

Avec *S. cavenessi* une faible reproduction n'a été observée que sur *A. holosericea* et *P. juliflora* et pour *D. elegans* seul *A. holosericea* a permis une multiplication.

En ce qui concerne *S. cavenessi* et *D. elegans*, ces expériences, conduites dans des conditions très éloignées de celles existant au champ et avec des nématodes difficiles à manipuler au laboratoire, n'ont donné que peu d'indications. Par contre, avec les deux souches de *Meloidogyne* elles ont permis de caractériser les qualités d'hôtes des différentes essences. A notre connaissance à l'exception de *P. juliflora* aucune des autres essences n'a été signalée comme plante hôte pour les deux espèces de *Meloidogyne* considérées.

Dans le cas de leur utilisation en agroforesterie, les essences classées comme bons hôtes ou très bons hôtes pour les *Meloidogyne* devraient être limitées aux associations avec des cultures non sensibles à ces parasites. Si ces essences étaient associées avec des cultures sensibles elles pourraient ainsi jouer le double rôle de réservoir et

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de refuge pour les *Meloidogyne*, rendant alors inefficaces tous les moyens de lutte.

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ON THE DEFINITION OF HETERODERID CYSTS

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The cyst is a key character in the systematics of the Heteroderidae *sensu* Wouts, 1973 but there is disagreement about the definition of this character. In a recent treatment of the phylogeny of Heteroderidae Wouts (1985) defines cyst-forming nematodes as "... those species that show a change in colour of the female cuticle upon death of the female, regardless of the extent of this colour change..." (p. 310). Perhaps to emphasize this usage, in his definitions of subfamilies and genera Wouts (1985) excludes the terms cyst-forming and non-cyst-forming in favour of females changing or not changing colour after death. The question arises whether or not this is an adequate definition and even one which has historical veracity.

In some "classical" publications the definitions/descriptions of cysts are as follows :

Filipjev and Schuurmans Stekhoven (1941) : "Part of the eggs remain within the female worm, which now forms a brown cyst, a saclike structure, consisting of the female cuticle in which egg-masses are contained." (p. 499).

Franklin (1951) : "... transformation of the body wall of the adult female into a tough resistant cyst or sac containing the embryonated eggs..." (p. 1).

Thorne (1961) : "... the female cuticle... transform(s) into a tough, brown, cystlike sac protecting the eggs which have been formed within the body" (p. 271).

Caveness (1964) : "At maturity the body wall of the *Heterodera* female thickens, becomes resistant to decay and turns brown as the worm dies resulting in a protective shell for the eggs and is termed a cyst." (p. 17).

Franklin (1971) : "The transformation of *Heterodera* females into cysts involves the tanning of the cuticle on death and the formation of a white subcrystalline layer initiated before the nematode dies, possibly during the last larval molt." (p. 144).

Dropkin (1980) : "... The female develops a thick cuticle, its uterus becomes packed with fertilized eggs that mature to second-stage juveniles but not further..."

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When the adult female dies, its cuticle tans into a brown leathery sac, the cyst". (p. 207).

Maggenti (1981) : "The cyst is the tanned cuticle of the mature female body in which eggs are retained." (p. 197).

Siddiqi (1986) in referring to cyst-forming genera of Heteroderidae states "... the female body turns into a hard-walled protective cyst" and divides heteroderids into... "cyst and cystoid (when the cysts are not formed) nematodes..." (p. 322).

There appears to be a consensus that two characteristics define cysts : *i*) transformation of the body wall of the female into a hard, tanned or brown structure; *ii*) retention of all or some of the eggs within the so modified female body wall. Only Franklin (1971) adds the presence of the subcrystalline layer as a character of the cyst applying this qualification to cysts of *Heterodera* and *Cryphodera* as defined at the time. To supplement these concepts we have tried to discover which author produced the first definition of a heteroderid cyst.

The first described species, *Heterodera schachtii* Schmidt, 1871, was extensively studied in Germany in the second half of the 19th century, so we have examined early German publications on the subject. In none of the publications of Schacht (1859*a,b*), Schmidt (1871, 1872), Kühn (1877, 1880) is the term "cyst" applied to female nematodes, neither is the presence of dead brown females recorded. Schmidt (1871) used "Eiersack" (egg-sac), but for the gelatinous matrix containing eggs outside the female body, and he first used "... cystenartige..." (cystlike), but to refer to the adult male enclosed in the sac-like juvenile cuticle. Later, Strubell (1888) used the term "Brutkapsel" (brood capsule) for the brown and hardened dead female of *H. schachtii*.

The description of cysts of *H. schachtii* apparently was first elaborated by the French author Chatin (1887) in a note to the French Academy of Sciences (presented by Louis Pasteur!). He wrote as follows :

« ... dans certaines circonstances et spécialement à l'approche de l'hiver, on constate chez les femelles d'importants changements qui offrent un intérêt tout particulier. Le tégument, d'abord très mince, s'épaissit progressivement; ses glandules fournissent une abondante sécrétion qui, agglutinant des substances organiques et minérales, forme ainsi autour de la femelle une sorte de test adventice, de nature mixte. En se développant, cette carapace finit même par obturer les ouvertures buccale, anale et vulvaire; l'aiguillon céphalique qui maintenait le parasite fixé dans les tissus du végétal ne peut, dès lors, plus fonctionner et toute adhérence se trouve rompue entre le ver et la plante nourricière. Ce n'est plus un animal qu'on a sous les yeux, mais un kyste rempli d'œufs, comparable à une oothèque, et qui tombe dans la terre mêlée aux racines.

De forme variable (ovoïde, naviculaire, biconique, etc.) ce kyste mesure en moyenne 0,6 mm suivant son grand axe. Il est de couleur brunâtre, protégé par des parois très épaisses et difficilement perméables. On voit combien il diffère de la femelle fécondée, telle qu'on l'observe avec sa teinte blanche, son tégument mince et fragile, se rompant sous le moindre choc ou sous la moindre action osmotique. On s'explique facilement comment un kyste ainsi constitué peut traverser la mauvaise saison, assurant une puissante protection aux œufs qu'il renferme. »

Translated as : "... in special circumstances, and especially when winter is approaching, changes of particular interest are observed in the female. The integument, previously very thin, thickens progressively; its glands provide an abundant secretion which, agglutinating organic and mineral substances, forms around the female a type of adventitious test of mixed composition. While developing this covering ends in obscuring the buccal, anal and vulval openings; the cephalic stylet that maintained the parasite fixed in the plant tissue can no more act and any contact is ruptured between the worm and the nourishing plant. It is no longer an animal we see before our eyes, but a cyst, full of eggs, similar to an oothecum, which falls into the soil mixed with the roots. Of variable shape (ovoidal, spindle-shape, biconical, etc.), such a cyst measures on average 0.6 mm, on the longest axis. It has a brownish colour, and it is protected by very thick and hardly permeable walls. One may see how such a cyst differs from the fecund female as she is observed with white colour, thin and fragile integument that ruptures following the smallest shock or under the smallest osmotic pressure. One may easily understand how a cyst having such a structure can overcome the unfavourable season, assuring a powerful protection to the eggs it contains. »

Chatin's description, which equates the cyst to an oothecum, emphasizes : *i*) that the cyst differs from the fecund female which is white and has a thin, fragile body wall; *ii*) the cyst contains eggs and protects them against adverse environmental conditions. These criteria are essentially the same as those most commonly used today. In a subsequent publication, Chatin (1891) was the first to observe under experimental conditions the life cycle of *H. schachtii* from cyst to cyst, confirming his usage of the term.

The structures contributing to the formation of the cyst require further consideration in the light of contemporary studies.

Chatin (1887) apparently considered the subcrystalline layer fundamental to the formation of the cyst and this was reiterated by Franklin (1971). It is only very recently that the distinct origin of the subcrystalline layer has been investigated (Brown *et al.*, 1971; Zunke, 1986). However, the subcrystalline layer is not useful in

the definition of the cyst because it occurs in only some species of *Heterodera sensu lato* and is highly developed in certain genera which clearly lack a cyst (e.g. *Atalodera*).

While the cyst wall of Heteroderidae is generally believed to be derived from the female body wall, it is not known if all body wall components (e.g. hypodermis) contribute to the cyst wall. Shepherd, Clark and Dart (1972) demonstrated that the body wall cuticle of heteroderid females have either of two patterns of layering: with or without a "D" layer. Subsequently, Baldwin (1983) and Cliff and Baldwin (1985) showed that both types of layering also comprise the body wall cuticle of non-cyst-forming species. In addition, they demonstrated that thickness of the cuticle is not correlated with the capacity to form a cyst; frequently very thick cuticles occur in species that do not tan or retain eggs. Thus, layering of the female cuticle appears to be independent of cyst formation, and its consideration does not contribute to a generally applicable *ad hoc* definition of the concept.

We propose the definition:

A heteroderid cyst is a persistent tanned sac which retains eggs and is derived from some or all components of the mature female body wall.

The proposed definition is empirical and is not intended to imply that all cysts of Heteroderidae are necessarily homologous. Conversely, Wouts' phylogenetic tree requires repeated evolution of the cyst; if this hypothesis is correct it is possible, and even likely, that cysts having different ancestors are not equivalent in details of development, morphology and biochemistry.

The definition of a cyst which includes tanning after death and retention of eggs, clearly applies to *Afenestrata* Baldwin & Bell, 1985, *Cactodera* Krall & Krall, 1978, *Dolichodera* Mulvey & Ebsary, 1980, *Globodera* Skarbilovich, 1959, *Heterodera* Schmidt, 1871, and *Punctodera* Mulvey & Stone, 1976. The very thick body wall cuticle of dead *Bellodera* Wouts, 1985 and *Sarisodera* Wouts & Sher, 1971 may occasionally be found empty and coloured brown. Fixed white females with eggs may eventually develop brown colouration, but the combination of an intact tanned cuticle and retained eggs apparently does not naturally occur. If this is indeed the case, *Sarisodera* and *Bellodera* do not have a cyst by the proposed definition. Furthermore, the dead females appear to lack the persistence, strength and rigidity characteristic of *Heterodera sensu lato*. Indeed the brown colouration of the former may not result from the same tanning process which is implied in true cyst formation, and which presumably involves crosslinking of structural proteins of the female body wall (Hesling, 1978). It is noteworthy that Wouts, while referring to species in these genera as cyst-forming, places them in a phylogenetic tree which precludes homology of the

character with that of, for example, *Heterodera*, and again with *Globodera*. Tanning of *G. rostochiensis* (Woll.) is attributed to the release of phenoloxidase, partitioned in the female body wall and released after death whereupon it catalyses the tanning process (Awan & Hominick, 1982). Detection of this enzyme in the female body wall of putative cyst-forming species may provide a biochemical test for cyst formation, providing it is linked with the other criteria in the proposed definition, i.e. persistence of the cyst and retention of eggs therein.

Thecaverniculatus Robbins, 1978 species and perhaps others retain eggs and even second stage juveniles within the female which apparently does not persist after death as a tanned sac, and is not considered a cyst. Analogous cysts may occur in non-heteroderids. For example, *Meloidoderita* Poghossian, 1966 (Criconematoidea) is also described as having a cyst or "cystoid body" (Kir'janova & Poghossian, 1973; Golden & Handoo, 1984) which is a resistant, non-living sac retaining eggs. Clearly this cyst is not homologous with that of Heteroderidae, apparently being derived from the persisting wall of the uterus rather than the body wall as in Heteroderidae.

Tanning and retaining eggs might best be considered as two independent characters which, in some cases, occur in combination; it is in such a combined form that the condition is a cyst.

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