

A redescription of *Heterodera arenaria* Cooper 1955, a cyst nematode from marram grass

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Summary – *Heterodera arenaria* Cooper, 1955 is redescribed from marram grass (*Ammophila arenaria*) from Gibraltar Point, Eastern England. The same species was also found on marram grass from seven other dune sites in Britain. *H. arenaria* belongs to the *H. avenae* group of *Heterodera* species, the cyst cone is bifenestrated with prominent bullae but no underbridge. *H. arenaria* differs from *H. avenae* in having a shorter vulval slit, longer second stage juveniles and larger females; in juveniles and males of *H. arenaria* the stylet basal knobs are indented more anteriorly.

Résumé – *Redescription d'Heterodera arenaria Cooper, 1955, un nématode à kyste de l'oyat* – Redescription est donnée d'*Heterodera arenaria* Cooper, 1955 parasite de l'oyat (*Ammophila arenaria*) à Gibraltar Point, dans l'est de l'Angleterre. La même espèce a aussi été trouvée sur oyat dans sept autres sites de dune en Grande-Bretagne. *H. arenaria* appartient au groupe *H. avenae* du genre *Heterodera*, le kyste étant bifenestré avec bullae proéminentes mais sans sous-pont. *H. arenaria* diffère d'*H. avenae* par la fente vulvaire plus courte, la plus grande longueur des juvéniles de deuxième stade et des femelles; chez les juvéniles et les mâles d'*H. arenaria*, les boutons basaux du stylet sont plus profondément indentés.

Key-words : *Ammophila arenaria*, *Heterodera arenaria*, nematode, taxonomy.

A cyst nematode species was first recorded on marram grass, *Ammophila arenaria* (L.) Link., in 1929 by Triffitt. She regarded it as a strain of *Heterodera schachtii*, but her measurements and illustrations resemble a *Meloidogyne* species. Franklin (1938) illustrates lemon shaped cysts from marram grass, which are much larger than those of most *Heterodera* species. Cooper (1955) includes a marram root eelworm, *H. major* var. *arenaria*, in his key to British species of *Heterodera*. The availability of the new names first used in combination with *Heterodera* by Cooper (1955) have, at the request of Stone (1974), been considered by the International Commission on Zoological Nomenclature which ruled them to be available in its opinion 1336 (ICZN), 1985). Unfortunately neither Stone (1974) nor ICZN (1985) actually referred to *H. major* var. *arenaria*. However, this combination appeared in the same diagnostic key as did the other names now ruled available. Also, "variety" published before 1961 and adopted before 1985 is, according to Article 45 g (ii) of the International Code of Zoological Nomenclature, considered to be at the subspecies level and is therefore available. This point has been confirmed by the Secretary of the Commission (P. K. Tubbs, *in litt.* 9 Dec. 1994). *H. arenaria* was subsequently raised to the species level: *H. arenaria* Cooper,

1955, by Kirjanova and Krall (1971); it was then transferred to *Bidera* by Krall and Krall (1978) but returned to *Heterodera* by Mulvey and Golden (1983) where it has been retained (Luc *et al.*, 1988; Baldwin & Mundo-Ocampo, 1991). Following the application by Franklin *et al.* (1959) the name "avenae" was preferred to "major" hence Cooper (1968) describes *H. avenae arenaria* cysts collected from marram grass at Gibraltar Point as resembling large *H. avenae*, but having thicker walls, longer eggs and very long juveniles. A *Heterodera* species with similar characters to Cooper's has been collected from marram grass at eight coastal sites in the British Isles and appears to be widespread. A redescription of this species is given below.

Materials and methods

The following redescription is based on material from Gibraltar Point Nature Reserve, Skegness, Lincs, England. Sand samples were collected in July 1979 from around the roots of *Ammophila arenaria* growing in dunes 100 m from the sea. Cysts were extracted using a fluidising column (Trudgill *et al.*, 1973); juveniles were obtained by soaking cysts in water and allowing them to hatch. Further sand samples and roots were collected in

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May 1980; males were extracted using a tray method (Whitehead & Hemming, 1965) and females were picked off the roots. Samples from *A. arenaria* were also examined from three other UK dune sites at Camber, Rye, Sussex; West Wittering, Sussex and Port Eynon, The Gower Peninsular, South Wales. Cysts of *H. arenaria* were also found on *A. arenaria* from sand dunes at Rock, Cornwall and Southwold, Suffolk, England; also from Carnoustie and Montrose, Tayside, Scotland.

Males, females and juveniles were killed by gentle heat and fixed in TAF. Males and juveniles were mounted and measured in TAF, female heads and cones in warm lactophenol, and eggs in water. Cyst cones were mounted in Euparal. For studies with the scanning electron microscope (SEM), specimens were fixed in 4% glutaraldehyde in 0.05 M sodium phosphate buffer at pH 6.8 using the microwave fixation technique of Jones and Ap Gwyn (1991). Fixed specimens were transferred to modified "Beem" capsules and dehydrated to 100% ethanol; specimens were then critical point dried using CO₂, mounted onto stubs, coated with gold and examined with an Hitachi S-450 SEM at 20 kV. More

details of the above fixatives/methods are given in Southey (1986).

Heterodera arenaria Cooper, 1955 (Figs 1-4)

MEASUREMENTS

Gravid (white) female (n = 30) : L (excluding neck) = 748 ± 23 (480-940) µm; body diam. = 589 ± 20.3 (380-840) µm; neck = 160 ± 4.4 (100-200) µm; L/D ratio = (n = 6) 1.27; stylet = 30.1 ± 0.1 (28.4-31.0) µm; DGO = 4.7 ± 0.1 (3.9-5.2) µm; median bulb length = 37.2 ± 0.1 (36.8-37.4) µm; median bulb width = 37.1 ± 0.1 (36.8-37.4) µm; ant. end to median bulb = 114.2 ± 0.7 (103.2-120.0) µm.

Cysts, eggs and second-stage juvenile : see Tables 1, 2, 3, respectively.

Males (n = 25) : L = 1604 ± 14.4 (1492-1778) µm; diam. at excr. pore level = 32 ± 0.2 (31-34) µm; a = 46 ± 0.5 (43-52) µm; b = 11 ± 0.1 (10-12) µm; stylet = 33 ± 0.1 (32-34) µm; spicules = 40 ± 0.5 (36-44) µm; gubernaculum = 10 ± 0.3 (9-12) µm.

Table 1. *Heterodera arenaria* : cyst measurements (µm) of various populations.

	Gibraltar Point	West Wittering	Camber	Port Eynon	Culture ex Hesling*
n.	35	35	14	7	35
Cyst width	602 ± 17.6 (395-790)	640 ± 15.2 (437-765)	653 ± 27.4 (475-792)	503 ± 39.5 (363-632)	620 ± 13.8 (360-760)
Cyst length (excluding neck)	799 ± 22.2 (600-1027)	906 ± 19.4 (656-1078)	899 ± 41.1 (633-1155)	693 ± 47.1 (553-916)	846 ± 15.1 (580-1060)
Length/diam.	1.3	1.4	1.4	1.4	1.4
n.	25	25	6	5	25
Vulval slit	9.4 ± 0.2 (8.3-11.5)	9.0 ± 0.2 (7.7-10.2)	9.3 ± 0.3 (8.9-10.1)	10.1 ± 0.3 (9.0-10.3)	9.1 ± 0.2 (7.7-10.3)
Vulval bridge length	21.2 ± 0.4 (16.6-26.8)	20.0 ± 0.5 (15.4-25.6)	24.5 ± 1.6 (19.1-27.9)	22.7 ± 1.3 (19.4-25.8)	21.1 ± 0.5 (15.5-25.8)
Vulval bridge width	8.3 ± 0.3 (5.1-11.5)	8.3 ± 0.4 (5.1-11.5)	8.0 ± 0.9 (6.4-11.4)	7.7 ± 0.9 (5.2-10.3)	6.9 ± 0.3 (3.9-9.0)
Fenestral length	46.9 ± 0.9 (38.4-55.0)	45.6 ± 0.6 (37.1-49.9)	49.7 ± 1.0 (47.0-52.1)	48.8 ± 1.2 (45.2-51.6)	45.2 ± 1.1 (36.1-52.9)
Semi-fenestra length	20.2 ± 0.4 (15.4-24.3)	19.3 ± 0.4 (15.4-24.3)	22.2 ± 0.8 (20.3-25.4)	22.4 ± 0.7 (20.6-25.5)	18.8 ± 0.5 (14.2-21.9)
Fenestral width	22.1 ± 0.5 (17.9-26.9)	21.5 ± 0.6 (16.6-29.4)	23.9 ± 1.2 (21.6-27.9)	25.8 ± 1.6 (20.6-29.7)	20.4 ± 0.5 (15.5-25.8)
Fenestral length/width	2.1	2.1	2.1	1.9	2.2

* Collected by B. A. Cooper from Gibraltar Point in 1950's.

Table 2. *Heterodera arenaria* : egg measurements (μm).

	Gibraltar Point	West Wittering	Camber	Port Eynon	Culture ex Hesling*
n.	60	60	60	60	60
Length	150 \pm 0.8 (140-164)	154 \pm 0.8 (142-168)	139 \pm 0.9 (125-155)	143 \pm 0.7 (134-160)	135 \pm 0.7 (124-146)
Width	54 \pm 0.4 (48-63)	56 \pm 0.4 (48-62)	52 \pm 0.3 (48-55)	55 \pm 0.3 (50-58)	51 \pm 0.4 (46-62)
Length/width	2.8	2.8	2.7	2.6	2.6

* Collected by B. A. Cooper from Gibraltar Point in 1950's.

Table 3. *Heterodera arenaria* : juvenile measurements (μm ; n = 50 for each population).

	Gibraltar Point	West Wittering	Camber	Port Eynon	Culture ex Hesling*
Stylet length	28.6 \pm 0.1 (26.8-29.4)	28.2 \pm 0.1 (27.5-29.4)	28.4 \pm 0.1 (27.1-29.7)	28.7 \pm 0.1 (27.1-29.7)	29.0 \pm 0.1 (27.1-30.3)
DGO	5.9 \pm 0.1 (5.1-7.0)	6.0 \pm 0.1 (4.5-7.7)	6.0 \pm 0.2 (3.8-7.6)	6.0 \pm 0.2 (4.5-7.1)	5.3 \pm 0.1 (3.9-6.5)
Ant. end to median valve	93 \pm 0.7 (85-102)	88 \pm 0.7 (81-96)	88 \pm 0.7 (80-97)	88 \pm 0.6 (80-95)	85 \pm 0.5 (79-89)
Ant. end to excretory pore	123 \pm 0.7 (116-129)	119 \pm 0.8 (113-129)	123 \pm 0.6 (118-130)	120 \pm 0.6 (112-125)	113 \pm 0.7 (107-120)
Diam. at excretory pore	22 \pm 0.1 (21-24)	22 \pm 0.1 (20-23)	22 \pm 0.1 (20-23)	22 \pm 0.1 (21-23)	21 \pm 0.1 (21-22)
Tail length	79 \pm 0.1 (72-84)	80 \pm 0.7 (73-87)	80 \pm 0.5 (75-85)	82 \pm 0.1 (76-86)	74 \pm 0.6 (67-80)
Hyaline tail part	51 \pm 0.7 (41-58)	53 \pm 0.7 (47-59)	53 \pm 0.5 (47-57)	53 \pm 0.7 (46-58)	48 \pm 0.7 (37-53)
Body length	639 \pm 2.7 (590-677)	633 \pm 3.0 (586-682)	663 \pm 3.0 (597-713)	647 \pm 4.0 (562-697)	587 \pm 6.7 (549-617)
Hyaline tail part/stylet	1.8	1.9	1.9	1.8	1.6
Stylet knob width/height (n = 20)	1.8	1.9	1.9	1.9	1.9
a	28.4	28.5	30.2	29.7	27.4
c	8.1	7.9	8.3	7.9	8.0

* Collected by B. A. Cooper from Gibraltar Point in 1950's.

DESCRIPTION

Gravid female : Body ovoid in shape with a low but distinct vulval cone. Neck well defined and usually coated with a brown jelly-like substance on female removed from the root. Thick white sub-crystalline layer present

on females of all ages. No egg sac observed. Valve plates of the median bulb 12.2 (11.6-12.9) μm long and 9.0 (8.4-9.7) μm wide. Excretory pore situated on the "shoulder" 162.5 (161.2-163.8) μm from the anterior end. Cuticle thin in the neck region, thickening towards the "shoulders", where 10.4 (7.7-12.2) μm thick. Fe-

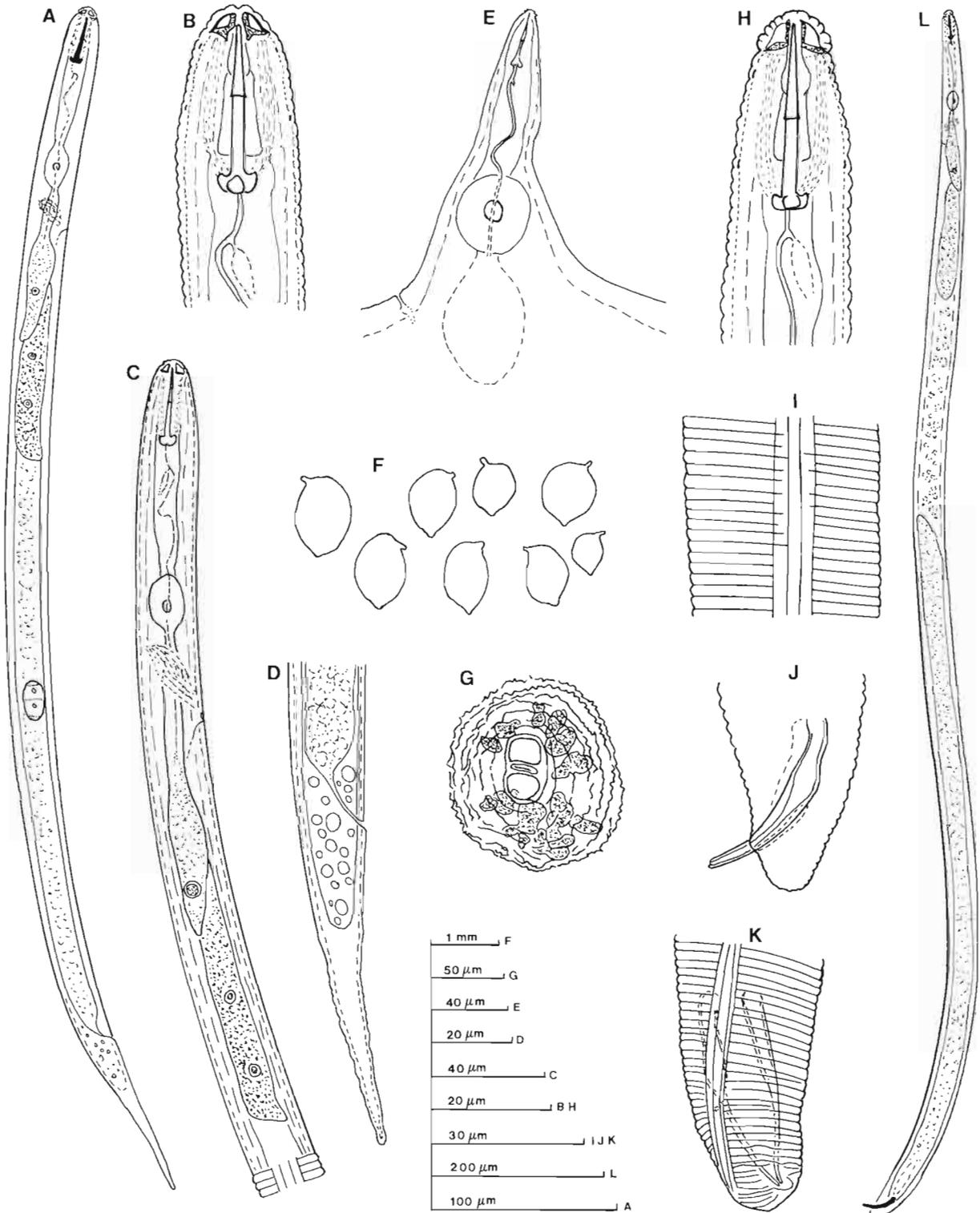


Fig. 1. *Heterodera arenaria* Cooper, 1955. A-D: Second stage juvenile. A: Whole specimen; B: Head region (lateral); C: Oesophageal region; D: Tail end – Female. E: Oesophageal region; F: Outlines of cyst; G: Fenestration pattern of mature cyst – H-L: Male. H: Head region; I: Lateral field in mid body region; J: Tail with spicules in lateral view; K: Tail end in sub-ventral view; L: Whole specimen.

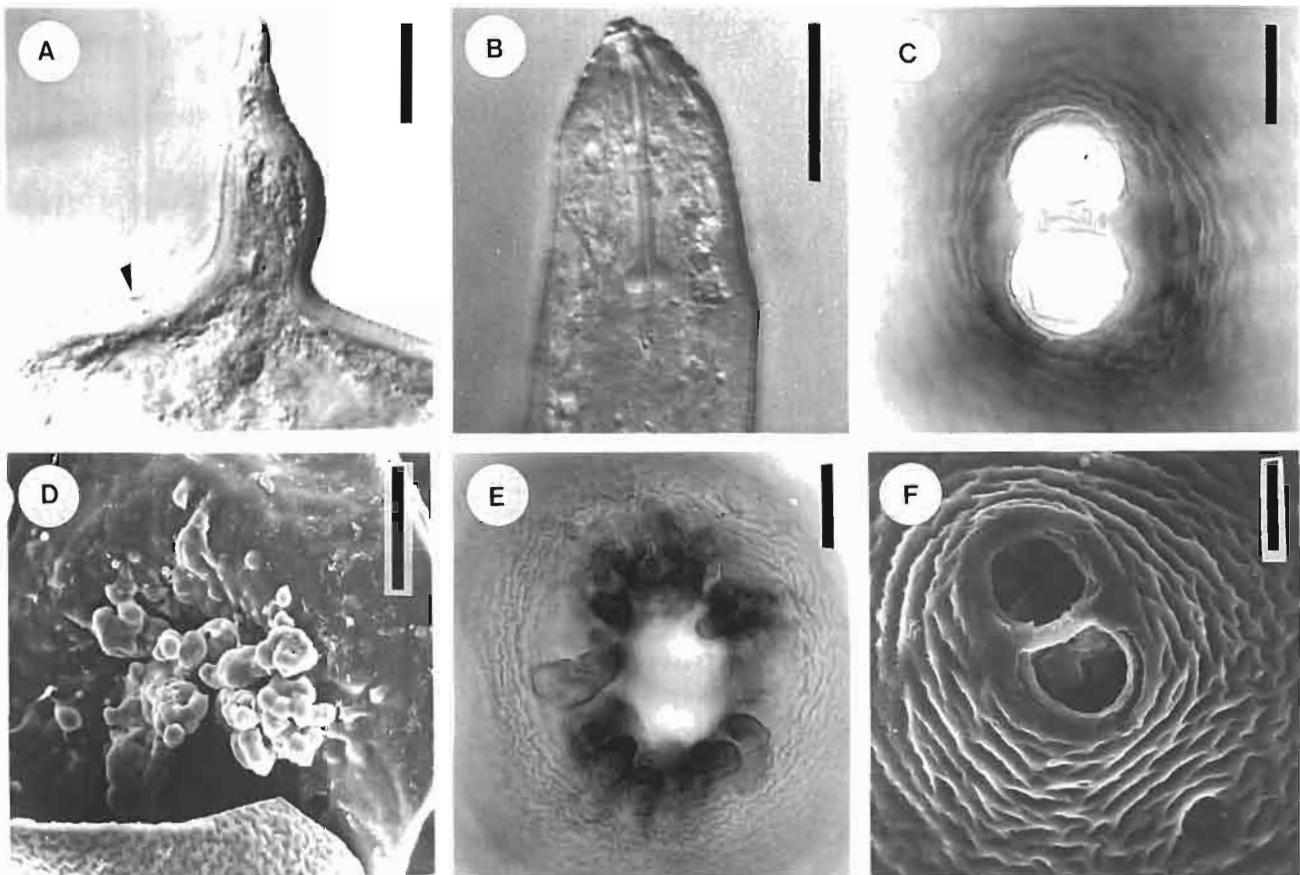


Fig. 2. *Heterodera arenaria* Cooper, 1955. *A*: Female oesophageal region, excretory pore arrowed; *B*: Female head region-lateral; *C*, *F*: Fenestration pattern of mature cyst; *D*, *E*: Bullae in cyst cone. (*A-C* & *E*, light micrographs; *D* & *F*, SEM's. Scale bars: *A* = 50 μm ; *B-F* = 20 μm .)

male labial area consisting of two distinct annules; cephalic framework indistinct. Stylet shaft narrow and flexible. Stylet basal knobs rounded and posteriorly directed 3.1 μm long by 6.2 μm broad. Anal-vulval distance 55 (48-64) μm .

Cysts: Mature cysts lemon-shaped, with a small vulval cone and distinct neck, and unusually large (some cysts over 1 mm in length). Cyst wall thick and dark brown in colour, often obscured by a thick white sub-crystalline layer. Vulval cone ambifenestrate to bifenestrate, with distinct fenestral outline. Semi-fenestrae horse-shoe shaped, bullae prominent, large, rounded, and located near top of cone, as in *H. avenae*. Anus 55 μm from the vulval slit. No underbridge.

Eggs: Cylindrical with rounded ends. Egg shell hyaline without visible markings. Juvenile folded four times within the egg.

Second-stage juveniles: Body usually slightly curved when heat relaxed. Labial area with three indistinct an-

nules. Cephalic framework strongly sclerotized. Anterior cephalids at 2nd or 3rd annule and posterior cephalids at 8th to 10th annule. Stylet with strong shaft and well developed basal knobs, with anterior faces distinctly concave. Stylet knobs width averages 6.6 μm and length 3.8 μm . Dorsal oesophageal gland orifice 5.9 (5.1-7.0) μm posterior to base of stylet knobs. Median bulb with well developed plates which occur 93 (86-102) μm behind the head. Oesophageal glands extending to 42.4 % body length. Excretory pore 123 (116-129) μm behind anterior end. Hemizonid two annules long and immediately in front of excretory pore. Hemizonion indistinct, nine annules posterior to excretory pore. Genital primordium consisting of two distinct nucleate cells, situated at 57.4 % body length. Lateral field with four incisures, the outer two being faintly areolated. Phasmids not prominent, found posterior to anus and slightly anterior to hyaline tail. Tail about 4.5 anal body widths long and gradually tapering to a narrow, rounded terminus.

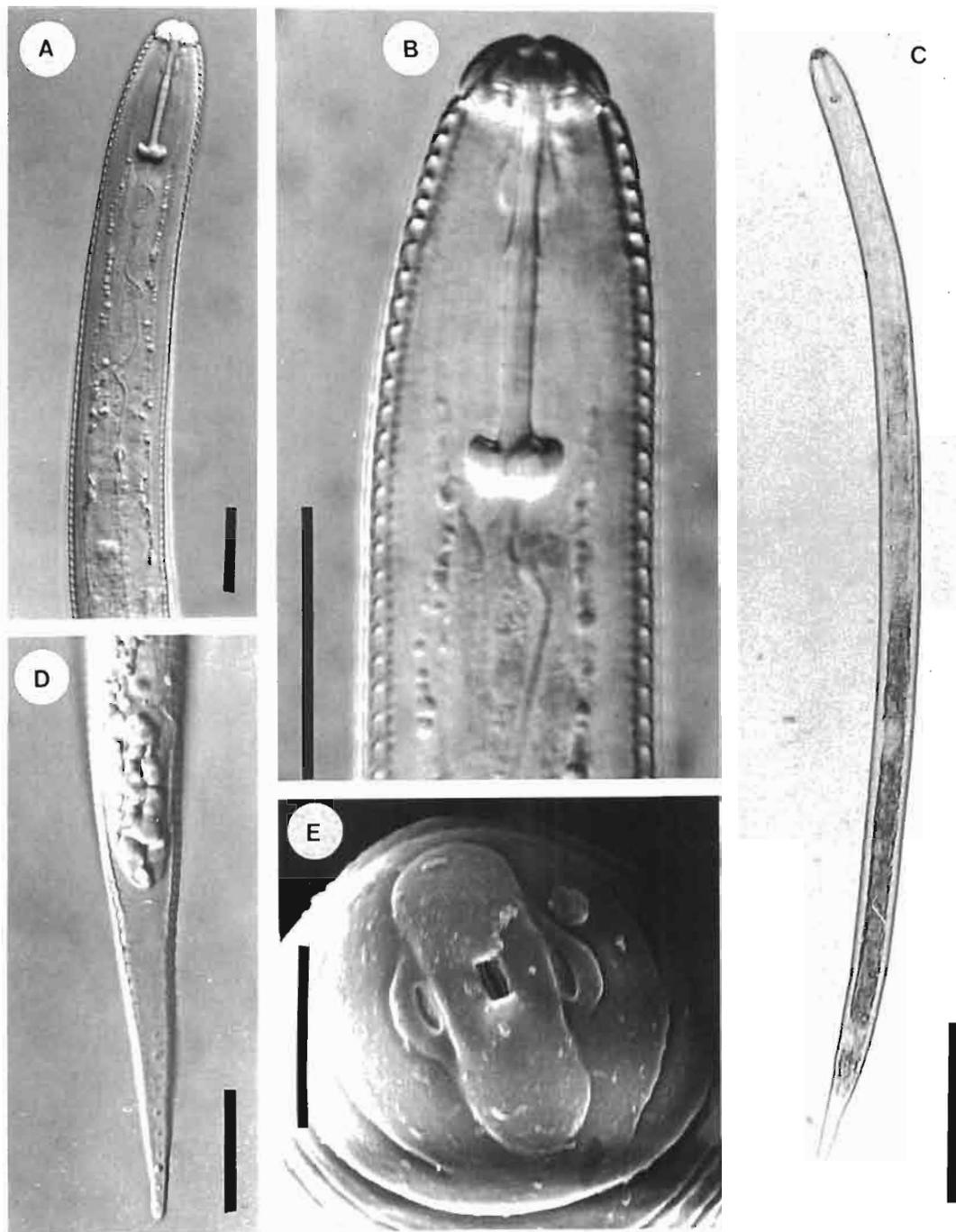


Fig. 3. *Heterodera arenaria* Cooper, 1955 juvenile (J2). A: Oesophageal region; B: Head region-lateral; C: Whole specimen; D: Tail end; E: En face view (A-D, light micrographs; E, SEM; Scale bars: A, B, D, = 20 μm ; C = 100 μm ; E = 5 μm .)

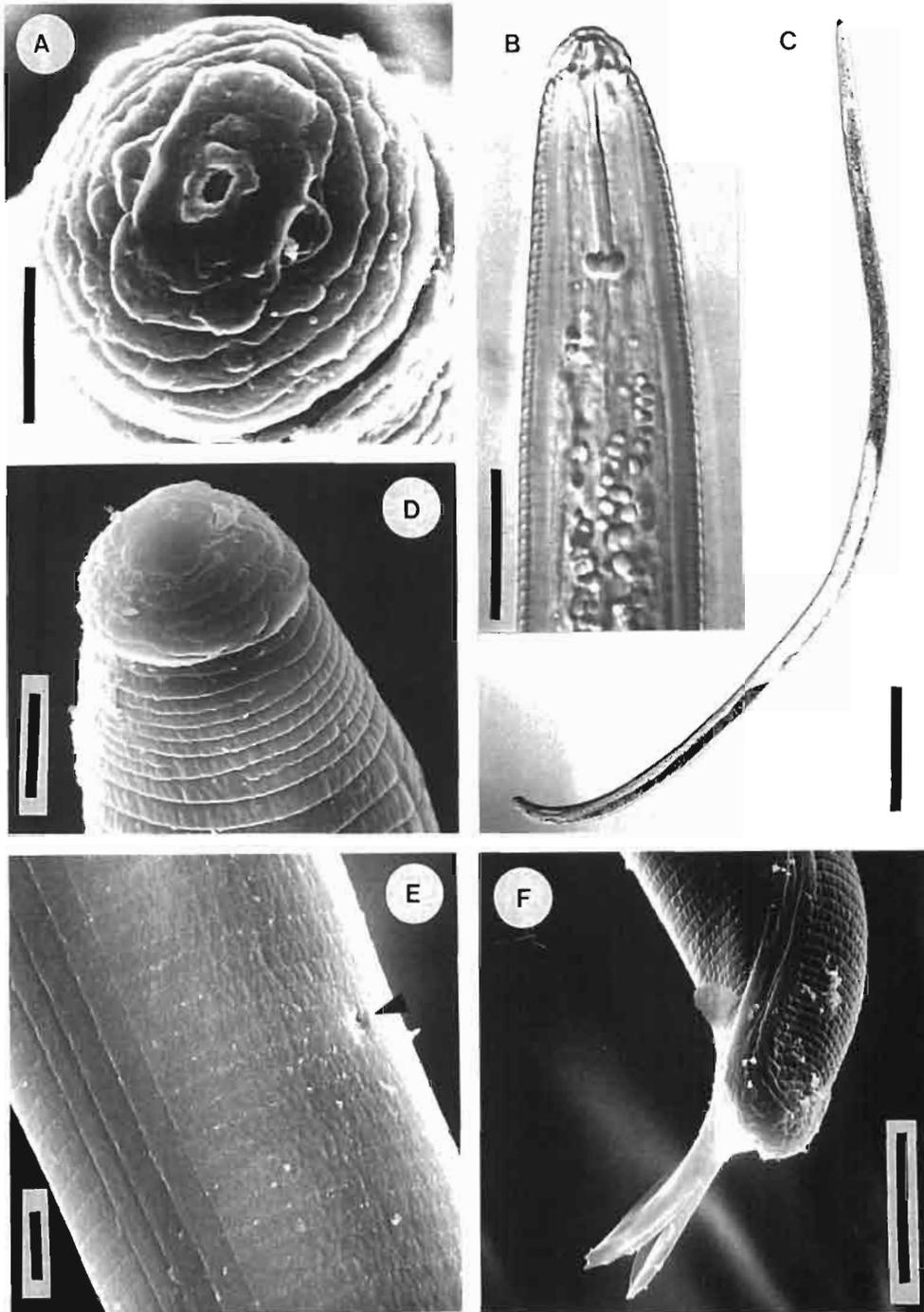


Fig. 4. *Heterodera arenaria* Cooper, 1955 male. *A* : En face view; *B* : Head region-lateral; *C* : Whole specimen; *D* : Head end-sublateral; *E* : Lateral field in excretory pore (arrowed) region; *F* : Tail end with protruding spicules. (A, D-F SEM's and B & C light micrographs; Scale bars : A, D, E = 5 μ m; B, F = 20 μ m; C = 200 μ m.)

Males : Rare. Body elongate and rounded at each end, usually assuming an open C-shape with a slight 90° twist in posterior half when killed by gentle heat. Labial area rounded and markedly offset, 7 µm long by 12 µm wide, with five or six annules. Cephalic framework heavily sclerotized. Cephalics indistinct; anterior cephalids two annules, and posterior cephalids nine to ten annules behind lip region. Stylet strong with rounded to angular basal knobs indented anteriorly, 5.7 µm wide and 3.4 µm long. Dorsal oesophageal gland orifice 5.2 (3.9-6.4) µm behind stylet knobs. Median bulb narrow and poorly defined; valve plates located 116 (108-123) µm behind head. Excretory pore 178 (165-186) µm from anterior end. Hemizonid prominent, two annules long and anterior to excretory pore. Hemizonion indistinct, posterior to excretory pore. Spicules arcuate, their shape varying considerably with the angle at which they are viewed; proximal third cylindrical, distal portion flattened laterally and tapering to a blunt, slightly bifid, terminus; gubernaculum linear, indistinct; phasmids generally indistinct but appearing on a few specimens in the centre of the lateral field some 25 µm from the tail tip. Lateral field with four lines (three bands), the outer bands partially areolated.

DIAGNOSIS AND RELATIONSHIPS

Heterodera arenaria belongs to the “*H. avenae* group” and cyst characters are similar to those of *H. avenae*. Cysts are larger, with thicker and darker walls and the subcrystalline layer is thicker. Cyst cones are ambifenestrate, with prominent bullae crowded beneath the vulval cone, as with *H. avenae*. The vulval slit in *H. arenaria* is slightly smaller than in *H. avenae* 9.4 (8.3-11.5) vs 10.1 (10-13) µm. It can be separated from *H. avenae* by the characters of J2 : stylet knobs more indented anteriorly, stylet length [28.6 (26.8-29.4) µm], L [639 (590-677) µm], and length of the protoplasmic part of the tail [79 (72-84) µm]. In *H. avenae* these characters measure, respectively, 27 (24-28) µm; 575 (540-580) µm, and 45-70 µm (Williams & Siddiqi, 1972). Males of *H. arenaria* are readily separated from *H. avenae* males by the somewhat stouter stylet with basal knobs indented anteriorly whereas spear knobs of *H. avenae* slope posteriorly. The anteriorly indented stylet knobs of the J2 of *H. arenaria* resemble to some extent those of *H. mani* described by Mathews (1971). However, the stylet knobs of the latter are even more indented appearing anchor-shaped. In *H. mani* the average stylet length (24 µm), tail length (67 µm) and hyaline tail length (40 µm) are all shorter than in *H. arenaria* (28, 79 and 51 µm, respectively). Cysts of *H. mani* have a weak underbridge whereas it is absent from *H. arenaria*. In males of *H. mani* the stylet knobs slope posteriorly whereas they are indented anteriorly in *H. arenaria*. Stone and Hill (1982), using principal co-ordinate analysis of six juvenile numerical characters, found that *H. arenaria* was well separated from various races of *H. avenae* and

H. mani. Ebsary (1991) made *H. mani* a junior synonym of *H. avenae*. Ibrahim and Rowe (1995) showed that *H. arenaria* could be readily separated from *H. avenae* and *H. mani* using nonspecific esterase profiles obtained by either isoelectric focusing or native gel electrophoresis from extracts of white females. Consequently that synonymy is not accepted here.

COMPARATIVE MORPHOLOGICAL STUDIES ON *HETERODERA ARENARIA*

Morphological comparisons were made on cysts, eggs and second-stage juveniles collected from *Ammophila arenaria* at four coastal sites in the British Isles, and on a population from *Agropyron pungens* which originated from Gibraltar Point, and has been cultured since 1958 (ex Cooper). The results of these studies are given in Tables 1-3.

Cyst characters were found to be similar for all populations. Fenestral length/width ratio in the Port Eynon population was slightly lower (1.88 compared with 2.12, 2.11, 2.07 and 2.21) but measurements were only taken from five cysts, due to lack of material.

Length/width ratios of the eggs were similar in all populations (2.8, 2.8, 2.7, 2.6, 2.6), although eggs from the culture were slightly smaller (135 × 51 µm).

Interesting differences in some characters of juveniles from the *A. pungens* culture and the field populations were found. Juveniles from the culture were shorter (587 compared with 639, 633, 663 and 647 µm); tail length was smaller (73.65 compared with 78.72, 79.94, 80.41 and 82.13 µm) as was hyaline tail length (47.57 compared with 51.25, 53.06, 52.52 and 52.77 µm). These differences could be due to the different host (*Agropyron pungens* as opposed to *Ammophila arenaria*) or the result of the nematode population being cultured continuously for 22 years in a glasshouse. However, when the cultured selection and the population more recently collected from Gibraltar point were cultured on *A. pungens* or *A. arenaria* their progeny from both plant species were of similar size to their parents. Hence the host does not have an immediate effect on their measurements.

Few morphological differences were found between populations of *H. arenaria* collected from *Ammophila arenaria* at four coastal sites in the British Isles. Juvenile characters in these populations were very constant.

Cooper (1968) states that “*H. avenae arenaria* attacks sea marram grass. The cysts resemble large examples of cereal cyst eelworm but have thicker cyst walls, longer eggs and very long larvae. Our specimens come from the Gibraltar Point Nature Reserve, Skegness, but the species is widespread”.

The population of *H. arenaria* cultured by J. J. Helling was originally supplied by B. A. Cooper from Gibraltar Point. We are therefore convinced that our description does indeed represent *H. arenaria*. Consideration has been given to the designation of a neotype of *H. arenaria* for which a second stage juvenile

could be appropriate. However, such juveniles when processed to glycerol are some 15 % shorter than those in TAF and so lack the distinctive length characteristic of this species. We therefore feel that the measurements and photographs presented here are a better representation for this species. Specimens of *H. arenaria* used in this study are deposited in the nematode slide collection of the Entomology and Nematology Department, Rothamsted, with the catalogue numbers 76/28/1-36.

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