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Maternal to offspring resource allocation in plants and mammals

J.F. Gutierrez-Marcos [a,*], M. Constância [b,c,d], G.J. Burton [c,d]

[a] School of Life Sciences, University of Warwick, Wellesbourne Campus, Coventry CV4 7AL, UK
[b] Metabolic Research Laboratories, Department of Obstetrics and Gynaecology, University of Cambridge, Cambridge CB2 0SW, UK
[c] National Institute of Health Research, Cambridge Biomedical Research Center, Cambridge, UK
[d] Centre for Trophoblast Research, Department of Physiology, Development and Neuroscience, University of Cambridge, Cambridge CB2 3EG, UK

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ABSTRACT

Appropriate allocation of resources to the offspring is critical for successful reproduction, particularly in species that reproduce on more than one occasion. The offspring must be provisioned adequately to ensure its vigour, whereas the parent must not become so depleted such that its survival is endangered. In both flowering plants and mammals specialised structures have evolved to support the offspring during its development. In this review we consider common themes that may indicate conservation of nutrient transfer function and regulation by genomic imprinting across the two kingdoms.

1. Introduction

The success of reproduction in plants and mammals relies to a large extent on the balanced allocation of resources to the developing embryo. Remarkably, the development and function of placental tissues in plants and mammals is in part epigenetically regulated. In this review, we discuss the similar strategies that have evolved in both kingdoms to support maternal nutrient transfer to the offspring, their regulation by genomic imprinting and we propose a hitherto unrecognized role for placentally-derived nutrients on ensuring the epigenetic stability of the offspring.

2. Placental/endosperm tissues support nutrition of the offspring in plants and mammals

The seeds of flowering plants are the result of a double fertilization event involving union of two sperm cells with a haploid egg and sister diploid central cell to form a diploid embryo and a triploid endosperm, respectively [1,2]. Hence, the endosperm has the same genetic composition as the embryo (Fig. 1). Whereas the embryo develops into a mature plant, the development of the endosperm is confined to the seed stage. The endosperm is a key feature of flowering plants, however its evolutionary origin is not yet clear. It is likely that the endosperm arose from a second successful fertilization event, which resulted in an altruistic embryo that could act as a nourishing placenta-like tissue. This is supported by the fact that basal seed-producing plants like conifers (Gymnosperms) produce supernumerary embryos that provide nutritive support to the development of the embryo [3], and by the recent finding in water-lilies (Nymphaeales), an ancestral flowering plant, that developing embryos are nourished by a reduced diploid endosperm [4].

Traditionally the endosperm has been considered a simple tissue that stores nutrients and supports the establishment of the embryo during germination. However, the role of the endosperm is more complex than initially thought. Upon fertilization of the central cell gamete, the endosperm rapidly divides through a wave of synchronous nuclear divisions to form a coenocyte or syncytium while the embryo remains as zygote [5]. At this stage of seed development nutrients can be freely transported to the developing embryo from the maternal tissues (Fig. 2A). The endosperm has nuclei arranged within a thin layer of cytoplasm at the periphery of the syncytium, which in some plant species undergoes synchronous cellularization until the cavity is filled. Cellularization of the endosperm constitutes a key stage in endosperm patterning [6], and thereafter the endosperm differentiates into various cell types, of which the nutrient-transfer cells are the first to become distinguishable and required to facilitate the active transport of nutrients to the embryo (Fig. 2B). Transfer cells are characterized by an extensive network of plasma membrane forming wall ingrowths, and are rich in mitochondria and rough endoplasmic reticulum, as well as abundant sugar translocating enzymes that convert sucrose into hexose sugars [6]. The action of invertases in establishing a sugar flux in the maternal–filial interface is of vital importance, as they regulate the development not only of the endosperm but also

* Corresponding author. Tel.: +44 2476575077.
E-mail addresses: j.f.gutierrez-marcos@warwick.ac.uk (J.F. Gutierrez-Marcos), jmasmc2@cam.ac.uk (M. Constância), gjb2@cam.ac.uk (G.J. Burton).

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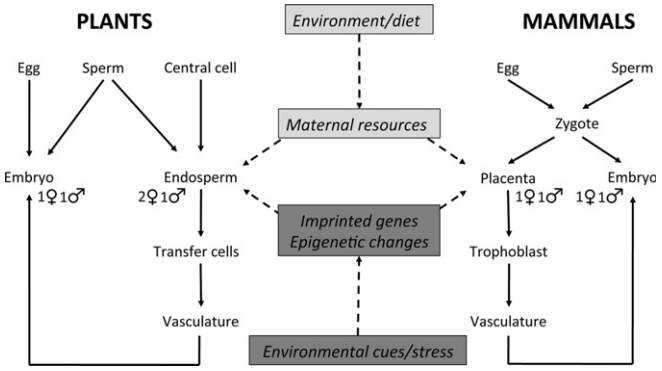

Fig. 1. Schematic diagram highlighting the strategies adopted in mammals and plants to translocate maternal resources to embryos. In plants, a sperm cell fertilises the haploid egg cell and the homo-diploid central cell gametes to give rise to a diploid embryo and a triploid endosperm. Endosperm transfer cells contribute to the active transport of nutrients to the developing embryo. In mammals, haploid sperm and egg cell gametes fuse to produce a diploid zygote, which later differentiates into a placenta with trophoblast cells actively translocating maternal nutrients to the embryo. Both endosperm and placenta function are regulated epigenetically by imprinted genes and environmental cues.

of the maternal surrounding tissue. The evolutionary origin of endosperm transfer cells is not yet understood but in species with persistent endosperms their function is critical for reproductive success and possibly in plant speciation [2].

During the final stages of seed development the endosperm acts as a nutritional reservoir to sustain embryo growth post-germination and the establishment of the next generation, much in the same way as the yolk and albumin of a reptilian or avian egg. By contrast in mammals, maternal nutrients are supplied during pregnancy via the placenta, and after birth through lactation. There is no doubt that the mammalian extraembryonic membranes and placenta have evolved from the reptilian egg. Indeed viviparity is seen in many reptilian species, in particular those living at high altitudes or in latitudes thought to allow for better thermoregulation during development [7]. Seed formation and oviparity arguably place a greater short-term drain on parental resources than viviparity, when the nutrients can be provided over the course of gestation. However, in mammals it is likely that the burden varies greatly depending on the length of pregnancy and the reproductive strategy employed. Thus in mice, where gestation is 21 days and the total conceptus weight of a litter represents 30% of maternal weight at term, the burden will be high compared to in humans where conceptus weight represents only 5% of maternal weight and gestation lasts for 9 months. These differences may explain why the epigenetic regulation by imprinting of placental function is more stringent in mice than in humans [8,9].

During early development of eutherian mammals, the first cell divisions of the fertilised egg create the morula, a ball of diploid totipotent cells. The first cell lineage divergence occurs in conjunction with the transformation of the morula into the blastocyst, which comprises an outer wall of trophoblast cells that contribute to the placenta, and the inner cell mass from which the embryo develops. The placenta therefore has the same genetic structure as the embryo (Fig. 1). In all species, the trophoblast of the placenta will interact with the uterus following implantation, but the nature of that interaction varies widely across species [10]. In those with non-invasive epitheliochorial placentas the trophoblast abuts the uterine epithelium, and nutrient exchange takes place between the underlying maternal and fetal capillary networks (Fig. 2C). In the most invasive forms the trophoblast erodes the maternal epithelium and endothelium so that maternal blood bathes the trophoblast. This is the haemochorial form of placentation, and is seen in rodents and the higher primates, including man (Fig. 2D). For many years it was assumed that these different forms represented an evolutionary progression, but molecular phylogenetics have revealed that the epitheliochorial form is an acquired state that has arisen in several different orders by convergent evolution [11,12]. The selective pressures that have favoured this development are uncertain, but greater control over resource allocation is a possibility.

Linked to the difference in invasiveness are changes in the histological nature of the trophoblastic epithelium. In epitheliochorial placentas the trophoblast generally remains cellular, whereas in the haemochorial forms it undergoes a syncytial transformation into a polarised, multinucleated epithelium devoid of intercellular clefts (Fig. 2B and C). Despite the different number of cell layers between the maternal blood and the trophoblast, comparative studies have shown considerable functional similarities between the different placenta types [10]. Placental exchange occurs by simple diffusion (e.g. respiratory gases, free fatty acids), facilitated diffusion (e.g. glucose), active transport (e.g. amino acids), and receptor-mediated endocytosis (e.g. immunoglobulins). Most relevant to the discussion here is the transport of glucose and amino acids, as capacity will be dependent upon the insertion of specific transmembrane proteins. Transport of glucose is facilitated

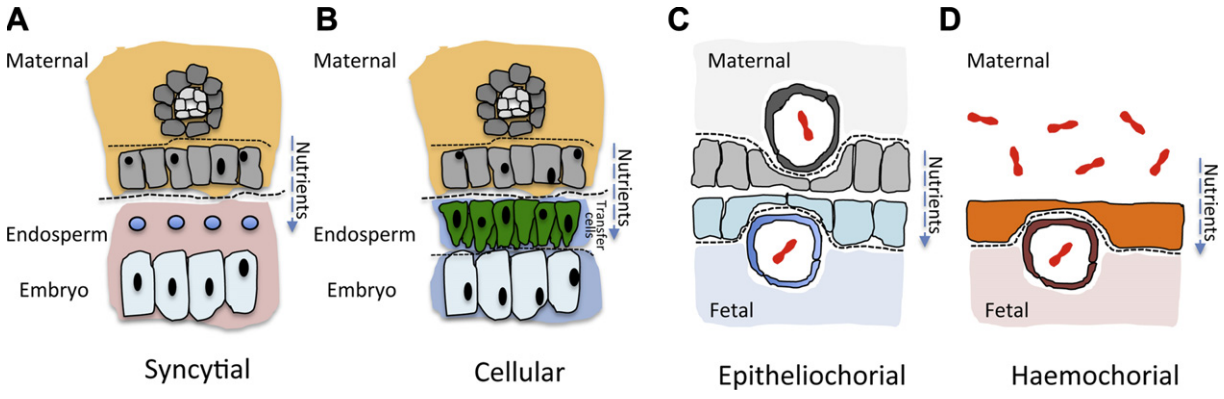

Fig. 2. Schematic diagram highlighting different strategies to translocate maternal resources to developing embryos in flowering plants and mammals. A, In syncytial endosperms, maternal resources are translocated to the embryo directly from vascular networks located in maternal tissues. B, In cellular endosperms, resources are translocated from maternal tissues into the embryo by specialized transfer cells (green) located at the maternal–filial interface. C, In epitheliochorial placentas, maternal resources are translocated between the underlying maternal (grey) and fetal (blue) capillary networks. D, In haemochorial placentas maternal resources are in direct contact with the trophoblast (orange) and are translocated directly to fetal (brown) capillary networks.