How long is a giant sperm?

SIR — In 1950, Cooper[1] reported that the spermatozoon of *Drosophila melanogaster* "proves to be a most impressive gamete", having a length of 1.76 mm, and commented, "just what the selective value of such a tremendously elongated spermatozoon may be is a matter of pure conjecture." These sperm were considered giants by any standard, being, for example, approximately 300 times longer than human spermatozoa. It has recently become clear, however, that by *Drosophila* standards, the sperm of *D. melanogaster* are tiny.

Here we report that males of *D. bifurca*, a distant relative of *D. melanogaster*, produce sperm that are 58.29±0.66 mm long (N=3 males); each gamete is approximately 20 times longer than the flies manufacturing them. Sperm length for this species was unambiguously determined using a dissection technique described elsewhere[2]. These sperm are two-and-a-half times longer than those of the sibling species, *D. hydei*, which held the previous record for sperm length[3].

The existence of such giant sperm poses a conundrum for evolutionary biology, for it seems to contradict established views on the evolution of sexes (anisogamy) and of male sexual strategy. Whereas males are expected to produce vast numbers of low-investment gametes which they use with minimal frugality, males of some giant-sperm-producing *Drosophila* use their sperm with female-like judiciousness, carefully partitioning their limited sperm among successive females[2]. Moreover, giant sperm are relatively costly to manufacture. First, comparative analyses of 11 *Drosophila* species reveal a trade-off between sperm length and the number of sperm produced and transferred to females by males (S. P., unpublished data). Second, to manufacture giant sperm, males must develop very long, energetically expensive testes. For example, the testes of *D. bifurca* are each 67 mm long and comprise nearly 11% of a male's total dry body mass (compare with 5% in *D. melanogaster*) (S. P, unpublished data). Third, studies of *D. pachea*[4] (sperm length 16.53 ± 0.29 mm) and *D. hydei*[3] (sperm length 23.32±0.51 mm) have suggested that time required to grow their large testes is causally responsible for the unusually delayed rates of male sexual maturation observed in those species. We therefore examined sex-specific ages of reproductive maturity in *D. bifurca* (N = 30 per sex), and found that females became sexually mature, on average, within 7 days of the final moult (eclosion), while males required 17 days (see ref. 4 for methods), thereby supporting the hypothesis that producing giant sperm constrains age at first reproduction.

What, then, are the selective advantages of producing such long sperm? It is likely either that longer tails confer some advantage in the competition to fertilize ova[2] or that they may contribute to some post-fertilization function, as illustrated by Karr[5]. In a recent report, Bressac *et al.*[6] claim giant *Drosophila* sperm represent "another way of being anisogamous", in which each sperm has a high prospect of fusion with an egg and serves the post-fertilization function of provisioning the zygote. These authors report that the sperm tail remains substantially intact throughout embryonic development and is ultimately eliminated with metabolic wastes on hatching, and therefore suggest that the function of giant sperm is to ensure the input of paternal mitochondrial DNA.

Although intriguing, this claim is based on limited data — that all or most of the giant sperm tail enters the egg in three species: *D. melanogaster*[5], *D. littoralis* and *D. hydei*, and that the efficiency with which sperm are used by females increases with increasing sperm length. Moreover, their claim appears unlikely for three reasons. First, detailed examination of fertilization in several *Drosophila* species with giant sperm reveals that, whereas the entire sperm tail is incorporated into the egg in some species, only a small fragment enters in other species. For example, in *D. bifurca*, < 3 mm of the 58.3-mm-long sperm enters the egg (T. L. Karr and S. P., unpublished data). Any hypothesis addressing post-fertilization functions are therefore refuted, at least as a general explanation for sperm length evolution in *Drosophila*. Second, comparing among species, the number of progeny produced per copulation declines drastically with increasing sperm length (compare 300–700 progeny per mating in *D. melanogaster*[7] versus about 70 in *D. hydei*[6]). Any increase in the efficiency with which females use longer sperm may ameliorate this reduction in fitness, but will be unlikely to compensate for it. Third, given the significant costs associated with the production of longer sperm, if the primary benefit is to increase the paternal representation of mitochondrial DNA in offspring, as Bressac *et al.*[6] suggest, this would represent an unlikely instance of 'selfish' mitochondrial genes winning out over nuclear genes. Further studies are required to resolve this enigma. Although our perspective of what represents a giant sperm has increased substantially, its selective value is just as conjectural as it was 45 years ago.

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A coral mitochondrial *mutS* gene

SIR — A high rate of evolution is a much mentioned characteristic of animal mitochondrial DNA (mtDNA). However, this claim is based on observations made principally for mammals, where mtDNA nucleotide substitutions occur at frequencies 5–17 times those of nuclear DNAs[1–3]. The differences in nucleotide substitution rates in mammals have been attributed to a lack of mtDNA repair mechanisms[1]: only enzymes that could carry out excision repair of DNA damaged by oxidation have been reported to occur in mammalian mitochondria[4]. Whether or not invertebrate mtDNAs evolve faster than nuclear DNAs is somewhat controversial[2,5]. Therefore it is of considerable interest that in the mtDNA of the octocoral, *Sarcophyton glaucum* (phylum Cnidaria) we have identified a gene for a homologue of MutS, a component of the bacterial MutSLH mismatch repair pathway. The octocoral *mutS* homologue is also of note because it is the only protein gene other than the constant set of 12 or 13 energy-pathway protein genes[6] so far reported for metazoan mtDNAs.

The Gram-negative bacterial MutSLH mismatch repair pathway is primarily a back-up for correcting replication errors that evade proofreading, although it also acts on mismatched bases in recombination intermediates[7,8]. As well as MutS, this

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