Sperms in 'parthenogenetic' freshwater gastrotrichs

from Geoffrey Fryer

PARTHENOGENESIS has been adopted as a means of reproduction by several groups of freshwater animals, among which the Cladocera and Rotifera are the best known. Such reproduction has several advantages, one of them being that, in climates where active life is profitable for only part of a year, populations can build up very rapidly if every constituent individual is a potential mother. The rapid increase of some planktonic populations of Cladocera in spring in temperate latitudes is an example. Such parthenogenesis is generally facultative and is followed by a period of sexual reproduction which results in the formation of 'resting' eggs that often overwinter or tide the population over other adversities such as a period of desiccation. By such means the ecological advantages of parthenogenesis and the genetic advantages of sexual reproduction are effectively combined in what is often referred to as cyclical parthenogenesis. In some populations of, for example, the cladoceran *Daphnia*, parthenogenesis has come to dominate the reproductive process and sexual reproduction takes place only at long intervals. The logical outcome of such a trend is to become completely parthenogenetic and some populations of planktonic *Daphnia* have conceivably achieved this status. Among the Rotifera, a whole group, the Bdelloidea, is believed to contain only obligate parthenogens, males being unknown, and the same is true of several species of freshwater ostracods. Such reproduction by means of which only female offspring are produced by a process not involving fertilisation is known as thelytoky. Thelytokous animals present problems to the taxonomist, who finds it difficult or impossible to apply the species concept to them, while their existence is something of an embarrassment to the student of evolution.

Another group of animals well represented in freshwater, and in that environment generally believed to include only obligate parthenogens, is the Gastrotricha. In the sea, however, some hermaphroditic forms are known. These microscopic animals — they seldom exceed 200 μm in length — sometimes regarded as comprising a distinct phylum and sometimes a class of the Aschelminthes, are common in a variety of habitats, usually associated with plants or mud surfaces over which they move by means of ventral cilia. Both quick-hatching (subitaneous) and resting eggs are produced but neither kind was believed to be fertilised, though in *Chaetonotus* two types of subitaneous egg

have been reported and the organism would not reproduce in culture unless two or more individuals were present, which hints at some sexual process. Now, following a tentative suggestion by Hummon that sperm heads may have been seen in *Lepidodermella squamata*, Weiss and Levy (*Science* 205, 302; 1979) have positively identified sperms in individuals of this species. These were grouped in packets, either singly or bilaterally, lateral to the intestine and seem not to be associated with any limiting membrane or ducts. Each packet contains only a few sperms — 16 is suggested as a possible maximum, a number that would correspond to the meiotic products of four spermatocytes. Individual sperms have also been found far removed from the packets but no signs of motility have been observed. Of the numerous individuals examined the proportion in which sperms were present never exceeded 8%. As ova are frequently present in sperm-carrying individuals these animals are not males but hermaphrodites.

In cultures, changes in the proportion of sperm-bearing individuals have been observed over short periods of time and the conclusion has been drawn that, as long assumed, parthenogenesis is indeed the usual means of reproduction but that the animals are really facultative hermaphrodites. It seems that hermaphrodites may appear only occasionally in nature, which may explain why they have been overlooked, and one now wonders whether, like the males of cladocerans and rotifers, they appear in response to certain conditions, and whether a kind of cyclical parthenogenesis occurs in some freshwater gastrotrichs.

Much remains to be learned about the sperms of *Lepidodermella*. It is not even known whether they actually fertilise the eggs, and although this has to be tentatively assumed it need not necessarily be the case. All kinds of peculiar cytological phenomena involving reproduction are displayed by small freshwater organisms — giant sperms in ostracods, resting eggs of *Daphnia* which, contrary to the general rule, can be produced without fertilisation, and so on — so caution is necessary. The small number of sperms produced and their lack of motility suggests internal fertilisation but it is not known whether self or cross-fertilisation occurs.

Provided cross-fertilisation is involved, the occurrence of a sexual phase, even if as a rare event, explains why one does not find a host of divergent 'strains' — a puzzle still presented by the apparently completely parthenogenetic bdelloid rotifers. It also makes it easier to understand speciation in freshwater gastrotrichs. There is now no

Lepidodermella squamata and details of its surface scales. (After Brunson).

need to invoke asexual speciation, at least in *Lepidodermella*, and this leaves the bdelloid rotifers — more than 200 species of them — as perhaps the only group in which this process seems likely to have occurred.

Thus the discovery of sperms in *Lepidodermella*, besides upsetting what is now seen to be a too easy generalisation, raises all sorts of interrelated problems of interest to the cytologist, ecologist, taxonomist and student of evolution, as well as to those who just like to understand how such minute creatures conduct their business. □

Squaring the circle

from Peter Lawrence

VERNON French's PhD thesis, an attempt to unravel the mysteries of insect leg regeneration, met with more success than he expected. His results revealed properties of insect legs that were similar to vertebrate limbs and in collaboration with Peter and Susan Bryant he launched the 'polar coordinate model' (*Science* 193, 969; 1976). In essence, this model attempts to explain formally why certain pieces of legs, insect imaginal disks and vertebrate limbs regenerate (remake the missing bits) and other pieces duplicate (make an extra set of the parts already present in the piece). For good measure the model also tackled a longstanding puzzle — the formation of supernumerary limbs after grafting. When a right leg is grafted onto a left stump two left appendages grow out from the graft/host junction, one on each side of the grafted right leg (Fig.1).

The model draws liberally on the observations of Bohn who grafted pieces of cockroach legs together which had been cut at different levels in graft and host. Intercalary regeneration occurred at the host/graft junction and replaced the parts normally lying between. The model also

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