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**A CULTURE METHOD FOR SOIL MEIOFAUNA AND ITS
APPLICATION TO THE STUDY OF NEMATODE
PREDATORS ¹⁾**

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Laboratory culturing of the soil meiofauna has been a problem for many years, and the lack of suitable techniques, a serious hindrance to progress. Existing methods have been developed primarily for life-history and biological studies of the Acarina and Collembola, the commonest members of the soil meiofauna. Some have been used in investigations of anoplocephaline cestodes, parasites of sheep, of which oribatid mites are intermediate hosts, and recently modifications have been devised by those concerned with trombiculid mites, important because of their connection with the transmission of 'scrub-typhus'. Some of the culture methods described here offer a means for biological studies of certain nematodes, and the observations on insect predators of soil and plant-parasitic nematodes outlined, demonstrate the possibilities of these culture techniques.

The minimum requirements for culturing meiofauna are a suitable vessel and cover, and a substrate which will retain sufficient water to provide the humid environment normally required by these creatures. MICHAEL (1884), in his studies of the Oribatoidea, used a cell formed from a glass ring cemented to a microscope slide, with a cover glass as lid, and a circle of filter-paper on the floor of the cell to provide the necessary reservoir of water. This method has been widely used in studying the Acarina and other organisms. For culture of cheese mites (Acaridoidea), ROBERTSON (1945) used a plastic strip in which a hole with inclined sides was drilled. Black filter-paper was cemented to the lower surface, and the upper was sealed with a cover glass held in position by a paraffin-vaseline mixture. This pattern can be suspended in a vessel containing a suitable solution, and in this way the relative humidity of the cell atmosphere can be controlled precisely. CUNNINGTON & SOLOMON (*in litt.*) have modified the Robertson cell

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by replacing the filter-paper with 200-mesh bolting silk dyed black, and by securing the cover glass with ticket clips. JONES (1951) used a further modification with which he cultured the harvest mite (*Trombicula autumnalis* Shaw) from larva to adult for the first time. His pattern consisted of a perforated plastic block with filter-paper fastened to the lower surface. The chamber was formed from a strip of filter-paper resting in the cavity, its ends being held in position by a cover glass placed on the upper surface of the perspex. A cotton-wool plug was inserted between the two pieces of filter-paper, and the cell placed in a larger vessel, its lower surface in contact with moist cotton wool.

Plaster of Paris has also been used to provide suitable humidity conditions. For culturing Trombiculidae — difficult creatures to rear and a good test of technique — MICHENER (1946), JENKINS (1947), LIPOVSKY (1953) and others, used a jar with the bottom removed, and replaced by a plug formed from a mixture of plaster of Paris and activated charcoal (JENKINS 1947). To prevent the formation of water droplets, the walls were also coated with this material (MICHENER 1946). Recently EDWARDS (1955) has used a modification for culturing Symphyla, in which the cells are formed from glass cylinders embedded in plaster of Paris. ROHDE (1956) has devised a somewhat similar modification for phthiracarid mites. SCHALLER (1953) and his students, used a cell formed entirely of plaster of Paris with a glass cover seated in plasticine. This receptacle has the advantage that water can be added from outside without disturbing the cell contents. It has proved suitable for a wide range of animals including Diplopoda, Acarina and Collembola. SCHUSTER (1956), for biological studies of soil-inhabiting Oribatoidea, used a porous clay pipe-filter placed on a surface of moist sand.

None of these methods is entirely suitable for studies requiring close observation of the culture subject, and for this reason the first author has developed a new technique, which has proved very suitable for this purpose. The second author has also found it a useful container for electronic-flash photomicrography of living material (Figures 5 & 6) and for studying predators of some nematodes, chiefly the Heteroderidae. In addition to the basic requirements — high humidity, adequate oxygen supply, food material maintained in a moist condition, and absence of water droplets — such studies require a culture receptacle with a small surface area, and reduction to a minimum of wall surfaces and other awkward parts, which make observation dif-

ficult. For studies of food habits particularly, the presence of filter-paper, plaster of Paris or a loose substrate such as sand (FRANZ & LEITENBERGER 1948) or vermiculite (FARRELL & WHARTON 1949), is undesirable. A completely inert, solid medium has the further advantage that sterilization of the cell becomes a comparatively simple operation.

Method

The culture chamber consists of a sintered-glass micro-immersion filter¹⁾ (Fig. 1) with sunk disk; it has an area of 64 mm²

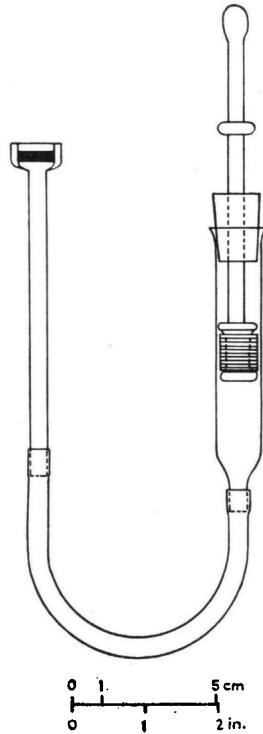


Fig. 1. Micro-immersion-filter culture cell with syringe.

(9 mm *d*), is 2 mm deep, and has a cover-glass lid. The glass syringe has a cotton-wound plunger. The filter is attached by rubber tubing

1) The micro-immersion filters (K902H) were obtained from Messrs. Baird & Tatlock (London) Ltd., Freshwater Road, Chadwell Heath, Essex, England. They are available in two porosities: No. 1 (pore size: 90-150 μ) and No. 2 (40-90 μ). No. 2 is preferable as the surface of the former is rather coarse.

to the syringe, and is mounted in a suitable framework (Fig. 2). The system is filled with water, and when the plunger is depressed it is possible to irrigate the cell; on withdrawing the plunger, the water can be brought below the level of the sintered disk, and no water droplets should remain on the glass parts of the cell. The only troublesome feature is condensation on the cover. Avoidance of large temperature fluctuations and a fairly thick glass for the lid reduce condensation to a minimum. Demisting compounds also help.

There is frequently need for a larger culture vessel (e.g. for stock cultures) and for this purpose a Gooch-type filter crucible²⁾ with sintered-glass plate (Fig. 3) is used. The crucible is inverted, inserted in a cork with a tube connected to a large syringe of the type already described. This arrangement provides a very shallow cell with a large surface area ($27 \text{ mm } d \times 2\text{-}3 \text{ mm deep}$; area = 573 mm^2). It is covered with a large cover glass, and the lower edge of the crucible is ground with carborundum powder if a tight seal is required. Alternatively, if there is need for a deep cell (4 cm) the crucible is turned right way up and inserted in a rubber cone adapter. This arrangement is particularly suitable for collecting live material from litter and soil samples when a funnel-type extractor is used.

It is important to ensure that the glass walls of the cell are thoroughly clean as a dirty surface traps water droplets during irrigation. For this reason cells should be cleaned in dichromate solution and then rinsed in distilled water.

Handling individuals of the soil meiofauna is a slow and tedious operation. Immersion in water for a short period does not harm some groups (e.g. the majority of the Oribatoidea) and this provides a convenient means for transferring live material. The animals are collected from a funnel extractor in a deep Gooch-crucible cell. The latter is flooded until the water reaches the upper rim of the cell, and the individuals, which usually float on the water surface, are removed with a fine brush, and placed in a miniature cell flooded in a similar manner. When the required number have been transferred, the water is withdrawn, thus completing the preparation of the culture.

2) The Gooch filter crucibles (a-4840, $1 \times$ porosity $1 = 100\text{-}120 \mu$) and matching rubber cone adapters were supplied by Messrs. A. Gallenkamp & Co. Ltd., 17-29 Sun Street, London, E.C. 2. The crucible pattern may vary slightly, especially the depth of lip which forms the cell wall. For this reason it is worth obtaining a sample before ordering in quantity.

Studies on animal predators of the Heteroceridae and other soil nematodes.

In July and August, 1956, while examining rape seedlings from a plot on which the cabbage-root nematode (*Heterodera cruciferae* Franklin) had been cultured for about seven years, it was found that whereas moderate infestations of larvae up to late third or early fourth stage occurred in the roots, the number reaching maturity appeared rather low. Moreover, of the few mature females found attached to the roots, sometimes up to about 30 per cent. had large irregular perforations through the cuticle and the body contents had usually disappeared (Fig. 4).

Although perforations of various forms have often been noticed in *Heterodera* cysts, so far as the writers are aware, no animal predators causing this type of damage have hitherto been identified. THORNE, however, reported *Mononchus papillatus* Cobb on two occasions attacking and drawing out the body contents of a young female *Heterodera schachtii* Schmidt, which was attached to a rootlet. He and other workers have also frequently observed *Mononchus* species feeding on mature males and larvae of *H. schachtii* and other soil nematodes and also attacking the eggs of *H. schachtii* in cysts, which had been opened, presumably by artificial means (THORNE 1927). THORNE (1928) also listed a number of species of *Acrobeles* and *Cephalobus*, *Dorylaimus obtusicaudatus* Bastian, *Tylenchus* sp. and *Plectus* sp. which he had found inside cysts of *H. schachtii*. Three *D. obtusicaudatus* were found with eggs of the sugar-beet nematode impaled on the mouth stylet, but as this nematode is not usually predacious, THORNE concluded that these occurrences were probably accidental. *Acrobeles* and *Cephalobus* are probably saprozoic and were not considered likely predators of eggs or larvae of *H. schachtii*.

Amongst others, J. J. HESLING and J. F. SOUTHEY (*in litt.*) have found species of *Dorylaimus* within *Heterodera* cysts, and these occurrences have sometimes coincided with the presence of a small circular perforation in the cyst wall. Although it seems probable, it has not been definitely established that these nematodes were preying on the living cyst contents.

Other soil-inhabiting organisms have been reported preying on heteroderas: SCHAERFFENBERG and TENDL (1950, 1951) concluded from experiments that young enchytraeids of the genera *Fridericia* and *Enchytraeus* fed on larvae of *H. schachtii* within the host plants, prob-

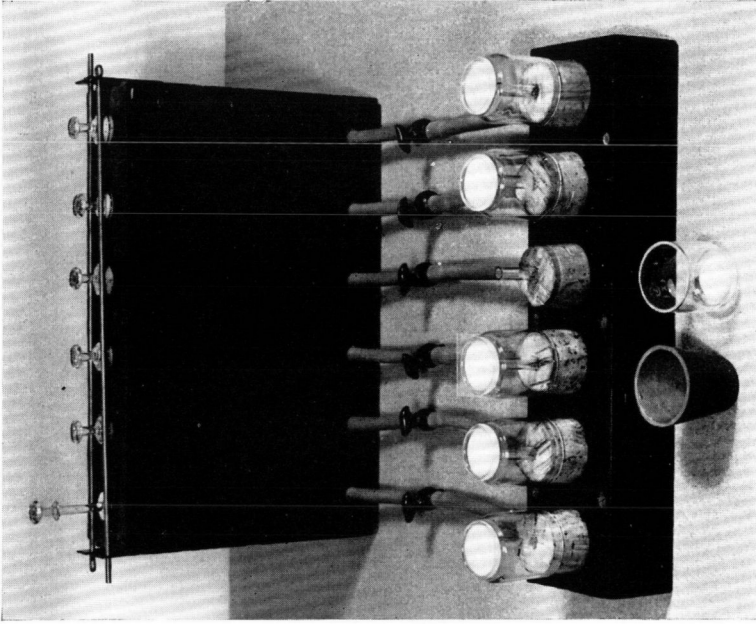


Fig. 3. Gooch filter-crucible cells with rubber cone adapter in the foreground for converting cell to deep form.

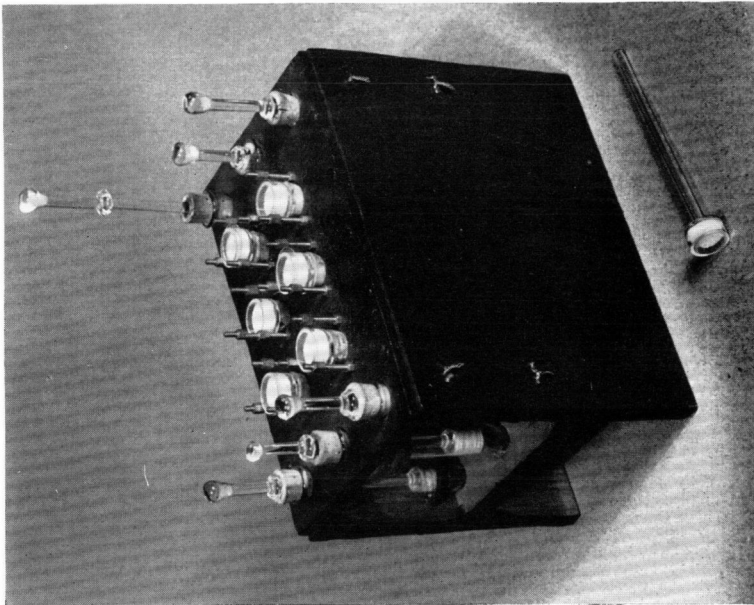


Fig. 2. A battery of micro-immersion-filter culture cells. A separate filter is shown in the foreground.



Fig. 4. Young adult females of *H. cruciferae* removed from rape plants in July, 1956. The damage shown is characteristic of that caused by Collembola.

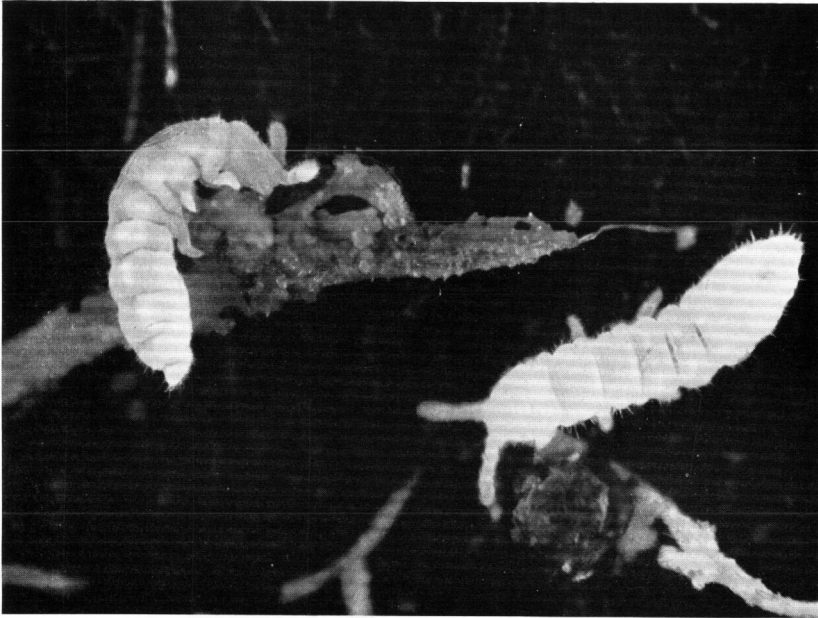


Fig. 6. The same culture as that illustrated in Fig. 5, photographed five hours later. Note the enlarged perforations in the white *H. cruciferae* and the characteristic feeding attitude of *O. armatus*.

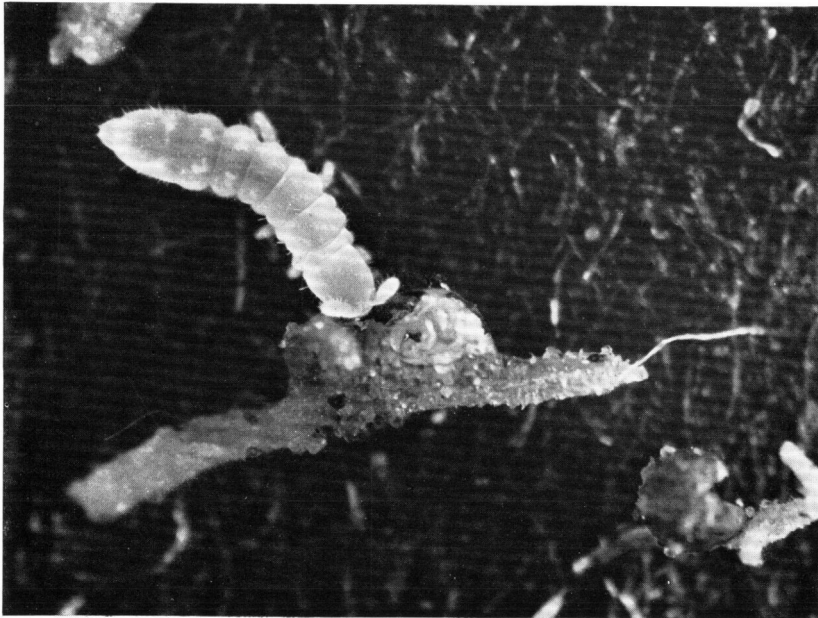


Fig. 5. *Onychiurus armatus* feeding on mature female *Heterodera cruciferae* (centre). A brown cyst of *H. cruciferae* which has been opened and the contents removed by *O. armatus* is also seen (bottom, left).

ably by means of extra-intestinal digestion, and WEBER, ZWILLENBERG and VAN DER LAAN (1952) reported an amoeboid organism engulfing and digesting larvae of *Heterodera rostochiensis* Wollenweber. This organism was later named *Theratromyxa weberi* Zwillenberg (ZWILLENBERG 1953 and VAN DER LAAN 1954).

Methods

In an attempt to find predators of *H. cruciferae*, soil samples collected from the top four inches of the culture plot in July and August, were elutriated in a 1 litre measuring cylinder and numerous Collembola and soil mites were recovered, together with a few Symphyla. By the 25th August no more Symphyla were being recovered and the most abundant soil animals were *Onychiurus armatus* (s. lat.) Tullb., *Folsomia* sp., *Hypogastrura* sp., *Isotoma viridis* Bourlet and other Collembola; various soil mites were also present in fair numbers. Later the meiofauna was extracted from the soil samples by means of a split-funnel extractor (MURPHY 1956) and most species recovered were cultured in selected groups in P. W. MURPHY'S culture cells. Each group was supplied with a new cyst of *H. cruciferae* and the culture cells were irrigated daily.

Predators of *Heterodera*

By 31st August none of the cysts in the culture cells had been eaten and a soil sample was taken from a pot culture of *H. cruciferae* from which damaged cysts had been recovered. This culture contained *O. armatus* in large numbers as well as most of the other forms recovered from the plot. On 1st September one specimen of *O. armatus* was seen nibbling away part of the cuticle of a cyst which had recently turned brown. Feeding continued until a shallow depression had been made in the cyst contents, when the insect was removed for mounting.

About a week after its introduction into a culture cell containing a mature female *H. cruciferae*, an *Isotoma viridis* was seen feeding intermittently on the nematode. Damage to the nematode did not progress far and the contents had not completely disappeared. This springtail fed more intensively on cortical tissues of the root to which the cyst was attached.

In a mixed culture of Collembola consisting of *Folsomia* sp., *Hypogastrura*, sp., *Lepidocyrtus* sp., *Orchesella villosa* (Geoffroy) and *Iso-*

toma notabilis Schäffer, a fresh brown cyst of *H. cruciferae* was found to have been perforated and a juvenile *Hypogastrura* sp. (probably *denticulata* Bagnall) was seen feeding on the cyst contents. In the same culture cell, which did not then include the *Orchesella villosa* a fourth stage female *H. cruciferae* was completely consumed.

The *O. villosa* was placed in a separate culture cell where it was seen feeding on the cortices of root fragments. But a fortnight after its introduction it was found to have eaten away an area of cuticle of a cyst of *H. cruciferae*, which was turning from white to brown. However, feeding on the cyst was neither sustained nor extensive.

J. J. HESLING informed the authors that he had seen soil mites of the Suborder Mesostigmata feeding on egg-sacs of *Heterodera schachtii* var. *trifolii* Goffart and mites from this group were kept with both white and brown females of *H. cruciferae*. On one occasion a small part of the egg-sac of a cyst was found to have been removed, but there was no evidence that anything more than the gelatinous matrix had been eaten. On several occasions it was thought that mature female heteroderas placed with these mites turned a dark brown colour unusually quickly: on two occasions this happened within five hours of placing in the culture cell, whereas previously they had remained in the white condition in a similar storage cell for about a week. Similar cysts believed to have been affected by Mesostigmata were transferred to a separate culture cell and three to four weeks later were placed in a watch glass of Brussels-sprout root diffusate. There was a fair emergence of larvae, indicating that if the mites had in some way killed the adult nematodes there was not, at any rate, complete mortality of the eggs within the cysts.

Nematodes recorded as food of Onychiurus armatus

As *O. armatus* was by far the most voracious predator on *H. cruciferae*, a variety of nematodes were placed in culture cells each with 7 to 9 freshly caught Collembola of this species. Two large *Dorylaimus* and a *Mononchus* from soil were both partially eaten, one of the *Dorylaimus* within an hour of introduction into the cell: it was showing little activity when introduced and no evidence has been obtained that nematodes are ever attacked when actively moving. BROWN (1954) however, reports actively moving nematodes (not identified) being smoothly and rapidly ingested by isotomid Collembola, as if sucked in by them; the *O. armatus* ate through the vermi-

form nematodes transversely and made no attempt to ingest entire eelworms.

Table I summarizes observations on the feeding of *O. armatus* on *H. cruciferae*, and provides data on the time elapsing before feeding commenced together with its extent and duration for each nematode. It is seen that living white females were preferred to brown cysts, although cysts were sometimes eaten if there were no live females available.

Attempts were made to feed *O. armatus* on white females of other species of *Heterodera*. Only *H. schachtii* and *H. schachtii* var. *trifolii* were then available (17th October), although rearing of suitable stages of other species is now being attempted. In the first culture, containing *H. schachtii* var. *trifolii*, there were 4 adult females, some with egg-sacs, and one fourth-stage larva. Within an hour of introduction, one young white female had been partially ingested and during the following night the fourth-stage female had been completely devoured. Three days later one specimen had turned brown, but was apparently undamaged and one mature white female remained unchanged. The remaining two specimens had been emptied of their body contents. No further change occurred.

The second culture contained three live females of *H. schachtii* with incompletely developed egg-sacs. One of these nematodes was punctured two days after its introduction, the head of another was eaten away at about the same time and some feeding from the base of egg-sacs was noticed. All three females had turned to brown cysts three days after their introduction and in this condition appeared to be immune to attack in this culture.

The usual behaviour of *O. armatus* when provided with fresh white *Heterodera* females on roots, was to spend a variable time examining the food with the antennae. Sometimes this would continue intermittently for several days. Finally, an insect would scrape a definite area of the nematode, employing a gentle abrasive action with the mandibles and persisting for up to an hour at a time. The antennae would be directed backwards, and other Collembola were apparently mildly deterred from interfering, by the predator pointing the tip of the abdomen and anal spines towards each intruder. The scraping period varied considerably and was usually interrupted more than once, but it is believed that the nematode cuticle was usually perforated within six to twelve hours of the commencement of scraping and sometimes within a much shorter period. Once the cuticle had been penetrated

TABLE I
 Observations on *O. armatus* cultures provided with living females and cysts of *H. cruciferae*

Culture number (<i>O. armatus</i>)	Number of <i>O. armatus</i> in culture	Dates of introduction of <i>H. cruciferae</i>	Condition of <i>H. cruciferae</i>	Duration of feeding	Extent of damage to <i>H. cruciferae</i>	Other food present
1	?	25th August	Recently turned brown	1st Sept.-1st Sept.	None	None
2	9	31st August	Recently turned brown	21st-25th Sept.	Cuticle perforated; some contents removed	Root fragment
3	9	18th September	White		Contents removed	Rootlets and brown cyst
		18th September	Recently turned brown		None	Rootlets and white female
		25th September	White	27th Sept.-1st Oct.	Most of contents removed	Rootlets and brown cyst
4	9 reduced by death to 6	25th September	Recently turned brown		None	Rootlets and white female
		17th October	Small, white	17th-19th October	Completely ingested	Rootlets and brown cyst
		17th October	Recently turned brown	19th-22nd October	Part of cuticle only remained	Rootlets and white females
		18th October	White	18th-19th October	Part of cuticle only remained	Rootlets and brown cyst
4	9 reduced by death to 6	18th October	White	18th-19th October	Fragment of cuticle only remained	Rootlets and brown cyst
		22nd October	Dry, brown cyst		None	Root fragments
		26th October	White; turned brown in culture		None	Root and peat-moss fragments
		3rd December	White; turned brown in culture		None	Rootlets, peat-moss and cyst

other *O. armatus* would find the food supply and frequently as many as four or five individuals were seen simultaneously devouring a single nematode. During this time competition for the food was most acute and individuals were often seen attempting to repel each other, on these occasions by lunging at one another and by free use of the mandibles, when they bit antennae, head or thorax. This was sufficient to cause abrupt cessation of feeding or to drive off an intruder, although no permanent injuries were apparently ever sustained. During this period a single *Heterodera* female might be perforated in as many as three or four places, the holes being progressively enlarged as the insects ate deeper into the interior. Providing that suitable conditions were maintained in the culture, the predator always consumed the contents of the nematode whether in the white or brown state, except in the case of the single *H. schachtii* female which was only punctured. Young females with relatively thin, soft cuticles were sometimes completely devoured, but it appeared probable that the cuticle was less attractive than the contents and became even less so as it aged.

Estimation of damage by Collembola to a population of H. cruciferae

No attempt was made to obtain an accurate quantitative estimate of the amount of predation by Collembola in a population of *H. cruciferae* because the age of the *Heterodera* females seemed to have an effect on the amount of damage done to them and it is probable that some were completely ingested. However, a pot culture of *H. cruciferae* was examined in order to obtain a minimum estimate of springtail predation.

In October a cabbage root system infested by *H. cruciferae*, together with its adhering soil was weighed and then washed. The soil and washings were collected in a flask and all floating material was collected on a filter-paper for examination. The remaining soil was collected on a 100 mesh-to-the-inch sieve, dried and finally re-washed in order to recover floatable material. From the root system and the first and second floats, counts were made of the numbers of *O. armatus*, undamaged heteroderas, those damaged by unknown causes and those showing characteristic damage by Collembola. The results are given in Table II. The mean number of *O. armatus* per gram of soil and roots was 1.0 and of *H. cruciferae* 5.3.

In interpreting these results it must be borne in mind that only partially eaten heteroderas could be counted. Some damaged cysts still

TABLE II
 Numbers of *Collembola*, normal and damaged *Heterodera cruciferae* individuals recovered from a cabbage root system (11th October)
 (Fresh weight of root system and soil = 247 g)

	<i>O. armatus</i>		<i>H. cruciferae</i>		
	Undamaged	Cause unknown	Damaged		Per cent, of total
			Numbers	Damaged by <i>Collembola</i>	
<i>H. cruciferae</i> attached to cabbage root system	8	1	3		25.0
Float from moist soil	328	29	26		6.8
Float from dried residual soil	706	60	55		6.7
Totals	1,042	90	84		
Grand Totals		1,216			6.9

contained eggs and the remainder were identified from fragments of cuticle of various sizes which were apparently sufficiently tough and resistant to survive the processes involved in their collection. However it is probable that during extraction many remnants of the more fragile white females were lost or damaged beyond recognition.

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ZUSAMMENFASSUNG

Nach einem Rückblick auf die Methoden der Kultivierung von Acariden, Collembolen und anderen Bodenorganismen werden zwei neue Kulturkammern beschrieben. Die kleinere besteht aus einem gläsernen Mikro-Immersions-Filter, der mit einer Spritze verbunden ist. Die Zelle wird mit Hilfe der Spritze befeuchtet. Sie ist besonders für Nahbeobachtungen bei Untersuchungen an Collembolen als Räuber von bodenbewohnenden und pflanzenparasitischen Nematoden, z.B. bei *H. cruciferae*, geeignet. Bei der grösseren Kammer wird anstelle des Immersionsfilters ein Gootsch-Filter-Schmelztiigel verwendet. Dieses Verfahren dient besonders zum Sammeln von lebendem Material aus Streu und Boden mit einem Extraktor nach Trichter-Art.

Zysten von *Heterodera cruciferae* aus Kulturen haben in der Kutikula häufig Löcher aufzuweisen. Die Collembolenarten *Onychiurus armatus*, *Isotoma viridis*, *Hypogastrura* sp. und *Orchesella villosa* frassen an ihnen. Milben der Unterordnung Mesostigmata töteten wahrscheinlich erwachsene Weibchen von *H. cruciferae* und fressen zu einem gewissen Grade an dem Eiersack. *O. armatus* war der wichtigste Räuber in den Kulturen; dieser frass auch an inaktiven Nematoden der Gattungen *Dorylaimus* und *Mononchus*, an Weibchen von *Heterodera schachtii* var. *trifolii* und bis zu einem gewissen Grade an *H. schachtii*. Auszählungen im Oktober zeigten, dass wenigstens 6,9 % der *H. cruciferae*-Zysten in Topfkultur von Collembolen geschädigt waren. Dabei war das Verhältnis der Zysten zu *O. armatus* wie 5: 1.

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ERRATUM

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Page 10, fig. 2.

Nematodes per 10 milligrams of root *should read* Nematodes per 40 milligrams of root.