

in part, by bodies that formed closer to the Sun; one need not assume that the solar nebula extended to such a distance. The efficiency of placing such bodies into the disk is uncertain, but Stern estimates that of the order of 1 per cent of the original plutons may reside there; most would be beyond 50 AU.

Observational limits are not too restrictive. Tombaugh's new search<sup>11</sup> was essentially complete for plutons within 50 AU. Searches to fainter limits necessarily cover smaller areas. The most stringent limit implies an upper limit of about ten objects within 80 AU, unless

they are extremely dark<sup>12</sup>. Deeper but less extensive searches formally allow up to 20,000 plutons to hide between 80 and 140 AU, but surely such a population would be accompanied by a significant number at smaller distances. A search that can detect bodies out to 100 AU will have a good chance of finding one or more objects. If none are out there, we will need greater ingenuity to explain the existence of Pluto and Triton. □

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## EVOLUTION

## Matriarchal liberation

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THE rules of molecular evolution seem made to be broken, and no piece of genetic material has shattered more evolutionary principles than has mitochondrial (mt) DNA<sup>1</sup>. Do genes within an organismal lineage share a single evolutionary history? Not necessarily, as exemplified first and most forcefully by the disclosure that mtDNA is endosymbiotic in origin<sup>2</sup>. Is the genetic code universal? No, as first demonstrated with the discovery of modified codon assignments in mammalian mtDNA<sup>3</sup>. Do functionally constrained sequences evolve slowly? Not invariably, as indicated by the rapid pace of nucleotide substitution in the functionally conservative animal mtDNA<sup>4</sup> (probably due in part to inefficient DNA repair mechanisms). Do all genes in higher animals obey mendelian laws of segregation and independent assortment during sexual reproduction? No, as exemplified by the fact that mtDNA exhibits a strict maternal transmission.

Or does it? On page 255 of this issue<sup>5</sup>, Gyllensten *et al.* report the detection of paternally derived mtDNA sequences in experimental backcross hybrids between the mice *Mus musculus* and *M. domesticus*. The proportion of paternal mtDNA within the heteroplasmic individuals was low (at most, one molecule in 1,000, the remainder being of maternal source), but the results nonetheless provide the first direct genetic evidence of effective leakage of paternal mtDNA in a vertebrate.

This finding comes on the heels of two other reports of departures from the axiom of complete maternal inheritance of mtDNA in higher animals. Kondo *et al.*<sup>6</sup> used paternal-specific mtDNA probes in Southern blot experiments to reveal instances of paternal leakage in experimental populations of *Drosophila*; among 331 lines derived from hybrid progeny unidirectionally backcrossed to

genetically marked males, three strains (all from interspecific crosses) exhibited a complete replacement by paternal mtDNA within ten generations. Hoeh *et al.*<sup>7</sup> used restriction digestion procedures to document the occurrence in mussels (*Mytilus edulis*) of heteroplasmic individuals carrying two highly distinct mtDNA genomes (sequence divergence  $\approx$  20 per cent). Such sequences are unlikely to have arisen by the accumulation of mutations within female lines, so the results were attributed to paternal input probably associated with recent interspecific hybridization.

Individual sperm carry small numbers of mtDNA molecules (about 50–100, compared to the 100,000 or more copies in a mature oocyte), and in some species they are known to penetrate the egg during fertilization (for discussion of this, and other aspects of mtDNA inheritance, see refs 1, 8 and 9). Earlier studies that employed less sensitive molecular assays may have failed to detect paternal input in hybrid progeny simply because of this numbers game. Another conventional speculation is that the usual maternal mode of inheritance may in some cases be strengthened by active oocyte involvement in the exclusion, degradation or under-replication of paternal mtDNA. Intriguingly, all three instances of paternal leakage found thus far involve inter- rather than intraspecific crosses. Gyllensten *et al.*<sup>5</sup> suggest that genetically distinct mtDNA from foreign sources might escape the exclusionary mechanisms normally aimed at closely related paternal molecules derived from fertilizations within species.

In any event, why all this fuss over low-level leakage of paternal mtDNA? The reason is that these discoveries raise evolutionary possibilities that previously were neglected, but now will require careful re-examination.

First, paternal leakage at least opens a

window of opportunity for physical recombination between mtDNA molecules from separate parents. Although such intermolecular recombination has not yet been discovered in higher animal mtDNA (in heteroplasmic *Mytilus*<sup>7</sup>, the distinct mtDNAs retained their separate identities), such a phenomenon could complicate reconstruction and interpretation of genealogies based on mtDNA. Second, because mtDNA numbers probably go through bottlenecks during oogenesis<sup>10</sup>, paternal mtDNA might occasionally be the 'lucky' survivor and take over a maternal lineage (as in the *Drosophila* study<sup>6</sup>). Such paternal invasions would provide a mtDNA genetic bridge between otherwise isolated cytoplasmic matrilineages. And, depending on frequency, they could have ramifications in such areas as the interpretation of mtDNA gene trees as estimates of strict matriarchal phylogeny; estimation of sex-specific demographic parameters, including effective female population size and gene flow<sup>6</sup>; the likelihood of occurrence of repetitive selfish elements within mtDNA (in principle, genes with selfish motives gain no fitness advantage by becoming repetitive within a uniparentally transmitted, non-recombining genome<sup>1</sup>); and, finally, the degree to which potential conflicts of interest between nuclear and cytoplasmic genes stem from the contrasting evolutionary strategies expected for biparentally as opposed to uniparentally transmitted genomes<sup>1,11</sup>.

As to the evolutionary significance, it remains to be seen whether leaks of paternal mtDNA are analogous to drips from a leaky tap (an inconsequential source of noise), or to seepage from cracks in a dike (perhaps a prelude to the bursting of yet another genetic principle, in this case one of mtDNA's own making). Given the history of mitochondrial incursions into conventional evolutionary doctrine, it may be wise to keep an eye on this trickle. □

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1. Avise, J. C. *A. Rev. Genet.* (in the press).
2. Margulis, L. *Origin of Eukaryotic Cells* (Yale Univ. Press, New Haven, 1970).
3. Barrell, B. G., Bankier, A. T. & Drouin, J. *Nature* **282**, 189–194 (1979).
4. Brown, W. M., George, M., Jr & Wilson, A. C. *Proc. natn. Acad. Sci. U.S.A.* **76**, 1967–1971 (1979).
5. Gyllensten, U., Wharton, D., Josefsson, A. & Wilson, A. C. *Nature* **352**, 255–257 (1991).
6. Kondo, R., Satta, Y., Matsuura, E.T., Ishiwa, H., Takahata, N. & Chigusa, S. I. *Genetics* **126**, 657–663 (1990).
7. Hoeh, W. R., Blakley, K. H. & Brown, W. M. *Science* **251**, 1488–1490 (1991).
8. Avise, J. C. & Vrijenhoek, R. C. *Molec. Biol. Evol.* **4**, 514–525 (1987).
9. Gyllensten, U., Wharton, D. & Wilson, A. C. *J. Hered.* **76**, 321–324 (1985).
10. Hauswirth, W. W. & Laipis, P. J. *Proc. natn. Acad. Sci. U.S.A.* **79**, 4686–4690 (1982).
11. Alexander, R. D. & Borgia, G. A. *Rev. Ecol. Syst.* **9**, 449–474 (1978).