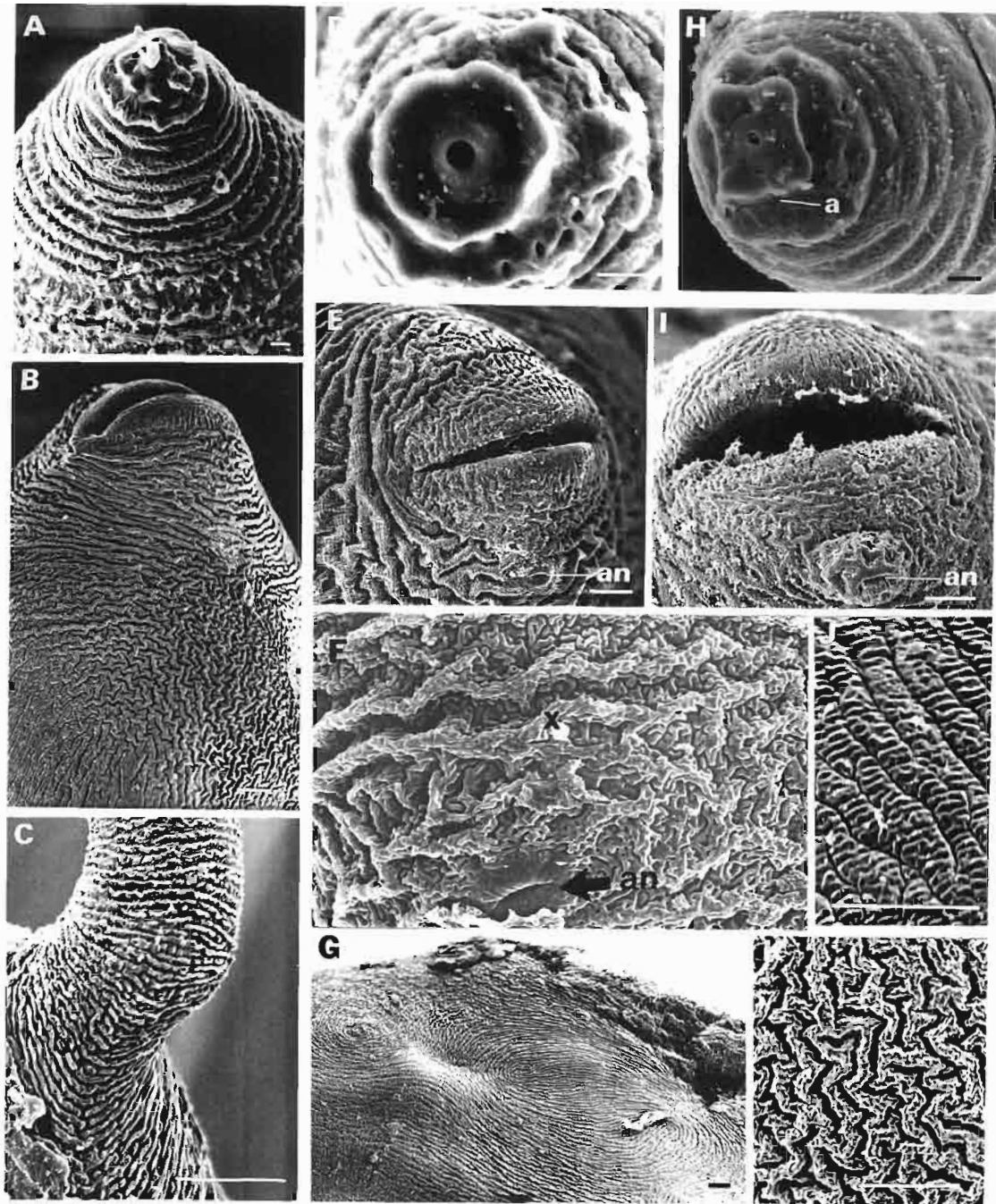
*Atalodera* comes close to *Sarisodera* Wouts & Sher, 1971 and *Bellodera* Wouts, 1985. The difference between *Atalodera* and *Sarisodera* is the shape of vulval lips (flush with body contour to protruded in vulval cone vs hypertrophied without forming vulval cone). *Atalodera* can be distinguished from *Bellodera* by cuticle pattern (lace-like vs pits and striae) and excretory pore position (at the level of "shoulder" vs stylet).

#### DISCUSSION

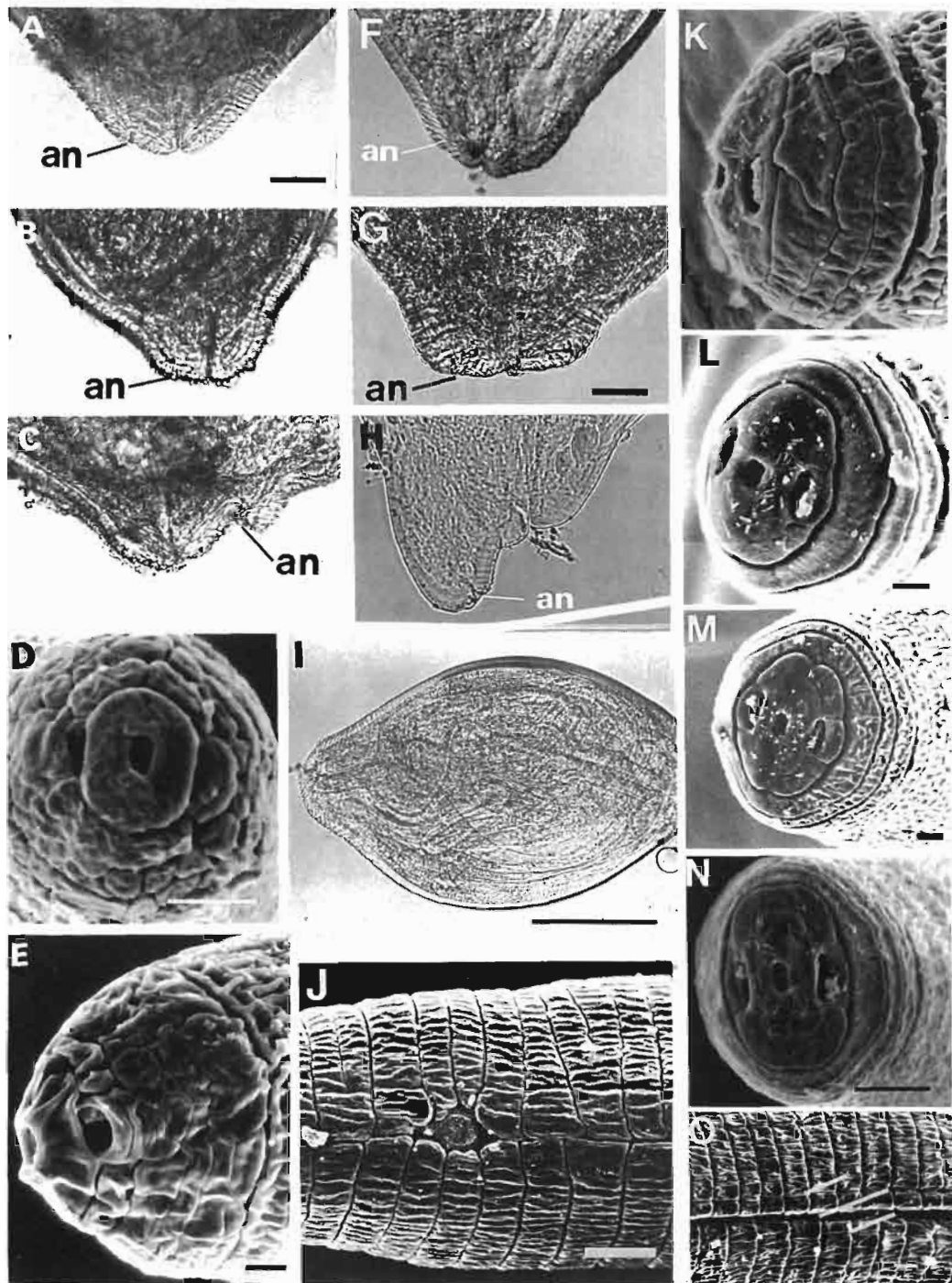
*Thecavermiculatus* Robbins, 1978 and *Atalodera* Wouts & Sher, 1971 share many morphological characters (Luc *et al.*, 1988), and in evolution studies were

considered to be closely related (Ferris, 1979 & 1985; Wouts, 1985; Baldwin, 1986; Baldwin *et al.*, 1989), and to be a monophyletic tribe (Baldwin & Schouest, 1990).

One of the two criteria used by Robbins (1978) for diagnosis of *Thecavermiculatus* was only hatched J2 retained in mature female body, which does not occur in *Atalodera*. However, hatched J2 were found in female body of *A. ucrici*, *A. festucae* and *A. gibbosa* n. sp. (Othman *et al.*, 1986; Baldwin *et al.*, 1989; this article, Fig. 4 I). In the present ecological study of *A. gibbosa* n. sp., it was observed that hatched J2 retained in the female body were abundant in the dry season. A similar observation was also reported by Baldwin and Schouest (1990). Luc *et al.* (1988) considered the parameter not to be significant for taxonomy.

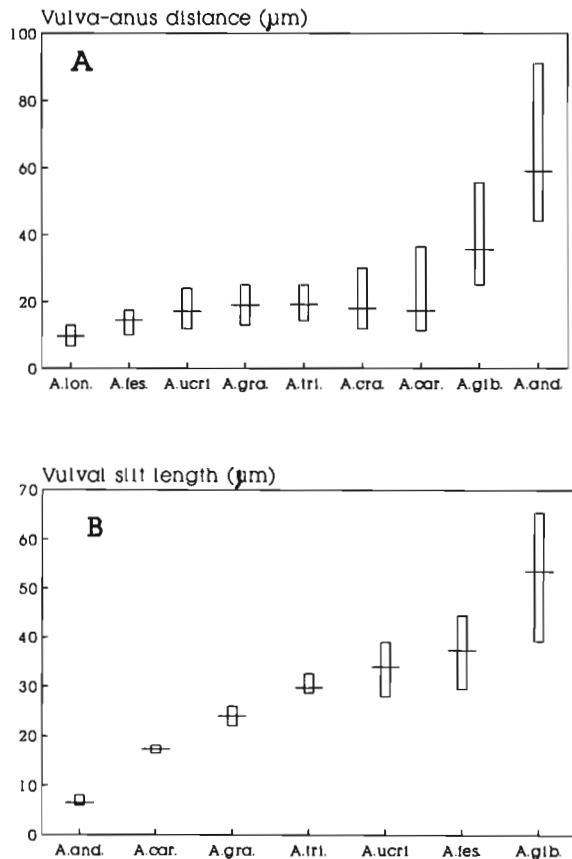


**Fig. 3.** *Atalodera gibbosa* n. sp. Female : A, D, H : Anterior region; B, E, I : Vulval region; C, F, G, J, K : Surface cuticular patterns (a = amphid; an = anus). (Bar equivalent : A, D, H = 1  $\mu$ m; B, C, E, G, I-K = 10  $\mu$ m; F = 3  $\mu$ m.)



**Fig. 4.** *Atalodera gibbosa* n. sp. *A, C, F-H*: Profiles of vulval region; *D, E*: Anterior region of male; *I*: Female body with hatched J2; *J*: Lens-like phasmid of J2; *K, N*: En face patterns of J2; *O*: Lateral field of J2 (bars indicate incisures). (Bar equivalent: *A, C, F, H* = 50  $\mu\text{m}$ ; *D, N* = 2.5  $\mu\text{m}$ ; *E, K, M, O* = 1  $\mu\text{m}$ ; *G* = 11  $\mu\text{m}$ ; *I*: 50  $\mu\text{m}$ ; *J* = 2.5  $\mu\text{m}$ ).





**Fig. 5.** Vulva-anus distance (A) and vulval slit length (B) of *Atalodera lonicerae* (= *A. lon.*) (Wouts, 1973); *A. festucae* (= *A. fes.*) (Baldwin et al., 1989); *A. ucrici* (Wouts & Sher, 1971); *A. gracililancea n. comb.* (= *A. gra.*) (Robbins, 1978); *A. trilineata* (= *A. tri.*) (Baldwin et al., 1989); *A. crassicutata n. comb.* (= *A. cra.*) (Bernard, 1981); *A. carolynae n. comb.* (= *A. car.*) (Robbins, 1986); *A. gibbosa n. sp.* (= *A. gib.*), and *A. andinus n. comb.* (= *A. and.*) (Golden et al., 1983) (Vulval slit lengths of *A. lonicerae* and *A. gracililancea* are not available in literature).

Another criterion for diagnosis of *Thecavermiculatus* was a slight terminal prominence, as against a distinct vulval cone in its closest relative, *Atalodera*. However, mature females of *A. gibbosa n. sp.* show four types of profile of the vulval region: 1. vulval protuberance absent; 2. distinct vulval protuberance, but still not forming a typical vulval cone; 3. typical vulval cone with narrow top; 4. typical vulval cone with wide top (Fig. 4 A, F, B & G, relatively). The frequency was highest in group 3, followed by groups 2, 4 and 1. The dimension of vulval cone on the lateral view in groups 3 and 4 with a total of 50 individuals observed was 52.2 (25.1-70.8) µm high and 137 (99.4-175) µm wide at the base. In comparison, *A. trilineata* was 60 µm high and 120 µm wide at base, *A. festucae* 64 × 101 µm (measured from

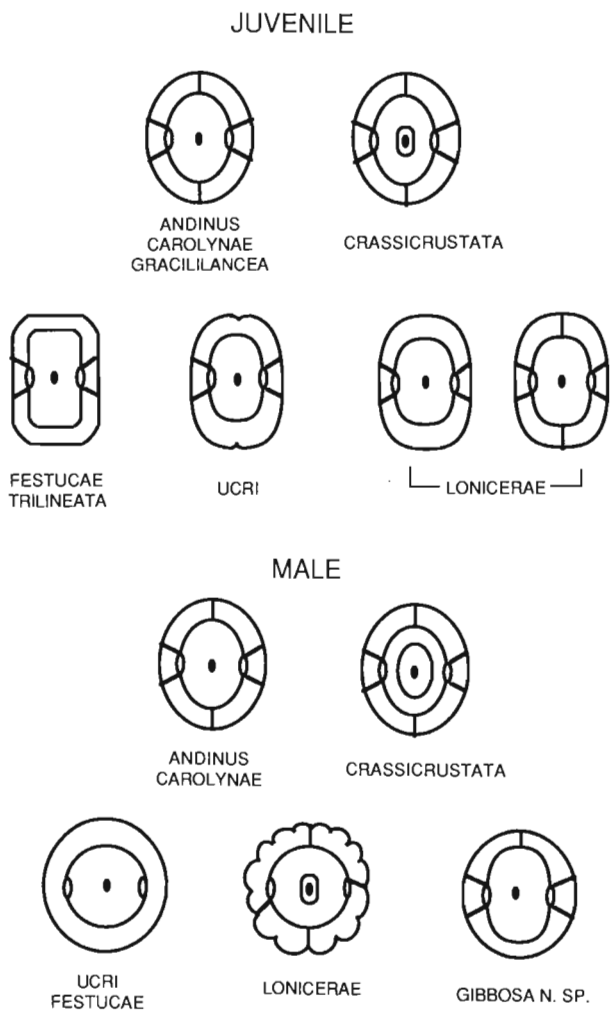
the drawings of Baldwin et al., 1989), *A. lonicerae* 92 × 140 µm (from photography of Wouts, 1973) and *A. ucrici* 70 (56-85) × 92 (83-110) µm (Wouts & Sher, 1971). Thus, there is a continuum in the profile of vulval region, from high vulval cone with narrow base (*A. ucrici* and *A. lonicerae*), low and wide vulval cone (*A. festucae*, *A. trilineata* and *A. gibbosa n. sp.*), distinct protuberance (*A. gibbosa n. sp.* and *A. carolynae n. comb.*; Robbins, 1986), slight protuberance (*A. gracililancea n. comb.*; Robbins, 1978) to no protuberance (*A. crassicutata n. comb.* and *A. andinus n. comb.*; Bernard, 1981; Golden et al., 1983). This continuum confirms previous provisions (Othman et al., 1986; Baldwin et al., 1989).

The separation of *A. andina n. comb.* and *A. crassicutata n. comb.* into a new genus has been discussed by some authors (Wouts, 1985; Othman et al., 1986; Baldwin et al., 1989; Baldwin & Schouest, 1990). This problem was justified in *A. andina* by its large vulva-anus distance, small vulval slit and oesophageal glands filling more than half of body cavity in J2, and in the both species by morphology of vulval region. However, with the present description of *A. gibbosa n. sp.*, the measurements of the first two characters become continuous among in the ataloderines (Fig. 5).

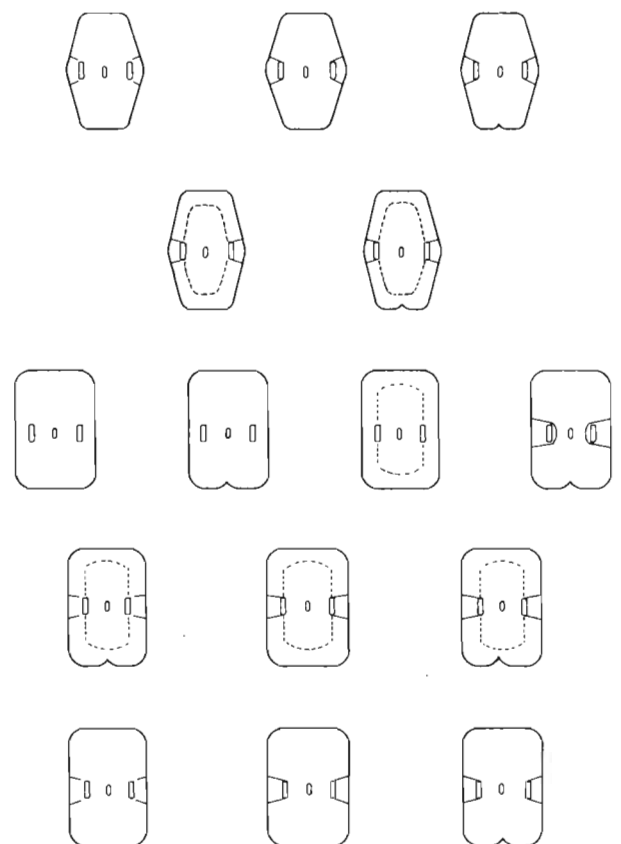
The third character cannot be justified because in *Atalodera n. comb.*, there are oesophageal glands occupying less than half (*A. lonicerae*, *A. carolynae n. comb.*, *A. gracililancea n. comb.* and *A. festucae*; Wouts, 1973; Robbins, 1986; from the drawings of Robbins, 1978 and Baldwin et al., 1989), half (*A. ucrici* and *A. trilineata*; from the drawings of Wouts & Sher, 1971 and Baldwin et al., 1989), more than half the body cavity (*A. andina n. comb.*; Wouts, 1985) or all the body cavity (*A. crassicutata n. comb.* and *A. gibbosa n. sp.*; from the drawings of Bernard, 1981; Luc et al., 1988; this article, Fig. 1 D). Similarly, the filling level of oesophageal glands in J2 was used as one criterion to differentiate *Meloidodera* species (Cid Del Prado Vera, 1991).

In the study of the vulval region (the fourth character), Othman et al. (1986) observed *Thecavermiculatus* having smooth perivulval region and only trace internal (*T. andinus*) or external vulval lips (*T. crassicutata*), in comparison with *Atalodera* possessing rough perivulval region and defined internal and external vulval lips (*A. lonicerae* and *A. ucrici*). However, these characters do not clearly distinguish the both genera because *A. carolynae n. comb.* had similar morphology to *Atalodera* (Othman et al., 1986), and *A. gracililancea n. comb.* had an intermediate pattern (rough perivulval region and only defined internal vulval lips; Robbins, 1978).

With the above judgments, we synonymize *Thecavermiculatus* Robbins, 1978 to *Atalodera* Wouts & Sher, 1971. The major differential characters among the nine species of *Atalodera* are shown in Table 2 and Figures 5-7.



**Fig. 6.** Atalodera. *En face* patterns of ♀2 and male (♀2 of *A. gibbosa* n. sp. not included).



**Fig. 7.** *Atalodera gibbosa* n. sp. *En face* patterns of ♀2.

Table 2. Main characters of *Atalodera* n. comb. species

Parameter	Species								
	<i>crassi-</i> <i>crustata</i>	<i>andinus</i>	<i>gracili-</i> <i>lancea</i>	<i>caro-</i> <i>lynae</i>	<i>gibbosa</i>	<i>trili-</i> <i>neata</i>	<i>festucae</i>	<i>lomi-</i> <i>cerae</i>	<i>ucri</i>
FEMALE									
profile of vulval region	0*	0	1	2	0-4	3	3	4	4
hatched J <sub>2</sub> inside female	+	+	+	+	+	-	+	-	+
morphology of vulva region	S,E**	S,I	R,I	R,I,E	R,I,E	R,I,E	R,I,E	R,I,E	R,I,E
vulva-anus distance (µm)	18 ± 6.4	59 ± 12	19 ± 3.3	17 ± 5.5	36 ± 5	19 ± 2.0	15 ± 3	10	18
length of vulval slit (µm)	NO DATA	7 ± 0.6	24 ± 1.4	17 ± 0.9	53 ± 6.1	30 ± 4.1	37 ± 14.3	NO DATA	34
stylelet (µm)	26 ± 1.2	24 ± 0.6	25 ± 0.9	21 ± 1.0	39 ± 2.3	30 ± 0.8	26 ± 2.7	30	29
MALE									
stylelet (µm)	30	25 ± 0.3	UNKNOWN	25 ± 0.8	39 ± 2.3	UNKNOWN	31	29	27
spicules (µm)	33	31 ± 1.6	UNKNOWN	26 ± 1.6	39 ± 3.0	UNKNOWN	35	33	35
striae in cephalic region	+	-	UNKNOWN	+	+	UNKNOWN	-	+	-
en face pattern	(SEE FIGURE 6)		UNKNOWN	(SEE FIGURE 6)		UNKNOWN	(SEE FIGURE 6)		
lip anuli	5	4-5	UNKNOWN	4	3-5	UNKNOWN	5-7	4-7	3-6
JUV. 2									
esophag. glands in body cavity	FILL	> HALF	< HALF	< HALF	FILL	HALF	< HALF	< HALF	HALF
en face pattern	..... (SEE FIGURES 6 AND 7) .....								
incisures	4	4	4	4	3	3	4	4	3
lip anuli	4	4	3	3-4	3	6	5	3-4	2-3

\* no (0), slight (1) or distinct (2) protuberance; low and wide (3) or high and narrow (4) vulval cone.

\*\* smooth (S) or rugose (R) perivulval region; defined external (E) or internal (I) vulval lips.

There are certain levels of coefficient variations shown in the studied population of *A. gibbosa* n. sp. (Table 1), but this variation is certainly not due to mixture with other nematodes. Within about 200 females studied, there were ten subterminal, one equatorial and one aberrant vulval region (Figs 1 J & 4 H). Also, six females were found to have protrusion next to anus (Fig. 4 C), the character which was observed in *Zelandodera* Wouts, 1973 and not accepted as one criterion for generic differentiation from *Cryphodera* Colbran, 1966 (Luc *et al.*, 1978).

The "collar" (Fig. 2 C & D) in the anterior female neck is the first report in Heteroderinae. The cuticle, thicker after the collar, probably resulted in the emergence of a new cuticle layer. Shepherd and Clark (1978)

demonstrated one cuticular thickness in the thorax as a consequence of emergence of C-layer in *Heterodera goettingiana* and C- and D-layer in *Globodera rostochiensis*. The collar described here is not similar to the cuticular thickness in *Hylonema ivorense* (Luc *et al.*, 1978).

Inter- and intraspecific variations in the en face pattern of J<sub>2</sub> and male of *Atalodera* n. comb. were shown in Figures 6 and 7, as described by Robbins (1978, 1986), Othman *et al.* (1986), Baldwin *et al.* (1989) and this article. The en face patterns of J<sub>2</sub> were round, oblong or ovoid, with fused or separated submedian lips. In *A. gibbosa* n. sp., a great number of variations were found in the 130 J<sub>2</sub> observed in SEM. Males of *Atalodera* n. comb. present round en face pattern, but many differences can be easily distinguished among the species.

Variations of the en face pattern were also reported in *Meloidodera*, *Globodera*, *Rhizonema sequoiae* and *Afenestrata africana* (Othman & Baldwin, 1985; Baldwin, 1986; Othman & Baldwin, 1986; Othman *et al.*, 1988). Because of these inter- and intraspecific variations, it becomes difficult to utilize this criterion for the evolution studies.

The principal characters of the non-cyst forming heteroderids with terminal and subterminal vulva were listed in Table 3. It is evidently difficult to study phylogenetics because five of seven genera in this group are monospecific. With description of new species in future, they may be expected to have more morphological overlapping among them, allowing them to be joined together as proposed in this article.

ECOLOGY

Figure 8 A shows two seasons, one dry (from August

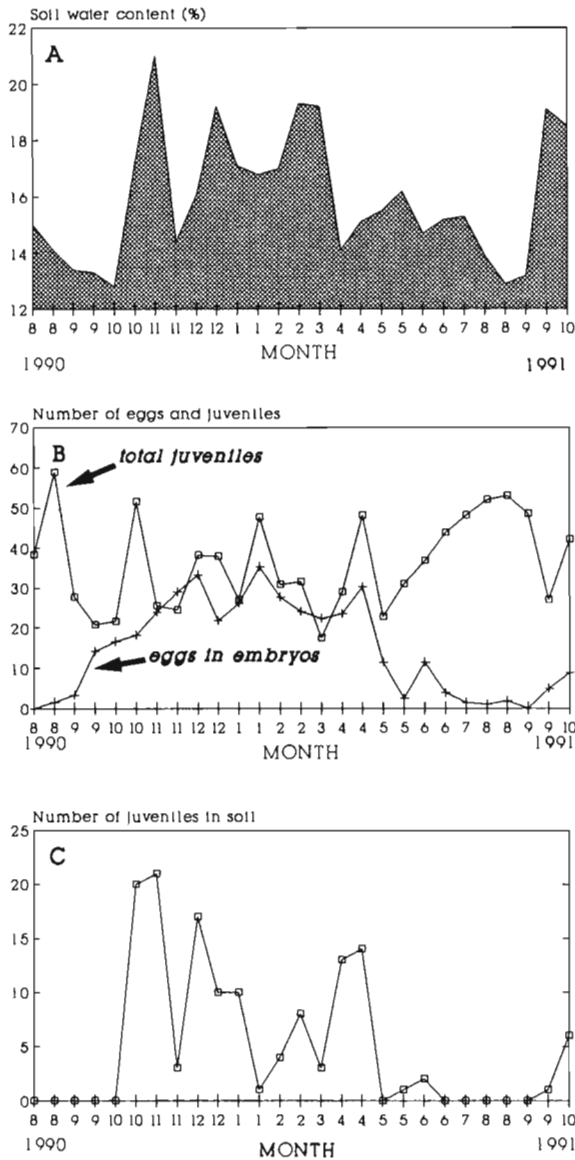
to September, 1990 and from April to September, 1991) and one wet (from October of 1990 to March of 1991, and from September to October, 1991). The number of eggs in embryo-stage was zero near the end of the dry season (August, 1990 and September, 1991), but increased rapidly in the transition months to the rainy season (Fig. 8 B). During the rainy season, hatched J2 inside females were never found, and the numbers of eggs in embryo- and juvenile-stage were high and fluctuated. The numbers of total juveniles (eggs in juvenile-stage and hatched J2 inside females) were high at the end of the dry season. They drastically decreased at the beginning of the rainy season, with increase in numbers of J2 in soil (Fig. 6 C). The correlation coefficients between soil water content and eggs in embryo-stage, and total juveniles, and J2 in soil were 0.46 ( $p = 0.018$ ),  $-0.33$  ( $p = 0.095$ ) and 0.50 ( $p = 0.008$ ), respectively.

**Table 3.** Main characters of the non-cyst forming Heteroderinae genera with subterminal vulva

Parameter	Genera						
	<i>Cryphodera</i>	<i>Hylonema</i>	<i>Rhizonema</i>	<i>Ekphymatodera</i>	<i>Bello-dera</i>	<i>Sarisdodera</i>	<i>Atalodera</i>
<b>FEMALE</b>							
cuticle pattern	ANNULATED	LACE-NIKE	ANNULATED	TUBERCLES	PITS/STRIAE	LACE-LIKE	LACE-LIKE
vulval position	TERMINAL	TERMINAL	TERMINAL	TERMINAL	TERMINAL	TERMINAL	SUB/TERMINAL
profile of vulval region	F*	F	C	P	C	H,S	F,P,C
vulva-anus distance ( $\mu\text{m}$ )	38-70	16-20	15-33	74-140	53-88	15 (A)	7-91
vulval slit ( $\mu\text{m}$ )	44-49	40-46	NO DATA	40-59	48-51	62-85	6-66
D-layer	-(B)	NO DATA	-	NO DATA	-(C)	+	+
level of excretory pore	SHOULDER	SHOULDER	SHOULDER	SHOULDER	STYLET	SHOULDER	SHOULDER
<b>MALE</b>							
spicules ( $\mu\text{m}$ )	21-29	27-37	22-34	34-46	22-31	33-46	23-44
cloacal tubus	-	+	+	+	+	+	+
<b>JUVENILE</b>							
oesoph. glands in body cavity	FILL	FILL	FILL	FILL	FILL	FILL	< HALF TO FILL
phasmids	LENS-LIKE	PORE-LIKE	LENS-LIKE	PORE-LIKE	LENS-LIKE	LENS-LIKE	LENS-LIKE
FEEDING SITE	GIANT (B) CELL	GIANT CELL	GIANT CELL	SYNCITIUM	GIANT CELL	GIANT CELL	SYNCITIUM/ GIANT CELL (D)
No. OF SPECIES	4	1	1	1	1	1	9

\*Vulval region flush with body contour (F), on protuberance (P), forming vulval cone (C) or with hypertrophied lips without vulval cone (H); anus sunken (S) in vulval slit.

(A) from drawing of Wouts & Sher (1971), (B) Baldwin & Schouest (1991), (C) Luc *et al.* (1988), (D) Souza (1992).



**Fig. 8.** *Atalodera gibbosa* n. sp. A: Fluctuations of soil water content (%); B: Eggs and juveniles in female body; C: J2 in soil.

The low number of eggs in embryo-stage and the absence of J2 in soil during the dry season indicate a drastic reduction in nematode reproduction, which accords with fading of the host plant in this period. It is clear that the nematode as eggs in juvenile-stage and hatched J2 inside females survived during the dry season. The two surviving forms were computed together because hatching of some J2 occurred at the moment of dissecting female for counting; this avoided to overcounting of hatched J2.

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