necessity to wait for fertilisation enables the oocytes of one generation to begin embryogenesis before the mother is born, so that three generations exist in the form of a single pregnant individual.

Grandmaternal effects can also occur during the course of sexual reproduction, wherever a specific area of germplasm is segregated in the oocyte before fertilisation. This is the case in *Drosophila* as described by R. M. Warn (University of East Anglia, Norwich). The germplasm determinants are located in the pole plasm of the egg; during early stages of cleavage some nuclei move down into this area, and most of the cells which form from the combination of nuclei and pole plasm become germ cells. In the 'grandchildless' mutants the pole plasm is not utilised in this way, so that germ cells fail to form and the adults are sterile. Of the vertebrates commonly used in embryological investigations, it is probable that only anuran amphibians have a real area of germplasm in the oocyte (L. D. Smith & M. A. Williams, Purdue University). Ultraviolet irradiation of the germplasm area of the egg results in the very late arrival of germ cells in the genital ridges, an effect which seems to be mediated through cleavage abnormalities in the germplasm area, and to damage to a (maternal) component of the migratory mechanism (probably mitochondria). Irradiated eggs can be 'rescued' by the injection of cytoplasm from another egg.

A mother can endow her oocytes with an embryolethal component. G. M. Malacinski and J. Spieth (University of Indiana) described a number of maternal effect genes in the Mexican axolotl. In the case of the *o* gene, homozygous embryos can be rescued from their fate of developmental arrest at gastrulation by injection of normal cytoplasm into the egg before the first cleavage division. Maternal effect mutant genes are also known in mammalian (mouse) embryos (A. McLaren, MRC Mammalian Development Unit, London). For instance, the hairpintail (T^{hp}) gene is expressed as polydactyly and spina bifida only when it is inherited maternally; matroclinous and patroclinous matings have shown that this is a cytoplasmic and not a uterine effect.

How much do the cytoplasmic components of maternal origin contribute to post-fertilisation development? The role of maternal mitochondria in chick development has been studied using chloramphenicol, which prevents synthesis of new mitochondria (F. S. Billett, University of Southampton). Embryogenesis was normal at first, but blood islands failed to form and the neural tube did not close, suggesting that the maternal contribution is sufficient for development to the headfold stage.

Yolk is another component of the oocyte cytoplasm which contributes to post-fertilisation development in most animal species. Yolk proteins are stored in the oocyte in insoluble form in the yolk platelets; they are derived from the soluble precursor vitellogenin, which is synthesised by the maternal liver and secreted into the bloodstream. J. R. Knowland and B. R. Westley (University of Oxford) described some aspects of vitellogenin synthesis in the frog *Xenopus laevis*. One of the most interesting aspects of their work is that vitellogenin synthesis is under hormonal control, and can be stimulated in the male liver by exogenous oestrogen. The capacity of the liver to respond to oestrogen in this way is gained around the stage of mid-metamorphosis, coinciding with the appearance of oestradiol-binding protein in the liver cells.

In discussion, J. B. Gurdon (MRC Laboratory of Molecular Biology, Cambridge) suggested that in Amphibia some gene repressors or activators might be synthesised in the oocyte, and subsequently segregated into different cells, thus determining them as ancestors of specific cell types. Such morphogenetic determinants almost certainly do not exist in the oocytes of amniote vertebrates (reptiles, birds and mammals), but they have been clearly established in gastropod molluscs (N. H. Verdonk & M. R. Dohmen, Utrecht). The determinants appear to be located in the 'vegetal body', a mass of vesicles filled with electron-dense material, which is segregated into a 'polar lobe' at the first cleavage division. The polar lobe is a small sac-like structure attached to the blastomeres, from which it can be removed without damage. The result of this operation (on *Dentalium*) was the formation of a larva without eyes, tentacles, mantle cavity, or heart. Some of these structures, the heart, for example, are directly lobe-dependent; others, such as eyes and tentacles, depend on a tissuue interaction involving the polar lobe.

In mammals, the opportunities for maternal effects are greatly increased as a result of intrauterine development: deleterious environmental effects on the maternal body may have adverse effects on the embryo or fetus, and the maternal genotype acting through the uterine environment may modify development. But several recent studies suggest that mammalian embryos have a considerable ability to defend themselves against adverse environmental factors. In a demonstration M. H. L. Snow (MRC Mammalian Development Unit) showed that when 7-day pregnant mice are injected with the mitotic inhibitor mitomycin C there is a temporary developmental arrest at the primitive streak stage, followed by resumption of development and the formation of embryos at day 10 with almost perfect form but only 15% of the normal number of cells in each structure; by 13½ days these embryos have achieved weights which are 90% of control values. In my own laboratory we have demonstrated a shorter-term example of morphogenetic regulation: rat embryos were exposed to cytochalasin B *in vitro* just before brain tube closure; the cranial neural folds collapsed, but on later transference of the embryos to control medium, the curvature was regained and neural tube closure effected even though it was by then out of phase with the morphogenesis of other structures.

C. Jones and J. Robinson (University of Oxford) described the fetal response to less than ideal maternal conditions at later developmental stages. Guinea pigs were growth-retarded by artificial reduction of the uterine blood supply; various essential proteins (such as components of the pathway of myelin synthesis, and the liver enzyme pyuvate carboxylase) were first detectable 2-3 days later than in controls, but subsequently reached normal levels. The morphogenetic examples of embryonic regulation described above are similar to these biochemical observations in that in both, adverse environmental conditions delay the synthesis or post-synthetic organisation of proteins which are essential for normal development. The ability of mammalian embryos and fetuses to adapt to such condtions may be an important protection against potentially detrimental maternal effects. □

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Errata

In the article 'Nucleon-nucleon interactions' (*News and Views* **275**, 589; 1978) Bedford College, London, was inadvertently omitted from the reference to results from the BASQUE group.

The Conveners of the London Conference reported in the article 'Echinoderm biology' (*News and Views* **275**, 268; 1978) were R. E. Emson (King's College, London) & E. P. F. Rose (Bedford College), from whom abstracts of the proceedings are available.