Hermaphroditism in *Paratrichodorus* species (Nemata : Dorylaimida)

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SUMMARY

In *Paratrichodorus allius* females of several populations sperm was commonly observed in the uterus or at the distal ends of both branches of the genital tract and sometimes between gonocytes. Hermaphroditism of the syngonic type (automixis) is strongly suspected for this species. Apparently also *P. nanus* and *P. tansaniensis*-like populations from Italy reproduce hermaphroditically. Among additional *Paratrichodorus* species, in which males are also very rare or absent, generally no distinct sperm was seen in *P. renifer* females and in females of most *P. minor* populations studied (with the exception of populations from Madeira).

RÉSUMÉ

Hermaphrodisme chez Paratrichodorus *(Nemata : Dorylaimida)*

Chez les femelles de plusieurs populations de *Paratrichodorus allius* des spermatozoïdes ont été fréquemment observés dans l'utérus ou dans la portion distale des deux branches du tractus génital, ou parfois entre les gonocytes. Un hermaphrodisme de type syngonique (autofécondation) est donc fortement soupçonné chez cette espèce. De même *P. nanus* et les populations italiennes rapportées à *P. tansaniensis* auraient apparemment une reproduction de type hermaphrodique. Parmi d'autres espèces de *Paratrichodorus* chez lesquelles les mâles sont très rares ou inconnus, aucun spermatozoïde typique n'a été observé chez les femelles de *P. renifer* ni chez les populations de *P. minor* étudiées, à l'exception toutefois de celles provenant de Madère.

Hermaphroditism is known to occur in free-living rhabditids, in the predacious *Seinura* and in a few animal-parasitic nematodes. Among plant-parasitic nematodes this reproductive strategy is suspected only for members of the Criconematoidea. No reports on hermaphroditism are available for e.g. Dorylaimida and Enoplida. In almost all cases it is the syngonic type, where both types of gametes are produced in the same gonad, mostly sperm first (= protandric hermaphroditism). Reports on digonic hermaphroditism in nematodes, where sperm is believed to be produced in a spermagonium and eggs in the ovary, has not been confirmed in several instances (Triantaphyllou & Hirschmann, 1964; Poinar & Hansen, 1983).

Some *Paratrichodorus* species, in which males are absent or very rare, are now found to reproduce by syngonic hermaphroditism. Preserved specimens in glycerin mounts were available for study.

Anatomical observations

Paratrichodorus allius (Jensen, 1963) Siddiqi, 1974.

On examination of several populations of *P. allius* (syn. *P. tansaniensis* Siddiqi, 1974) of different origin, sperm was observed in the reproductive system of almost all adult specimens studied (Sturhan, 1989).

Among 37 " females " of a population from an onion field at Prosser, Washington State, USA, 25 had the uteri filled with sperm (up to a length of more than twice the body diameter), and both gonads exhibited the normal female appearance with oogonia and oocytes at various stages of development (Fig. 1. A). In ten of the " females " an accumulation of sperm was present at the distal ends of both branches of the genital tract where the gonads reflex. These ends are rather short in some specimens with closely packed sperm, or longer in other specimens in which the spermatozoa are more scattered (Fig. 1. B, C). In two additional individuals sperm resp. spermatids were present at the distal end of the anterior genital branch and in the central part of the posterior gonad, between large cells with large nuclei and nucleoli (Fig. 1. D). In none of these last twelve specimens sperm was present in the uteri. Not a single specimen was found with sperm in the gonad region and in the uterus at the same time. The spermatozoa in the uteri and in the gonads were slightly elongated, generally with rounded or sometimes rather pointed ends, about 2 µm long and 1 µm thick. Whereas in several specimens the tip of the gonad showed a few small gonial cells with more or less distinct nuclei (Fig. 1. A-C), in most specimens the gonad tip appeared coarsely granulated (Fig. 1. D, E). In the population from Prosser no male had been found among numerous " females " (Inserra, pers. com.).

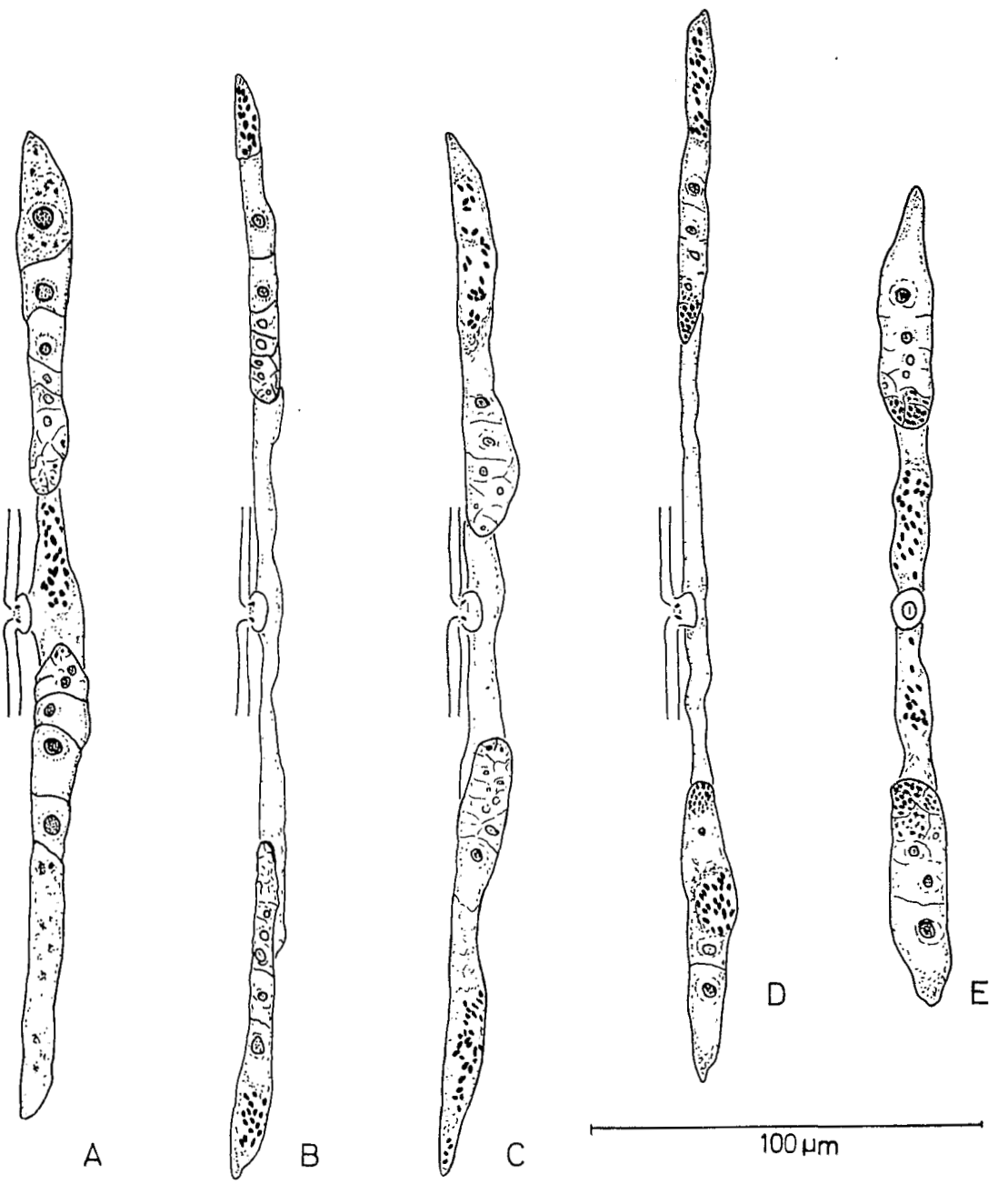

Fig. 1. *Paratrichodorus allius,* population from Prosser, Washington State, USA : Variation of genital tract of hermaphrodites (A-D = lateral view; E = ventral view).

Sperm was also seen in the genital tract of specimens considered to belong to the species *P. allius* and obtained from the following sources (cp. Sturhan, 1989) :

— Oregon, USA : Three out of five *P. allius* topotypes with sperm at the distal ends of the genital branches (material in poor condition, in particular the other two specimens);

— California, USA : Among four " females " one with sperm in uterus, one with sperm-like bodies at the distal ends of both branches of the genital tract (material in poor condition, no sperm detectable in the other two specimens);

— Tanzania : In nine out of ten paratypes of *P. tansaniensis* sperm present at the distal end of each genital branch;

— Madeira, Portugal : Among six " females " two with sperm in the uterus and four with sperm at distal end of the anterior and the posterior branch of the reproductive tract. One specimen apparently with a few spermatozoa also in the uterus;

— Continental Portugal : Several specimens with sperm in uterus.

P. " tansaniensis "

Some specimens of several populations from Toscana and Puglia, Italy, identified by Roca and Lamberti (1984) as *P. tansaniensis*, but possibly representing a different species (Sturhan, 1989), were available for study. In most " females " an accumulation of sperm-like bodies occurred in the central zone of the gonads. In three specimens rather large, elongate spermatozoa were present in the uteri, but no sperm was observed in the gonad region of these individuals. No males were found in these populations.

P. nanus (Allen, 1957) Siddiqi, 1974

Specimens of five populations from the Federal Republic of Germany were studied for the presence of sperm in the genital system. Among 33 " females " sperm was seen in the uteri of all except one, the spermatozoa being generally slightly shorter and more roundish than in *P. allius*, with a diameter of about 1-1,5 µm. Rarely sperm occurred in the uteri and at the distal ends of the branches of the genital tract at the same time. In many *P. nanus* populations collected in Germany, a male was found only once.

P. minor (Colbran, 1956) Siddiqi, 1974

Among 41 females of seven populations from Morocco, Israel, USA, Dominican Republic and Nicaragua only one had few roundish, sperm-like particles in the uterus, but thread-like structures of unknown nature were present throughout the uteri (similar inclusions were mentioned and/or figured by Vermeulen and Heyns, 1983, and Roca and Lamberti, 1984). However, in all fifteen adults examined of two populations from the island Madeira numerous roundish sperms with a diameter of 1-1,5 µm were observed in the uteri; at both sampling sites many additional females had been found, but not a single male.

P. renifer Siddiqi, 1974

In 32 females of four greenhouse populations from the Federal Republic of Germany no (distinct, roundish) sperm could be identified in the uteri or any other part of the genital system.

Conclusion

Though males are very rare in *P. allius* (only three males have been reported so far), sperm was observed in all " females " of this species studied, in which details of the genital system were visible. The common occurrence of sperm at the distal end of each branch of the genital tract, while generally no sperm was present in the uteri at the same time, strongly suspects that sperm did not originate from insemination by rarely occurring males. The observation of spermatids between large gonocytes indicates that both spermatozoa and oocytes are probably produced within the same gonad (= ovotestis). *P. allius* thus appears to reproduce by automixis (hermaphroditism of the syngonic type). Cross-fertilization through the rarely occurring males, which appear to have well-developed gonads, may also take place besides automixis.

According to the observations presented here, *P. " tansaniensis "*-like populations from Italy and *P. nanus* apparently also reproduce by syngonic hermaphroditism, but *P. renifer* does not. In *P. minor* automixis possibly occurs only in certain populations (since the Madeira populations appear to show also minor differences in certain morphological characters, their species identity needs reconfirmation).

For *P. anthurii* common occurrence of spermatozoa in the female genital tract has been recorded by Baujard and Germani (1985); since no males were found among many females, hermaphroditic reproduction may be assumed also for this species.

ACKNOWLEDGEMENTS

I thank R. Inserra, Gainesville, USA; D. J. Hooper, Rothamsted, England; P. A. A. Loof, Wageningen, Netherlands; M. T. M. Almeida, Braga, Portugal; and N. Vovlas, Bari, Italy, for supplying permanent slides or preserved specimens of *Paratrichodorus allius/tansaniensis*.

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Accepté pour publication le 5 octobre 1988.

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