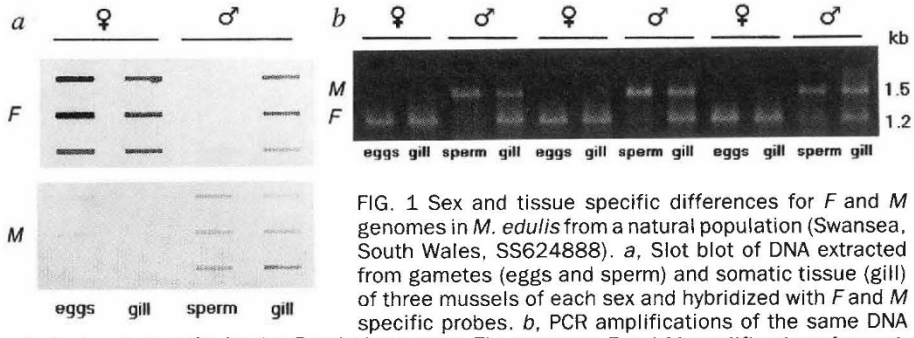

FIG. 1 Sex and tissue specific differences for *F* and *M* genomes in *M. edulis* from a natural population (Swansea, South Wales, SS624888). *a*, Slot blot of DNA extracted from gametes (eggs and sperm) and somatic tissue (gill) of three mussels of each sex and hybridized with *F* and *M* specific probes. *b*, PCR amplifications of the same DNA using primers specific for the *F* and *M* genomes. The separate *F* and *M* amplifications for each DNA sample were loaded in the same well of an agarose gel to facilitate comparison. The results shown are representative of a study in which gametes and somatic tissue were examined from 16 females and 17 males. Note the weak *F* signal obtained with sperm DNA for the male at the right of the panel. Further details are available from D.O.F.S. on request.

using genome specific PCR primers (*b* in fig. 1). Moreover, in females, the *M* genome is undetectable using PCR.

If females lack the *M* genome, males will inherit it from their fathers. If the *M* genome is partitioned preferentially into sperm, both sexes will inherit the *F* genome from their mothers. It can be concluded that the two genomes have separate transmission routes. Some males give a weak *F* signal for sperm (*b* in fig. 1), suggesting that the paternal transmission route might be leaky.

Separate maternal and paternal transmission routes could allow long-term maintenance of both mtDNA genomes within mussel populations in the face of genetic drift. This might explain the evolution of the high level of divergence between the genomes. In male zygotes, copies of the *F* genome derived from the egg will vastly outnumber the few copies of the *M* genome derived from sperm. It follows that in males, the *M* genome must replicate faster than the *F* genome to be detectable at a high level in blotting experiments. This implicates interactions between mtDNA and sex-determining factors.

Nuclear modifiers causing uniparental inheritance of cytoplasm might have been selected in evolution to prevent the rapid spread of selfish and harmful cytoplasmic particles to all lineages within species[7–9]. The maternal inheritance of mtDNA in most organisms could be accounted for in this way. *M. edulis* presents no contradiction. Although the inheritance of mtDNA is biparental, individual mtDNA genomes are inherited uniparentally through either the female or male line of descent. Thus, mussel populations might be safeguarded against the rapid spread of selfish mtDNA genomes by the restriction of such genomes to either male or female clones. The level of protection should depend on the amount of leakage.

The analysis of different tissues within individual animals is not usual in studies of mtDNA variation. Thus separate maternal and paternal routes of mtDNA inheritance might occur widely, but have been missed in other organisms.

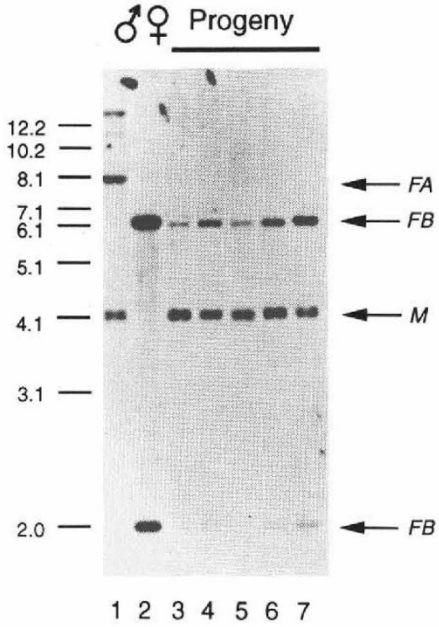

FIG. 2 DNA from the father (lane 1), mother (lane 2) and five sons (lanes 3 to 7) of family No. 16 (ref. 2) was restricted with *Eco*RI and probed with a mixture of clones that hybridize to 6-kb and 2-kb bands of the *FB* profile, the two 4-kb bands of the *M* profile and one of the two 8-kb bands of the *FA* profile (original descriptions of these profiles in refs 2, 5). The mother had the typical *FB* profile and the father was heteroplasmic having inherited the *M* type from the father (the *M* type does not occur in females[2,5]) and the *FA* type from the mother. All sons inherited the mother's mtDNA diagnostic bands (6 and 2 kb). No son had the diagnostic band of the father's maternal mtDNA (8 kb), but all had the diagnostic band of father's paternal mtDNA (4 kb). Bands in the male parent above 8 kb result from incomplete digestion.

1. Satta, Y. *et al. Genet. Res., Camb.* **52**, 1–6 (1988).
2. Gyllensten, U. *et al. Nature* **352**, 255–257 (1991).
3. Neale, D. B., Marshall, K. A. & Sederoff, R. R. *Proc. natn. Acad. Sci. U.S.A.* **86**, 9347–9349 (1989).
4. Zouros, E. *et al. Nature* **359**, 412–414 (1992).
5. Fisher, C. & Skibinski, D. O. F. *Proc. R. Soc.* B **242**, 149–156 (1990).
6. Hoeh, W. R., Blakley, K. H. & Brown, W. M. *Science* **251**, 1448–1490 (1991).
7. Grun, P. *Cytoplasmic Genetics and Evolution* (Columbia University Press, New York, 1976).
8. Hastings, I. M. *Genet. Res., Camb.* **59**, 215–225 (1992).
9. Law, R. & Hutson, V. *Proc. R. Soc.* B **248**, 69–77 (1992).

David O. F. Skibinski
Catherine Gallagher
Christine M. Beynon
School of Biological Sciences, University of Wales, Swansea, Swansea SA2 8PP, UK

SIR — The exceptionally high rate of biparental inheritance in the blue mussel *Mytilus*[1,2] appears to defy the view that uniparental transmission of organelle DNA evolved to prevent the spread of selfish deleterious mutations of cytoplasmic DNA throughout the species[3,4]. We have now grown progeny from the crosses in which we have demonstrated biparental inheritance[2] to the age they could be sexed and found that biparental inheritance was limited to sons.

In two crosses, the father's paternal and maternal mtDNA could be distinguished from each other and from the mother's mtDNA. In these crosses we found that male progeny inherited from the father only his paternal mtDNA (see fig. 2). Thus, in *Mytilus* mtDNA transmission is 'doubly uniparental', with non-anastomosing female and male lineages.

Deleterious mutations arising in a male's maternal mtDNA will not be passed to offspring, and mutations arising in a male's paternal mtDNA will affect only his sons and filial grandsons. Mutations arising in a female's mtDNA will affect her sons and daughters, but will be transmitted only through her daughters. In all cases mutations will be confined within the lineages they arose and will be removed from the population with the extinction of these lineages. Far from defying the theory of evolution of uniparental transmission of organelle DNA, mtDNA transmission in *Mytilus* provides a much needed empirical support for the theory.

Eleftherios Zouros
Amy Oberhauser Ball
Carlos Saavedra
Kenneth R. Freeman
Department of Biology and Marine Gene Probe Laboratory, Dalhousie University, Halifax, Nova Scotia B3H 4J1, Canada

E.Z. is also at Department of Biology, University of Crete and Institute of Marine Biology of Crete, Iraklion, Crete, Greece. Current addresses: Departamento de Biología Fundamental, Universidad de Santiago de Compostela, Santiago de Compostela (La Coruña), Spain (C.S.); Halifax Fisheries Research Laboratory, Department of Fisheries and Oceans, PO Box 550, Halifax, Nova Scotia B3J 2S7, Canada (K.R.F.).

1. Hoeh, W. R. *et al. Science* **251**, 1488–1490 (1991).
2. Zouros, E., *et al. Nature* **359**, 412–414 (1992).
3. Hoekstra, R. F. in *The Evolution of Sex and its Consequences* (ed. Stearns, S. C.) 59–91 (Birkhauser, Basel, 1987).
4. Hurst, L. D. & Hamilton, W. D. *Proc. R. Soc.* B **247**, 189–194 (1992).
5. Fisher, C. & Skibinski, D. O. F. *Proc. R. Soc.* B **242**, 149–156 (1990).

■ See News and Views, page 811