

ON *ENDOTOKIA MATRICIDA* AND INTRA-UTERINE DEVELOPMENT AND HATCHING IN NEMATODES

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A bibliographic study has established that Seurat (1914, 1920), the first author known to have used the term "*endotokia matricida*", gave it the meaning of cyst-formation as occurs commonly in the Heteroderidae. However, later workers have used the term to describe what Seurat (1920) himself called "éclosion intra-utérine" (hatching of larvae inside the body of the female, followed by destruction of the latter upon exiting) or even the simple "développement intra-utérin" (développement of larvae entirely inside the uterus of the female).

Therefore, the authors recommend:

- discontinuing the use of the term "*endotokia matricida*";
- the use of the term "female encystment" which corresponds to the original meaning of "*endotokia matricida*";
- to introduce the term "matricidal hatching", for the particular type of intra-uterine larval development leading to the destruction of the female by the larvae.

To the best of our knowledge, the first nematologist who used the term *endotokia matricida* (or "endotokie matricide" in French) was Seurat (1914, 1920).

Seurat (1914) described "endotokie matricide" in an oxyurid, *Oxyuris spinicauda* Duj. [now: *Pbaryngodon spinicauda* (Dujardin, 1845) Diesing, 1861], present in the rectum of a gecko from Algeria, in the following way:

"Les utérus, dans lesquels les œufs s'alignent par trois, puis par quatre, sont fortement distendus et finissent par occuper presque toute la cavité générale, refoulant et comprimant les autres organes: ce processus aboutit finalement à la mort de la femelle. Celle-ci se présente alors sous l'aspect de la figure 6: la cuticule détachée du corps, sert d'enveloppe protectrice à un véritable sac bourré d'œufs, dans lequel à part l'œsophage et le bulbe, on ne reconnaît plus traces d'organisation. Cette dépouille de la femelle, contenant 155 à 180 œufs volumineux, peu avancés dans leur évolution (non segmentés) parvient au dehors, rejetée par le Gecko avec les excréments. Ce phénomène d'endotokie matricide rappelle celui offert par l'*Heterodera schachtii* Schmidt de la Betterave." [Transl.: "The uteri in which eggs are arranged in three, then four, lines, are strongly distended and end by occupying nearly all the general cavity, forcing back and compressing the other organs: this phenomenon finally leads to the death of the female. At that time, the female has the aspect shown in Fig. 6 (= Fig. 1 A in this paper): the cuticle detached from the body, acts as a protective sheath, covering a veritable sac stuffed with eggs and in which no trace of organization can be recognized, except for the oesophagus and the bulb. These remains of the female, containing 155 to 188

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large and scarcely developed (unsegmented) eggs, reach the exterior by being ejected together with the faeces of the gecko. This phenomenon of *endotokia matricida* recalls that shown by *Heterodera schachtii* Schmidt of sugar beet.”]

This last sentence could mean that *endotokia matricida* was described previously in *H. schachtii*. Unfortunately, bibliographical searches for earlier reference(s) were unsuccessful. We can only state that in the first complete description by Chatin (1887) of the protective role of the cysts of *H. schachtii*, during the unfavorable season, the term *endotokia matricida* is not used. Possibly the term *endotokia matricida* was applied to *H. schachtii* between 1887 and 1914 by a yet unknown author. In any case we can consider Seurat as having given a valid definition of *endotokia matricida*, because this author later gave (Seurat, 1920) a detailed description of “endotokis (*sic*) matricide” in *H. schachtii*:

“Chez quelques Nématodes les œufs ou les larves sont protégés par la dépouille de la mère. L'exemple le plus connu est celui de l'*Heterodera schachtii* Schmidt: dans les conditions normales les œufs ou les embryons sont expulsés par la vulve; mais il n'est pas rare de voir, surtout à la fin de l'été, les tissus périphériques de la femelle subir des modifications d'où résulte une transformation du corps tout entier en un kyste brun, destiné à assurer la protection des œufs pendant la mauvaise saison; une fois cette période passée, ses parois se gonflent, se ramollissent et laissent échapper les œufs et les larves. Chacun de ces kystes bruns contient, comme une femelle normale, de 300 à 400 œufs” (p. 108-109). [Translation: “In some nematodes, eggs and larvae are protected by the remains of the dead mother. The best known example is *Heterodera schachtii* Schmidt. Under normal conditions, eggs or embryos are expelled through the vulva, but it is not uncommon to observe, especially at the end of summer, that the peripheral tissues of the female are modified so that the whole body is transformed into a brown cyst, designed to protect eggs during the unfavorable season. When this period is over, its wall swells, softens and allows escape of eggs and larvae. As is the case with normal females each of these brown cysts contains 300-400 eggs.”].

Thus, *endotokia matricida*, as defined by Seurat and as applied to plant parasitic nematodes, is synonymous with female encystment and this term must only be applied to those forms producing cysts, i.e. certain genera of Heteroderidae (*Heterodera*, *Globodera*, *Punctodera* and *Sarisodera*), perhaps to *Meloidoderella* (Meloidogynidae) and to *Meloidoderita* (Criconematoidea). In the latter genus, it appears that uterine tissue rather than body wall constitutes the cyst, thus resembling the oxyurid *Pharyngodon spinicauda*.

It is obvious that Seurat's (1914, 1920) definition of *endotokia matricida* differs from the way in which this term has been used by subsequent authors (Lordello, 1951; Paetzold, 1958; Loof, 1959; Hirschmann, 1960; Ivanova, 1962; Lordello & Koguti, 1962; Krall, 1967; Southey, 1969; Scott & Whittaker, 1970; Wehunt & Edwards, 1971; Jatala, 1975; Vovlas & Inserra, 1975; Lordello & Zem, 1977; Pinochet, 1978; Laughlin, *et al.*, 1978). Even Caveness (1964) gave an erroneous definition of this term in his nematological glossary.

These authors have misapplied the term *endotokia matricida* in describing a different phenomenon which may be described as "intra-uterine development" or "intra-uterine hatching". Seurat (1920) made a clear distinction between *endotokia matricida* and "éclosion intra-utérine" (intra-uterine hatching), and cited as an example of the latter observations of Maupas (1899) on *Rhabditis* spp. Rather than quote a lengthy passage in French (pp. 604-605), it suffices to paraphrase Maupas as follows: in some cases eggs developed into larvae which hatched directly within the uterus of the mother; these larvae progressively destroy the body contents of the female and finally reach the exterior through the anterior end or by breaking the cuticle. It is a form of ovovivipary — a matricidal one. Other workers (eg. Wehunt & Edwards, 1971) have also misused the term *endotokia matricida* in describing the occurrence of a fully developed second-stage juvenile within an egg in the uterus even though it may not have hatched.

TABLE I

*Examples of intra-uterine development and hatching among
plant-parasitic nematodes*

Nematode	Citation	Relationship *		
		1	2	3
<i>Aphelenchus avenae</i>	Jairajpuri, 1964	+		
" "	Hechler (unpublished; cited in Jairajpuri, 1964)	+		
<i>Aphelenchoides fragariae</i>	Loof, 1959		+	
<i>Anguina tritici</i>	Scopoli, 1777		+	
" "	Marcinowsky, 1909		+	
" "	Gupta & Swarup, 1968	+		+
<i>Anguina</i> spp.	Ivanova, 1962		+	
<i>Anguina</i> sp.	Southey, 1969		+	
<i>Paranguina agropyri</i>	Krall, 1967			+
<i>Helicotylenchus paxilli</i>	Yuen, 1965	+		
<i>Helicotylenchus</i> sp.	Yuen, 1965	+		
<i>Helicotylenchus vulgaris</i>	Yuen, 1966	+		
<i>Pratylenchus coffeae</i> **	Loof, 1959	+		
" "	Wehunt & Edwards, 1971	+		
<i>Pratylenchus minyus</i>	Vovlas & Inserra, 1975	+		
<i>Pratylenchus brachyurus</i>	Laughlin <i>et al.</i> , 1978	+		
<i>Radopholus similis</i>	Loos, 1962	+		
<i>Thecavermiculatus gracililancea</i>	Robbins, 1978			+
<i>Meloidogyne</i> sp. or spp	Atkinson, 1889		+	
<i>Meloidogyne</i> sp. or spp	Nagakura, 1930		+	
<i>Meloidogyne javanica</i>	Lordello & Koguti, 1962		+	
<i>Meloidogyne</i> sp.	Pinochet, 1978		+	
<i>Xiphinema</i> sp.	Jatala, 1975		+	
<i>Xiphinema insigne</i>	Jairajpuri & Bajaj, 1978	+		

* Definition of relationships: 1. Eggs contain fully developed J₂, but J₂ not reported in female body; 2. J₂ are free in female body and may have caused her death; 3. fully developed males within female body.

** Some authors have given credit to Cobb (1920) for the first observation of intra-uterine hatching in *P. coffeae*. But this author recorded only the presence of "embryos" in uterus, not of larvae.

The first mention of vivipary or ovovivipary for plant-parasitic nematodes, occurs in the first description of such a nematode, *Anguina tritici* (Scopoli, 1777), in which the following is found (p. 374): "*Fem. longior, vivipara et ovipara*" (reproduced in Chitwood, 1935, and cited by Krall, 1967). Such intra-uterine development from eggs to second-stage juveniles has been confirmed by several authors in *Anguina* and the related *Paranguina* (see Table I).

In the genus *Meloidogyne*, the presence of juveniles within the female cuticle was first reported by Atkinson (1889) who wrote: "Segmentation of the egg begins before it leaves the uterus, and we find, in the body cavity of live female cysts (*sic*) eggs in all stages of development, and free larvae, so that the female may be said to be oviparous" (p. 91). He illustrated this in his Figure 37 (reproduced here as Fig. 1B). The earliest photograph of this phenomenon that

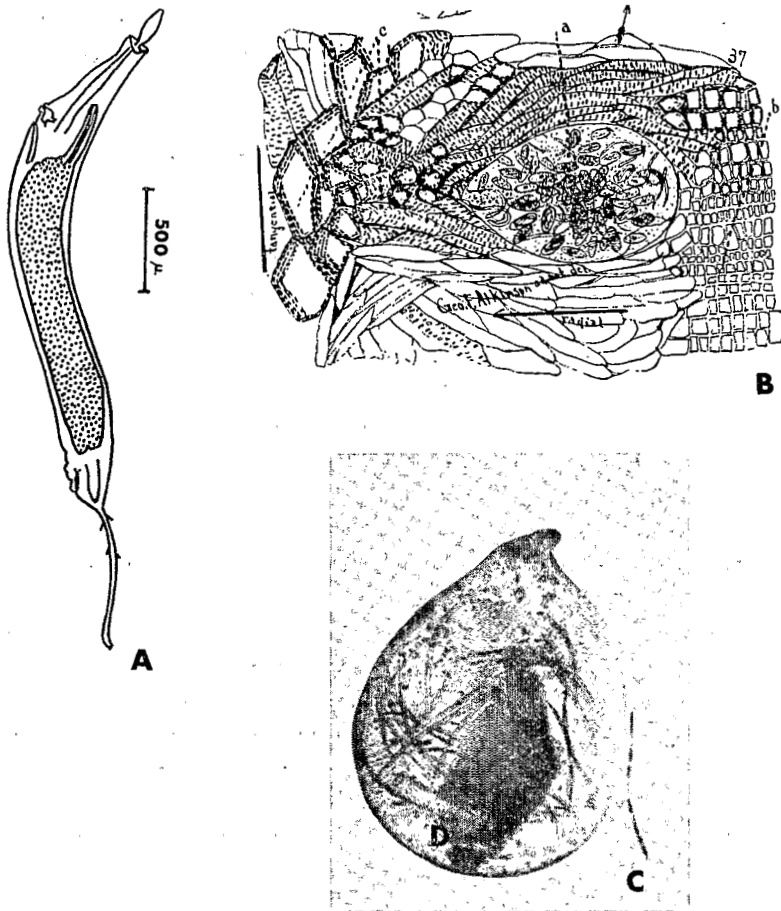


Fig. 1. A "cyst" of *Pharyngodon spinicauda* (from Seurat, 1914); B, C: Intra-uterine hatching in *Meloidogyne*; B: Reproduction of Fig. 37 of Atkinson (1889). C: Reproduction of Fig. 65 B of Nagakura (1930).

we have located, "Mutterkörper zur Brutkapsel verwandelt" (Nagakura, 1930: Fig. 65B), is reproduced here as Figure 1C. More recently Lordello & Koguti (1962) and Pinochet (1978) have published similar observations in *Meloidogyne*.

Other examples, especially involving plant-parasitic nematodes are given in Table I. Poinar (1969) recorded intra-uterine hatching, with fully developed males, in *Praecocilenchus rhabdiphorus* (Aphelenchoididae) parasitic in Coleoptera. With the exception of *Anguina* and related genera, intra-uterine hatching appears rather infrequently in the Tylenchida, and exceptionally in the Dorylaimida. This phenomenon appears to be more common in the Rhabditida. Most authors (e.g. Lordello & Zem, 1977) have given Maupas (1899) credit for the first mention of intra-uterine hatching in *Rhabditis*. However, Pérez (1866) described this phenomenon in *R. terricola* (pp. 294-295), and to the best of our knowledge was the first to do so. Several subsequent authors have recorded intra-uterine hatching in various Rhabditidae (Seurat, 1920; Ludwig, 1938; Lordello, 1951; Wessing, 1953; Paetzold, 1958; Lordello & Zem, 1977); Chabaud *et al.* (1965) observed it in *Gynopoecilia pseudovipara* (Diplogasteridae), a parasite of *Mantis* sp.; and Poinar (1978) in *Mesidionema praecomascularis*, a parasite of an earthworm.

Among nematode parasites of Vertebrata, intra-uterine hatching is notably more frequent. For example, it is the rule in the Camallanoidea and Filarioidea as well as in Atractidae (Cosmocercoidea); it is more or less frequently observed in other groups such as the Metastrongyloidea and Oxyuroidea.

Concerning physiological and phylogenetic aspects of intra-uterine hatching, Laughlin *et al.* (1978) discuss the observations and hypotheses made by various authors, and add their own. It is not in the line of the present paper to discuss these points.

Thus we have concluded from careful, but probably incomplete, study of the early literature that the term *endotokia matricida* has been erroneously used by all authors except Seurat (1914, 1920) and that this term is in fact synonymous with "female encystment".

From this we recommend the abandonment of the use of the term *endotokia matricida*, in both of the senses described here, namely that of Seurat, and that of subsequent authors. Concerning *endotokia matricida sensu* Seurat, the term "female encystment" appears more appropriate, being in general use and self-defining. For *endotokia matricida sensu* Lordello (= intra-uterine hatching of Seurat) we propose the term of "matricidal hatching", defining this peculiar intra-uterine hatching leading to the destruction of the female by the larvae.

Further, we suggest that careful attention to early nematological literature may avoid describing as new records observations that had been made, in some cases, many years previously.

RÉSUMÉ

Au sujet de l'endotoquie matricide, du développement intra-utérin et de l'éclosion intra-utérine chez les nématodes

Des recherches bibliographiques ont conduit à constater que Seurat (1914, 1920), premier auteur connu pour avoir employé le terme d'"endotoquie matricide", lui avait donné le sens d'enkystement des femelles, tel celui connu chez certains Heteroderidae. Par contre, l'ensemble des auteurs ultérieurs ont utilisé ce même terme pour décrire, soit ce que Seurat (1920) lui-même avait appelé "éclosion intra-utérine" (= L₂ éclochant dans le corps de la femelle et détruisant celui-ci pour gagner l'extérieur), soit même le simple "développement intra-utérin" (= L₂ entièrement formée dans l'utérus de la femelle).

Les auteurs recommandent donc:

- d'abandonner l'usage du terme endotoquie matricide,
- d'utiliser le terme d'enkystement des femelles, correspondant au sens primitif d'endotoquie matricide,
- d'introduire le terme d'éclosion matricide pour le type particulier de développement intra-utérin conduisant à la destruction de la femelle par les larves.

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