

Fig. 1. *Heterodera goettingiana*. A, B. Oesophageal regions of male and second-stage larva, respectively. C. Head, second-stage larva. D. Tail, second-stage larva. E, F. Lateral fields at mid-body of second-stage larva and male, respectively. G. Tail, male. H, I. Entire male and second-stage larva. J. Cysts, two with egg sacs. Figures of specimens from culture originally derived from type-locality.

*Heterodera goettingiana* Liebscher, 1892.

Syn. *H. schachtii* (pea strain) of Liebscher, 1890; *H. (Heterodera) goettingiana* Liebscher, 1892 (Škarbilovich, 1959).

**MEASUREMENTS** Mean measurements and standard deviations of specimens from a culture originally derived from type locality: 25 ♀♀: Stylet length =  $25.7 \pm 1.0 \mu$ ; stylet base to dorsal oesophageal gland duct =  $5.5 \pm 1.1 \mu$ ; number of head annules = 1-3; head tip to median bulb valve =  $71.8 \pm 8.4 \mu$ ; diameter of median bulb =  $32.7 \mu \pm 2.3 \mu$ ; head tip to excretory pore =  $131.1 \pm 20.4 \mu$ . Dimensions of genital region features similar to those of cysts.

25 cysts: Length excluding neck =  $521 \pm 53 \mu$ ; maximum width =  $372 \pm 44 \mu$ ; length of fenestra =  $35.3 \pm 5.9 \mu$ ; width of fenestra =  $37.4 \pm 4.3 \mu$ ; length of semifenestra =  $16.3 \pm 3.9 \mu$ ; anus to fenestral edge =  $36.2 \pm 4.6 \mu$ ; length of vulval bridge =  $33.0 \pm 5.4 \mu$ ; maximum width of vulval bridge =  $3.0 \pm 0.9 \mu$ ; length of vulval slit =  $39.9 \pm 7.2 \mu$ ; length of underbridge =  $117.2 \pm 13.1 \mu$ ; maximum width of underbridge =  $6.1 \pm 1.5 \mu$ .

Neotype cyst-cone dimensions: Length of fenestra =  $35 \mu$ ; length of semifenestrae =  $15 \mu$  and  $16 \mu$ ; width of fenestra =  $37 \mu$ ; anus to fenestral edge =  $30 \mu$ ; length of vulval bridge =  $36 \mu$ ; maximum width of vulval bridge =  $5 \mu$ ; length of vulval slit =  $36 \mu$ ; length of underbridge =  $125 \mu$ ; maximum width of underbridge =  $5 \mu$ .

50 ♂♂: L =  $1270 \pm 112 \mu$ ; a =  $51.4 \pm 4.6$ ; width at excretory pore =  $24.7 \pm 0.8 \mu$ ; stylet length =  $26.8 \pm 1.0 \mu$ ; stylet base to dorsal oesophageal gland duct =  $7.9 \pm 1.2 \mu$ ; head tip to median bulb valve =

100.9 ± 5.5 µ; head tip to excretory pore = 157.5 ± 9.9 µ; spicule length along axis = 26.5 ± 4.3 µ; gubernaculum length = 12.2 ± 2.0 µ; length of testis plus vas deferens = 663 ± 81 µ; tail length = 5.1 ± 1.0 µ. 50 second-stage larvae: L = 486 ± 22 µ; a = 25.1 ± 1.1; width at excretory pore = 19.4 ± 0.7 µ; stylet length = 24.6 ± 0.8 µ; stylet base to dorsal oesophageal gland duct = 5.3 ± 0.7 µ; head tip to median bulb valve = 70.3 ± 2.3 µ; head tip to excretory pore = 101.6 ± 4.0 µ; anus to terminus = 60.1 ± 5.3 µ; tail width at anus = 12.7 ± 0.9 µ; hyaline part of tail = 37.0 ± 3.2 µ. Some measurements are also given by Jones (1950), Fenwick & Franklin (1951), Goffart (1960), Macara (1963) and Matthews (1971).

**DESCRIPTION Female:** Body swollen, lemon-shaped, with projecting neck containing the oesophagus and part of oesophageal glands, bearing the head with one to three projecting head annules. Anterior part of neck irregularly annulated, remainder of body without annulations or lateral incisures but covered with reticulate ridges forming a brickwork-like pattern. Head skeleton weak, hexaradiate. Anterior part of stylet about 50% of stylet length and often detached in preserved specimens, stylet knobs rounded. Stomal lining forming a complex lyre-shaped tube around stylet shaft, extending back from basal plate of head skeleton for 70% of stylet length. Median oesophageal bulb large, sub-spherical, with prominent oval valve, oesophageal glands in a broad lobe, often displaced by massively developed paired ovaries. Prominent excretory pore at base of neck. Vulva and tail region carried on an obtuse cone-shaped projection opposite the neck, the vulva a transverse slit surrounded dorsally and ventrally by thin-walled crescent shaped areas leaving the vulva on a thicker-walled bridge-like structure. Vagina supported proximally by strongly developed lateral bands of muscle. Fenestral region surrounded by a zone of thickened cuticle (Fig. 2A). The fenestral region is at the posterior pole of the body with the anus in a dorsal position. Females are white on emergence from the root cortex and remain so throughout their development, turning brown at death. Females produce a gelatinous egg sac, exuded through the vulval aperture, into which some individuals lay a few eggs (Jones, 1950).

**Cyst:** Lemon-shaped with protruding neck and vulval cone but irregularly formed specimens are common (Fig. 1, J). **Ambifenestrate.** Vulval region may be intact in new cysts but in older specimens the thin-walled cuticle of the terminal region is lost leaving an open fenestra crossed by a vulval bridge bearing the vulval slit and dividing the fenestra into two semi-circular semifenestrae. The lateral muscles attaching the proximal part of the vagina to the body wall remain as an underbridge and the vagina remains as a sheaf-like structure between the vulval bridge and underbridge. Cyst wall dark brown and tough, with a thickened, strongly pigmented zone surrounding the fenestra. **Bullae absent.** Cyst wall bearing ridges forming a reticulate brickwork-like pattern. **Sub-crystalline layer not visible under light microscope** but a very fine layer is apparent with the scanning electron microscope. The egg sac is usually lost from cysts recovered from soil. For terminology of cyst-cone structures see Cooper (1955), Hesling (1965) and CIH Descriptions Set 1, no. 1.

**Male:** Vermiform, with a very short bluntly rounded tail. Body adopting a characteristically curved position on heat relaxation, the posterior part often twisting through 90° about the long axis (Fig. 1, H). Cuticle regularly annulated, 4 incisures in lateral field, appears un-areolated under the light microscope but is so in the scanning electron microscope. Head offset with prominent head cap and 5-6 annules. Head skeleton hexaradiate, heavily sclerotized. Anterior and posterior cephalids at level of 2nd and 8-9th body annules respectively. Well developed stylet, anterior portion 45% of total stylet length, knobs rounded with anterior faces sloping backward. Stomal lining forming a lyre-shaped tube around stylet shaft, extending from basal plate of head skeleton for 60% of stylet length. Median oesophageal bulb a slender ellipse with prominent crescentic valve plates. Dorsal and sub-ventral oesophageal gland lobes distinct, both lobes extending beyond excretory pore but sub-ventral lobe longer, extending to 15% of body length from head. Dorsal gland nucleus prominent, sub-ventral gland nuclei obscure. Broad nerve ring encircling oesophagus between median bulb and gland lobes. Hemizonid distinct, 2 annules long, usually 5-7 annules anterior to excretory pore, but in one specimen it was only 1 annule anterior to the excretory pore. Hemizonion not seen. Testis single, about 50% of total body length, packed with dense, spherical spermatogonia and terminating in a glandular-walled vas deferens with narrow lumen. Cloacal aperture small, surrounded by a raised collar-like lip. Spicules stout, curved with inner faces reflexed inward and interlocked proximally to form a tube (see Clark *et al.*, 1973). Spicule tips broad and said to be tridentate by many authorities but this character is difficult to resolve with the light microscope and electron microscope studies indicate that the spicules have bidentate tips (Clark *et al.*, 1973). Gubernaculum a simple rod. Phasmids and caudalids not observed.

**Second-stage larva:** Folded 3 times in egg. Vermiform, with regularly annulated cuticle, 4 incisures in lateral field along most of body, reduced to 3 at anterior and posterior. Lateral field appears un-areolated under the light microscope but is so in the scanning electron microscope. Cuticle thicker for first 7-8 body annules. Head slightly offset with 2-3 annules, a dorsoventrally elongate oral disc and lateral lips bearing amphid apertures—these characters are shown by scanning electron microscopy. Head skeleton massive, hexaradiate, often obscuring stylet tip. Cephalids at 2nd and 8th annules behind head. Stylet robust, knobs varying from smoothly rounded to slightly hooked shaped with recurved anterior surfaces. Stomal lining forming a lyre-shaped tube around stylet shaft extending from basal plate of head skeleton for about 60% of stylet length. Anterior part of oesophagus as in male. Oesophageal glands in an elongate lobe, extending for 33% of body length from head; broad posteriorly, dorsal gland and sub-ventral gland lobes less distinct than in male but distinguishable by texture; both lobes extend beyond excretory pore. Dorsal gland nucleus prominent, sub-ventral gland nuclei indistinct. Nerve ring as in male. Hemizonid 2 annules wide, 1 annule anterior to excretory pore. Hemizonion less than 1 annule wide, 7 or 8 annules behind excretory pore. Genital primordium a distinct two-celled structure about half-way along body. Tail tapering uniformly to a finely rounded terminus, posterior 60% of tail hyaline. Hyaline portion of tail often seen to contain 1 or 2 minute refractive bodies of unknown composition (see Stone, 1973). Caudalids and phasmids not observed.

**Note on identification:** *Heterodera goettingiana* cysts have a plump lemon shape with a wide vulval slit (exceeding 30 µ), are ambifenestrate, lack bullae and have a brickwork-like pattern of cuticular ridges. Second-stage larvae are characterized by the stylet knob shape and tail dimensions and the males by the broadly tipped spicules, apparently tridentate. Several characters must be used in making specific identification, preferably together with information on host. *H. cruciferae*, *H. carotae* and *H. urticae* are most similar but are distinguished by their shorter larval tails. In *H. goettingiana* the hyaline zone is 1.5× stylet length but less than 1.5× stylet length in the other 3 species. Of these 4 species only *H. goettingiana* has a brickwork-like pattern of ridges on the cyst surface and additionally *H. carotae* and *H. urticae* have more nearly spherical cysts. Females and cysts of *H. goettingiana* attached to pea or vetch roots may be distinguished from the other *Heterodera* spp. parasitizing these plants (*H. glycines*, *H. trifolii* and *H. schachtii* (Goodey *et al.*, 1965)) by the apparent absence of a sub-crystalline layer. Hesling (1965) and Mulvey (1972) give keys for separating *Heterodera* species.

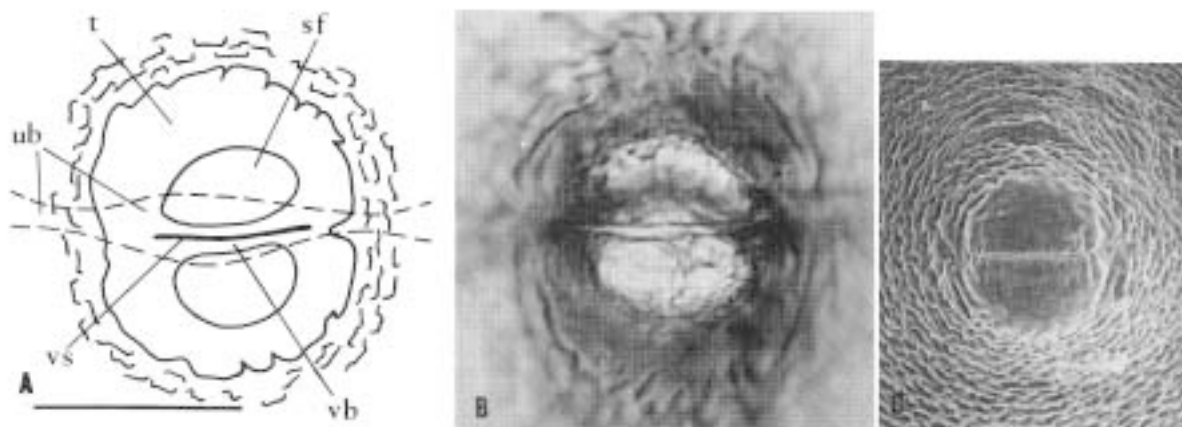


Fig. 2. A. Vulval cone, t, thickened band of cuticle; sf, semifenestra; vb, vulval bridge; vs, vulval slit; ub, underbridge; scale bar = 50  $\mu$ . B. Photomicrograph of cyst cone at same magnification. C. Scanning electron micrograph of unfenestrated cyst cone,  $\times 700$ .

**TYPE HOST AND LOCALITY** *Pisum sativum* L. The type locality was described by Liebscher as "local trial fields" near to Göttingen University Agricultural Institute.

**SYSTEMATIC POSITION** Tylenchida: Tylenchoidea: Heteroderidae: Heteroderinae: *Heterodera* Schmidt, 1871; *H. (Heterodera)* Skarbilovich, 1959.

**TYPE MATERIAL** Apparently type material of *H. goettingiana* does not exist (B. Weischer, pers. comm.) and no fully adequate description is available. A neotype cyst is here designated, taken from a culture on *Pisum sativum* and derived from soil removed from the type-locality at Göttingen, now no longer available, supplied by B. Weischer, Biologische Bundesanstalt, Münster, West Germany. The neotype is deposited at Rothamsted Experimental Station, Nematology Department type collection number 76/2/7.

**DISTRIBUTION AND HOSTS** *Heterodera goettingiana* has been widely reported from Northern Europe (see Goffart, 1941; Oostenbrink, 1951; Jones, 1965; and d'Herde, 1966 for details), from Spain (Tobar Jimenez, 1962) and Italy (Garofalo, 1964a). Kir'yanova & Krall (1971) illustrated populations from the USSR and Thorne (1961) reported isolated occurrences in the USA, probably chance introductions. Brown (1958) and Jones (1965) gave details of distribution in England and Wales and stated that many infestations were found in allotments and gardens as well as on agricultural land. Hosts of major agricultural importance are garden and field peas (*Pisum sativum*), broad and field beans (*Vicia faba*), vetches (*Vicia* spp.), soybean (*Glycine max*) and lentils (*Lens esculenta*). Three species of *Pisum*, 17 of *Vicia* and 9 of *Lathyrus* have been recorded as hosts including a number of European weeds. Thorne (1961) stated that sweet pea (*Lathyrus odoratus*) is a host but Jones (1950) and Winslow (1954) reported that it was not. Nearly all hosts are in the tribe Viciae of the family Leguminosae (Winslow, 1954). Many leguminous crops and weeds were found by these two authors to be non-hosts. For further details of host range see Goodey *et al.*, 1965 and for extensive host range tests Jones (1950), Winslow (1954) and Oostenbrink (1951) who found no resistance in 153 pea varieties.

**BIOLOGY AND LIFE-HISTORY** Development and basic biology are similar to those of other *Heterodera* spp. (see *CIH Descriptions* Set 1, Nos. 1 and 2, Set 2, Nos. 16 and 17). Macara (1963) gave illustrations of each stage in the life-history. The first moult occurs in the egg. Second stage larvae are the invasive stage, entering host plant roots and passing through three further moults to the adult. Males emerge from the host roots but females remain, rupturing the root cortex as they enlarge and often remaining partly buried in the root tissue especially in the thick main roots of beans. Guevara Benitez *et al.* (1970) reported that maximum invasion of larvae into roots of *Vicia sativa* occurred 65 days after commencement of growth; moulting larvae were most numerous 71–98 days later while males first appeared between the 58th and 98th day and numbers reached a maximum at 117–129 days. *H. goettingiana* is amphimictic and there is some evidence for environmental influence on sex ratio. In chick pea (*Cicer arietinum*) invading larvae induced a strong [necrotic?] host reaction and only male adults were produced (Vara Alcalá, Tobar Jimenez & Muñoz Medina, 1970). On peas at initial populations of 4 eggs/g soil 50% of eggs resulted in females but at 359 eggs/g less than 1% did so (Jones, Meaton, Parrott, Shepherd & King, 1965). Guevara Benitez *et al.* (1970) also found that a greater proportion of new adults were males at high population densities than at low ones. Numerous authors give evidence for extreme persistence of the nematode in the absence of a host crop, with crop damage occurring after breaks of 10–12 years (Brown, 1958). Moriarty (1963b) found that numbers of viable eggs in fen soil declined to 50% of the initial population in the first 3 years and thereafter declined at a rate of 50% of the surviving population each year. Hatch of larvae from eggs in field soils is stimulated by presence of a host crop (Brown, 1958; Jones & Moriarty, 1956; Anon., 1971). Shepherd & Wallace (1959) obtained a maximum emergence of only 1% from cysts in sand with growing pea plants but in field soil under peas they estimated emergence at 5% over the initial seven weeks of growth. Winslow (1955a) obtained 15% emergence in distilled water from cysts recently extracted from soil with growing peas. Host root diffusates, a wide range of organic compounds and extracts from cultures of pea rhizosphere fungi all failed to stimulate emergence *in vitro*; only treatment with 5% calcium hypochlorite induced a hatch, probably by dissolving the eggshell (Winslow, 1955a; Shepherd, 1963).

**HOST-PARASITE RELATIONSHIPS** Only one publication gives histological details, describing changes in *Vicia sativa* roots (Vara Alcalá *et al.*, 1970). After invasion, endodermal cells surrounding the head of a second-

stage larva form a syncytial transfer cell. As the female develops, suberin is deposited in the cortical parenchyma cells surrounding its enlarging body. The reaction is less marked around developing males.

Root growth of infected peas is reduced but without the excessive formation of small lateral roots characteristic of the hosts of other *Heterodera* species and plants may suffer water stress even at low nematode densities (Moriarty, 1962). Formation of nitrogen-fixing bacterial nodules on pea roots is suppressed and often absent, resulting in marked symptoms of nitrogen deficiency (Oostenbrink, 1955; Anon., 1971). Fungal infections are frequently associated with, and aggravate, pea cyst nematode infestations. Garofalo (1964b, 1964c) showed that damage to peas and lupins grown in sterile soil was more severe and developed earlier when inoculated with *H. goettingiana* and *Fusarium oxysporum* than with either pathogen alone and implicated *F. oxysporum* in damage to field crops of peas. However, Oostenbrink (1955) demonstrated the primary role of the nematode: surface sterilized *H. goettingiana* larvae inoculated onto a *Fusarium oxysporum*-resistant pea variety caused typical symptoms. Field infestations typically show patches of sick plants with yellow foliage, the patches spreading in successive years if no control measures are taken. The relationship between initial nematode density and yield in peas is variable (Stemerding, 1960; Moriarty, 1962; Jones & Moriarty, 1956) but Jones *et al.* (1965) and Winfield (1965) found a sigmoid curve best fitted the relationship over a range of initial populations from 4 to 359 eggs/g soil. Winslow (1955b) recorded total crop failure of peas at an initial density of 127 eggs/g soil; Winfield (1965) reported total crop failure at a minimum of 331 eggs/g soil and a reduction of 75% in yield from plots with 250 eggs/g compared with plots with 18 eggs/g. Field and broad beans are less susceptible to damage than peas and are less efficient hosts (Winslow, 1955b; Moriarty, 1963a). Jones & Moriarty (1956) found that over a range of 12 to 136 eggs/g soil, cyst numbers after vetch were double the initial number but eggs increased by only 27%. Under field beans a similar increase in cyst numbers occurred but with only a 5% increase in eggs. Windsor and Longpod beans caused a relatively small increase in cyst numbers and reduced the egg populations. Peas caused average increases of 265% of cyst numbers and 378% of eggs. All crops tested produced final egg densities sufficient to cause damage to pea crops.

**CONTROL** Small scale experiments have shown that some chemicals are effective. Nemagon at 30 lb a.i./acre gave some control (Proctor, 1960). Heat sterilization, chloropicrin at 0.3 ml a.i./litre soil and D-D at 0.15 ml a.i./litre soil gave complete control in pot experiments but aldicarb at 0.025g a.i./litre soil and captan at 0.3g a.i./litre soil were less effective and none of these measures was economic (Eissa, 1971). Whitehead (1974) obtained control of the nematode and increase in pea yields on clay and loam soil with a range of small amounts of aldicarb, Du Pont 1410 and Dowco 275 (*O,O*-diethyl *O*-(6-fluoro-2-pyridyl) phosphorothioate) incorporated in the seedbed before sowing. On sandy clay only aldicarb and Du Pont 1410 were effective.

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