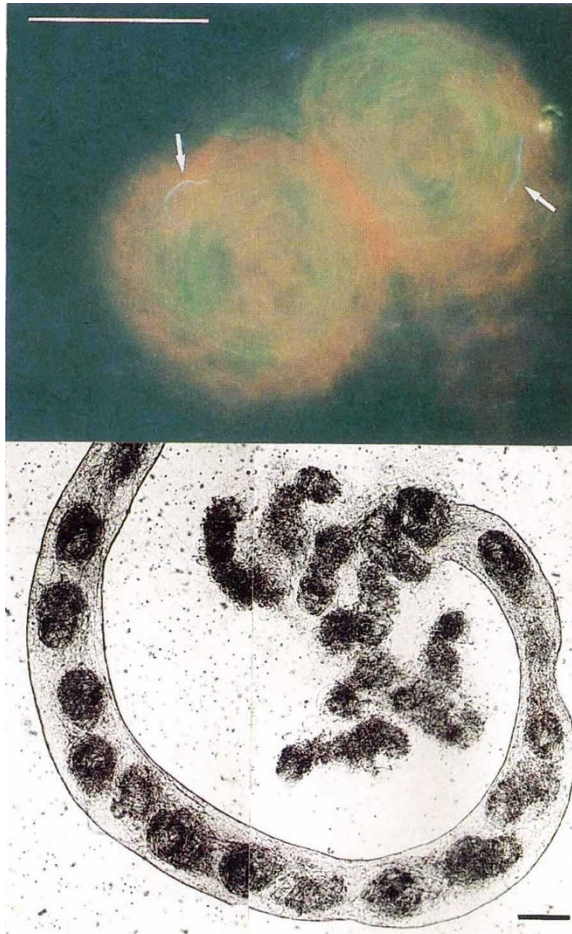# Disentangling giant sperm

SIR — The theory of the evolution of sex suggests that the greater the investment in individual gametes, the more parsimonious males should be in transferring sperm to females. It has been argued that physiological constraints may limit the range of allocation strategies available to males; therefore, the evolution of giant sperm up to 2 cm long in *Drosophila hydei* and 6 cm in *D. bifurca*, 7 and 20 times as long as the male body, respectively, could appear as one of the great paradoxes of sexual selection. The selective value of these giant sperm has become a matter for controversial and growing debate[1,2].

Concerning the anisogamous pattern, *Drosophila bifurca* is the most extreme and impressive example known of how far evolution can shift in unexpected directions. During the 17 days needed by *D. bifurca* males to become sexually mature, their testes increase from 11.95 ± 0.25 mm ($n=25$) to 68.89 ± 0.44 mm ($n=25$), at which size they occupy more than half the abdominal cavity. Using the correlation curve between testis and sperm length[3], we estimated the sperm length in 30-day-old *D. bifurca* males to be 58.36 mm, consistent with the direct measurements of Pitnick *et al.* (58.29 ± 0.66 mm, $n=3$)[2].

Drosophila bifurca displays an intriguing and unique way of offering sperm to the females which we call the 'pea-shooter effect'. Males transfer to females huge 80-μm-wide spermatic pellets, each made of a single 6-cm-long gamete (see figure, upper panel). Uniquely, these sperm are transferred one after another. This is made possible by the genital tract in *D. bifurca* males narrowing subterminally in a spiral duct which seemingly acts as a bottleneck constraining mature sperm to disentangle from one another, separate and roll up. The very end of the testicular tract is a straight tube, 'the pea shooter', where monospermatic pellets are stored in single file (lower panel). During each short mating, lasting 374.33 ± 14.63 s ($n=18$), 23-day-old males offer 25.61 ± 1.86 ($n=18$) such monospermatic pellets to females, around four times less male gamete supply than in *D. hydei* whose sperm are three times shorter and remain

mixed during transfer[1]. *Drosophila bifurca* males do not transfer all the monospermatic pellets that they manufacture (106.15 ± 30.35; $n=26$ per seminal vesicle). Curiously, the amount of monospermatic pellets offered corresponds almost exactly to the number of spermatids per cyst (that is, 24).

The mechanism evolved by *D. bifurca*

Single giant sperm pellets in *Drosophila bifurca*; above, two giant sperm disentangled and rolled up, head in blue (arrow), flagellum in green (methods as in Bressac *et al.*[6]; scale bar, 50 μm); below, giant sperm pellets ordered in single file in the outer part of the seminal vesicle and released one after another ('pea-shooter effect'), phase contrast (scale bar, 80 μm).

could be a sophisticated way to fragment the sperm supply within the seminal vesicles and hence facilitate flexible sperm ejaculate allocation. It may enable males to adjust sperm offer, depending on prevailing conditions. This may limit rapid sperm exhaustion in males in a highly promiscuous reproductive system.

Alternatively, transfer of single monospermatic pellets in succession may represent an efficient way of transferring extremely long sperm to females safely. The reason for manufacturing giant sperm is unclear; they may serve as a blocking device, reducing sperm competition by purely mechanical means[4]. This could not

satisfactorily explain why females have evolved co-adapted giant tubular storage organs (73 ± 1.57 mm; $n=25$) within which sperm are stored elongated. A way to counter this difficulty would be to assume that the evolution of co-adapted giant sperm, testes and female storage organs results from a maternal–paternal genetic conflict[5]. Giant sperm could, for instance, result from a coevolutionary arms race between the female and male genital tracts, the paternal genome trying to produce as long sperm as possible to saturate the storage organs of females and thereby limit sperm competition, and the maternal nuclear genome trying to remove the effect of such elongation to promote sperm competition.

Another possibility could be some post-fertilization paternal investment[1] from which females would also gain some benefit. Relevant to this is the seemingly controversial consideration that only incomplete fragments enter the eggs in giant sperm species[2]. Assuming giant sperm constitute a "direct paternal legacy to the embryo, which, in contrast to any male-derived nuptial gift, cannot be minimized by female remating"[1], females would nonetheless divert for their own benefit a part of the giant sperm otherwise used for the present fertilization (a resource for future offspring sired by subsequent males). These alternative views, however, remain purely speculative, and a difficulty in understanding the problem of why giant sperm have evolved can result from the fact that the various species may obey different selective rules. Sperm disentangling occurs in *D. bifurca* but not in any other giant sperm species so far studied. The existence of monospermatic pellets offered one after another indicates that there are in fact few physiological constraints limiting the range of allocation strategies available to males. It is certainly a quirk of evolution that these sperm mimic the size and form of ova.

D. Joly
C. Bressac
D. Lachaise
Laboratory Populations, Genetics & Evolution,
CNRS, 91198 Gif-sur-Yvette cedex, France

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