

The evolution of fetal nutritional adaptations

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Viviparous (live-bearing) vertebrates have evolved a variety of specializations by which the nutritional needs of their embryos can be satisfied. The enormous diversity of these adaptations has been well documented in reviews on fish (AMOROSO, 1960; HOAR, 1969; WOURMS, 1981), amphibians (WAKE, 1977, 1980, 1982), reptiles (WEEKES, 1935; BAUCHOT, 1965), and mammals (MOSSMAN, 1937; WIMSATT, 1962; LUCKETT, 1977). This paper is a preliminary attempt to examine these adaptations from an evolutionary standpoint. We shall summarize evidence that strong evolutionary convergence in fetal nutritional adaptations has occurred frequently in viviparous vertebrates. Hypothetical explanations for the observed trends are also suggested.

TERMINOLOGY. We classify reproductive modes according to the form of the reproductive product. «Oviparity» involves the laying of eggs with intact shells or membranes, and «viviparity» involves maternal retention of the eggs to term followed by parturition of living young. We recognize two nutritional patterns which represent extremes of a continuum: «lecithotrophy», in which energy for development is derived from the yolk of the ovum, and «matrotrophy», in which nutrients are supplied directly by the mother during gestation. Lecithotrophic viviparity is often called «ovoviviparity» (e.g., see WAKE, 1982).

Five types of matrotrophy can be distinguished (terminology of WOURMS, 1981): 1. Oophagy- embryos feed upon sibling ova; 2. Adelphophagy- embryos feed upon developing siblings (intrauterine cannibalism); 3. Histophagy- embryos ingest maternal secretions; 4. Histotrophy- embryos absorb maternal secretions; 5. Placentotrophy- nutrient transfer is accomplished via a chorioallantoic or yolk sac placenta. There are intergradations between these categories, and a given species may exhibit multiple forms of matrotrophy.

METHODS. Previous evolutionary analyses of viviparity (BLACKBURN, 1981, 1982, in press, ms.) were used to elucidate evolutionary trends in nutritional patterns. These analyses have identified a minimum of 124 independent origins of the viviparous mode. Each lineage was characterized according to the nutritional specialization exhibited. Lecithotrophy was assumed to represent the primitive viviparous condition. For references and detailed information on nutritional adaptations discussed, see the reviews cited above.

REPTILES. Although data are available for only a few of the approximately 1100 viviparous species, substantial matrotrophy is known to have evolved at least four times.

Nutrient transfer is accomplished by placental means. Certain New World skinks of the genus *Mabuia* have converged upon a «eutherian» reproductive pattern. Specializations of these lizards include: 1. ovulation of exceedingly small (1 mm) ova; 2. a prolonged gestation (9–12 months); 3. formation of a chorioallantoic placenta with an intimate association of fetal and maternal tissues; 4. placental transfer accounting for over 99% of the fetal dry mass (VITT and BLACKBURN, 1983; BLACKBURN et al., 1984).

MAMMALS. Nutrient transfer involves the omphaloplacenta in metatherians and the chorioallantoic placenta in paramelid marsupials and eutherians. This diversity in nutritional mechanisms may represent multiple origins of matrotrophy. A substantial histotrophic absorptive phase characterizes all mammals including monotremes, suggesting that matrotrophy may have preceded rather than followed the adaption of viviparous habits.

AMPHIBIANS. Matrotrophy in viviparous amphibians involves ingestions of oviductal secretions, although the urodele *Salamandra atra* also feeds upon breakdown products of sibling ova. Specializations believed to aid in histophagy include the labial filaments of the anuran *Nectophrynoides occidentalis* and the convergently derived fetal dentition of *Salamandra atra* and the caecilians (WAKE, 1980, 1982).

OSTEICHTHYES. In viviparous teleosts, gestation is ovarian rather than oviductal, and matrotrophy usually involves the absorption or ingestion of ovarian secretions (WOURMS, 1981). Frequently, the ovary has become specialized through hyper-vascularization and formation of folds or villi covered with secretory cells. In four histophagic lineages (clinids, anablepids, zoarcids, embiotocids) the gut has become enlarged and its epithelium hypertrophied. Three groups (ophidioids, parabrotulids, goodeids) have convergently evolved trophotaeniae, elongate projections from the proctodeal region, which are believed to function in histotrophy. In two cyprinodont groups (poeciliids, Anableps), a hypertrophied pericardial sac and extraembryonic coelom contribute to formation of a follicular pseudoplacenta. In some poeciliids, a pseudoplacenta is formed from the yolk sac and follicle wall (AMOROSO, 1960; HOAR, 1969; WOURMS, 1981).

CHONDRICHTHYES. Incipient oviductal histotrophy and histophagy are widespread among viviparous chondrichthyans. Species vary with respect to the degree of elaboration of the uterine epithelium and the organic content of its secretions. Myliobatoids and pristoids exhibit (independently derived ?) trophonemata, glandular villous projections of the uterine epithelium which, in some species, project into the embryonic spiracles and secrete histotroph into the gut. Yolk sac placentation has probably originated at least twice (Sphyrnidae, Carcharinidae) (WOURMS, 1981). Adelphophagy and oophagy, characteristic of lamnoid sharks, may have also evolved in the extinct holocephalan *Delphyodontos* and the carcharinid *Pseudotriakis* (see WOURMS, 1981).

PREADAPTIONS AND CONSTRAINTS. The discontinuous distribution of nutritional patterns (Table 1) supports the idea that the type of matrotrophy evolved is a function of preadaptions and constraints. For example, the emphasis on in utero feeding in anamniotes may reflect the fact that a free-living larval stage is commonly a feature of oviparous development. The extraembryonic membranes of amniotes probably preclude nutrition via adelphophagy and oophagy. Vascularized respiratory structures frequently have been recruited for nutrient transfer, such as the chorioallantois, the yolk sac, the gill, and the cyprinodont pericardial sac. Convergent trends towards reduction of the distance between fetal and maternal blood streams are apparent in numerous placental groups. In goodeids, trophotaenial histotrophy may have evolved from histophagy through heterochrony of genes regulating gut development (WOURMS, 1981). For most lineages, however, there is little evidence that one type of matrotrophy is ancestral to another.

Table 1. Evolution of matrotrophy in viviparous anamniotes. Figures represent minimum numbers of evolutionary origins of each nutritional pattern.

Nutritional pattern	Amphibia	Osteichthyes	Chondrichthyes
oophagy/adelphophagy	1	2	1
histophagy (ovarian)		6	
histotrophy (ovarian)		7	
histophagy (oviductal)	3		2
histotrophy (oviductal)			
placentotrophy		1	2

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