

REPRODUCTIVE ADAPTATIONS AMONG VIVIPAROUS FISHES (CYPRINODONTIFORMES: POECILIIDAE)

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Abstract

Within the family Poeciliidae, a wide range of adaptations accompanying viviparity has evolved. The reproductive mechanisms of five representative species were examined and related to the habitats in which they are employed. *Poecilia reticulata*, the guppy, represents the majority of poeciliids which have a single stage of embryos in the ovary at a time. Most of the nutrients are prepack-aged in the eggs before fertilization; no specialized placental adaptations have evolved. The major variable among species utilizing this mechanism is in the yolk loading time; some eggs are mature and ready to be fertilized immediately after the birth of a clutch of embryos, others take a week or more. The mechanism may be thought of as a generalist-type, being employed throughout the range of poeciliids and in all varieties of habitats. *Poeciliopsis monacha* has embryos of two different ages occurring simultaneously in the ovary. Its large eggs provide the embryo's entire nutrient supply. Mature embryos weigh 47% less than mature eggs. This species lives in a harsh, montane environment with an unpredictable food supply; its reproductive mechanism is well suited to fluctuating resources. When conditions are favorable, a large clutch of eggs is loaded, but if food is in short supply, clutch sizes are small or only one stage is produced. During starvation conditions, no eggs are produced; but, with restoration of food supply, reproduction resumes quickly. *Poeciliopsis lucida* has medium-sized eggs and three stages of embryos. At birth, young weigh slightly more than mature ova. This weight gain plus the energy utilized for embryonic metabolism constitutes a significant maternal contribution during development. *P. lucida* is wide-spread in the three rivers that comprise its range but it does not enter the depauperate rocky arroyos occupied by *P. monacha*. *P. lucida* requires a stable food supply characteristic of the fertile and productive downstream regions. *Poeciliopsis prolifica* carries as many as five stages of embryos which are born at short brood intervals of two to eight days. Ova sizes are small and embryos receive almost all of their nutrients through a placenta. *P. prolifica* lives in a rich environment where food resources are stable. It is the smallest species in the genus and it produces the smallest young, yet its habitat seems precarious. Living on the steep slope between deep and shallow water it is wedged between deep and shallow water competitors, having to cope with large deep water fish predators as well. *Poeciliopsis turneri* is the largest of the five species studied and occupies a habitat somewhat unusual for poeciliids. Three stages of embryos are present in the ovary but brood sizes are usually small (ave. 3.6). The ova are small yet the mature embryos are large, weighing almost 19 times more than the ova. Brood sizes in neither *P. prolifica* nor *P. turneri* become larger as female size increases. *P. turneri* is adapted to life in deep swift water where large adults, large offspring and streamlining are important. The other four species can risk the swollen pregnant-look typical of poeciliids, whereas *P. turneri* cannot. Superfetation (multiple stages of embryos) is advantageous in that it avoids the surge of energy required to load a single large clutch of eggs. The energy for reproduction is sequentially divided among two to five small clutches. Reduction of ova size increases the space available for more stages of embryos. Although embryos with small yolk supplies place a nutrient drain directly on the mother, surges in demand are avoided since embryonic stages enter the growth phase at different times. A continuous food supply to the female is essential; otherwise, embryos will die and the reproductive effort to that point is lost.

REPRODUCTION AND DEVELOPMENT IN CHONDRICHTHYAN FISHES

JOHN P. WOURMS

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Department of Zoology, Clemson University Clemson, South Carolina 29631

Patterns of chondrichthyan reproduction and development are diverse. Species either are reproductively active throughout the year, or have a poorly defined annual cycle with one or two peaks of activity, or have a well defined annual or biennial cycle. Based on embryological origin and adult morphology, their reproductive system is more similar to tetrapods than to teleosts. Primordial germ cells are of endodermal origin. The Wolffian ducts in males and Mullerian ducts in females become the functional urogenital ducts. Differentiation is under hormonal control. Unusual features of the reproductive system include an epigonal organ in males and females. It contains lymphoid and hemopoietic tissue. Leydig's gland, a modified region of the kidney, produces seminal fluid. In some species, sperm passing through the vas deferens, is enclosed in spermatophores. Rotating about their long axis, helical spermatozoa can move forward or reverse direction. Spermatogenesis often occurs in bicellular units, spermatocysts. These consist of a spermatogonium enclosed in a Sertoli cell. Fertilization is internal. Claspers, modified portions of the pelvic fins act as intromittent organs. In many viviparous sharks and rays, the female reproductive system is asymmetrical. Eggs of some sharks are the largest known cells. Yolk platelets contain lipovitellin. Oocytes have lampbrush chromosomes. Eggs released from the ovary into the body cavity are transported by ciliary action to the ostium of the oviduct. There they are fertilized. Physiological polyspermy is normal. The shell gland, a specialized region of the anterior oviduct, functions both in long term sperm storage and in egg case production. Egg cases of sharks and skates consist of unique collagenous protein with a 400 Å period, organized as a cholesteric liquid crystal. Chimaeroid egg cases contain 550 Å pseudotubules in orthogonal lattices. In small sharks, males copulate by coiling around the female. A parallel position is assumed by large sharks. Skates and rays copulate with ventral surfaces apposed or by a dorsal approach. Biting is a pre-copulatory release mechanism. Parental care, except for selective oviposition, is lacking. Heavily yolked eggs undergo meroblastic, discoidal cleavage. Development is lengthy, shortest (2–4 months) in rays, longer in skates (3–8 months) and longest (9–22 months) in sharks and chimaeras. Most sharks and all rays are viviparous. Chimaeras, skates, and some sharks are oviparous. Viviparity either involves a yolk sac placenta or is aplacental. If aplacental, the embryo derives nutrients either from yolk reserves, or by intra-uterine embryonic cannibalism, or from placental analogues which secrete "uterine milk." Phylogenetic position, geographical distribution, benthic vs. pelagic habitat, adult size, egg-embryo size, feeding ecology, and embryonic osmoregulation are factors in the retention of oviparity or the evolution of viviparity.

REFLECTIONS ON THE EVOLUTION OF PISCINE VIVIPARITY

JOHN P. WOURMS and JULIAN LOMBARDI

Department of Biological Sciences, Clemson University Clemson, South Carolina 29631
Department of Biology, The University of North Carolina at Greensboro Greensboro, North Carolina 27412

Viviparity first makes its evolutionary appearance within the craniate-vertebrate line among fishes. We estimate that it has independently evolved at least 42 times in five of the nine major groups of fishes. Viviparity is the dominant mode of reproduction among the cartilaginous sharks and rays, *i.e.*, 55% of approximately 900 living species. It is less prevalent among the five major groups of bony fishes, *i.e.*, 2–3% of an estimated 20,000 or more species. The evolution of viviparity from oviparity involves: 1) a shift from external to internal fertilization; 2) retention of embryos in the female reproductive system; 3) utilization of the ovary or oviduct as sites of gestation; 4) structural and functional modification of the embryo and the female reproductive system and; 5) modification of extant endocrine mechanisms controlling reproduction. Viviparity offers selective advantages to parents and offspring, such as: 1) enhanced survival of offspring; 2) compensation for low fecundity; 3) amplification of reproductive niches to reduce competition; 4) exploitation of pelagic niches; 5) colonization of new habitats; and 6) increased energetic efficiency in viviparous matrotrophes. Its principal disadvantages include: 1) reduced fecundity; 2) cost to the female; and 3) risk of brood loss through maternal death. Acquisition of viviparity establishes new maternal-embryonic relationships, namely: 1) trophic; 2) osmoregulatory and excretory; 3) respiratory; 4) endocrinological; and 5) immunological. In sharks, rays, and the coelacanth, gestation takes place in the oviduct, but in teleosts gestation occurs either in the ovarian follicle or ovarian lumen. The cystovarian teleostean ovary is hypothesized to function both as ovary and oviduct. Oviductal, ovarian luminal, and follicular epithelial cells are the maternal sites of metabolic exchange. Metabolic exchange in embryos takes place across the epithelia of the general body surface and its derivatives or across the gut epithelium and its derivatives. Four patterns of piscine placentation have evolved, namely: 1) yolk sac; 2) follicular; 3) branchial; and 4) trophotaenial placentae. The pericardial amniochorion, the embryonic portion of the follicular placenta, occurs in poeciliids and several other teleostean groups. Developmentally, it is nearly identical to the anterior amniochorionic fold of tetrapod vertebrates. Trophotaeniae are external rosette or ribbon-like structures that have evolved in four orders of teleosts by heterochrony, *i.e.*, accelerated outgrowth and differentiation of the embryonic hind gut. With the possible exception of the coelacanth, the yolk sac placenta occurs only in sharks. We estimate that it has independently evolved between 11 and 20 times. It displays considerable diversity. Evolution of the yolk sac placenta entails retention of the yolk sac and secondary differentiation of its distal portion for implantation and maternal tissue-embryonic tissue metabolic exchange and its proximal portion for oviductal fluid-embryonic tissue exchange. The yolk stalk lengthens, is modified into an umbilical stalk, and establishes a site of autotomy at the embryo-umbilical stalk junction. The luminal wall of the oviduct becomes competent to function as a site of implantation.

VIVIPARITY: THE MATERNAL-FETAL RELATIONSHIP IN FISHES

JOHN P. WOURMS

Department of Zoology, Clemson University Clemson, South Carolina 29631

SYNOPSIS. Viviparity in the vertebrate line first makes its evolutionary appearance among fishes. It has independently evolved in a number of divergent piscine lineages. The 54 families of extant fishes that bear living young include 40 families of chondrichthyans (sharks and rays), one monotypic family of coelacanth (*Latimeria*), and 13 families of teleosts. There is fossil evidence for viviparity in holocephalans and chondrosteans. Viviparity predominates among sharks and rays (40 families, 99 genera, 420 species) but is less widespread among teleosts (13 families, 122 genera, 510 species). Following an historical introduction, the organization of the female reproductive system, sites of gestation, developmental sequences and superfetation are considered. The evolution of viviparity establishes specialized maternal-fetal relationships, viz., 1) developmental, 2) morphological, 3) trophic, 4) osmoregulatory, 5) respiratory, 6) endocrinological, and 7) immunological. While the latter four categories are briefly noted the major emphasis is on the trophic relationship and its morphological and developmental basis. First, a general overview is presented and then the maternal-fetal trophic relationships in each of the major groups of fishes are systematically reviewed. Pertinent anatomical, histological, ultrastructural, developmental, physiological, and biochemical studies are considered. Viviparous fishes are either lecithotrophic, *i.e.*, exclusively yolk dependent, or matrotrophic, *i.e.*, in receipt of a continuous supply of maternal nutrients during gestation. Nutrient transfer is accomplished by 1) oophagy and adelphophagy, 2) placental analogues, and 3) the yolk sac placenta. Placental analogues include: external epithelial absorptive surfaces, *e.g.*, skin, fins, gills; trophonemata, modifications of the uterine epithelia for the secretion of histotrophe or "uterine milk"; branchial placentae, close apposition between gill epithelia and either uterine or ovarian epithelial villi; the yolk sac; pericardial amnion and chorion; follicular pseudoplacenta, close apposition between follicle cells and embryonic absorptive epithelia; hypertrophied gut; and trophotaeniae, external rosette or ribbon-like projections of the embryonic gut. Among chondrichthyans, the yolk sac placenta (840–1,050%), trophonematal secretion and embryonic absorption of histotrophe (1,680–4,900%) and oophagy and adelphophagy (1.2 x 106%) are the most efficient methods of nutrient transfer. Among teleosts, the follicular pseudoplacenta (1,800–3,900%), trophotaeniae (8,400%) and absorption of ovarian histotrophe through surface epithelia and a hypertrophied gut (1,100–34,000%) are the most efficient. These values stand in contrast to the 30%–40% loss of dry weight characteristic of oviparous fishes and viviparous lecithotrophes.

FOLLICULAR PLACENTA AND EMBRYONIC GROWTH OF THE VIVIPAROUS FOUR-EYED FISH (*ANABLEPS*)

Frank M. Knight¹, Julian Lombardi², John P. Wourms^{3*}, Dr. John R. Burns⁴

¹Department of Zoology, Michigan State University, East Lansing, Michigan 48824

²Department of Biology, The University of North Carolina, Chapel Hill, North Carolina 27514

³Department of Biological Sciences, Clemson University, Clemson, South Carolina 29631

⁴Department of Biological Sciences, George Washington University, Washington, D.C. 20052

*Correspondence to John P. Wourms, Department of Biological Sciences, Clemson University, Clemson, South Carolina 29631

ABSTRACT

In the four-eyed fish, *Anableps* (Atheriniformes, Anablepidae), eggs are fertilized and embryos develop to term within the ovarian follicles. Development is highly matrotrophic. During gestation, the largest term embryo of *A. anableps* examined had grown to a total length of 51 mm and attained a dry weight of 149 mg. The postfertilization weight increase is 298,000%. The largest term embryo of *A. dowi* examined had grown to a total length of 77 mm and attained a dry weight of 910 mg. The postfertilization weight increase is 843,000%. Embryonic weight increases result from nutrient transfer across the follicular placenta. This structure is formed by apposition of the maternal follicular epithelium to absorptive surface cells of the embryo's pericardial trophoderm. The latter, a ventral ramification of the pericardial somatopleure, replaces the yolk sac during early gestation. The external surface of the pericardial trophoderm develops hemispherical projections, termed *vascular bulbs*. Within each bulb, the vascular plexus of the trophoderm expands to form a blood sinus. Cells of the external surface of the bulbs possess microplicae. Microvilli are absent. During middle to late gestation, the juxtaembryonic follicular epithelium differentiates into two regions. One region consists of shallow, pitlike depressions within which vascular bulbs interdigitate in a "ball and socket" arrangement. Follicular pits are formed by the curvilinear distortion of the apical surfaces of follicle cells. The second region in contact with the dorsal and lateral surfaces of the embryo, is comprised of villous extensions of the hypertrophied follicular epithelium. In both regions, follicle cells appear to constitute a transporting rather than a secretory epithelium. In terms of percentage of weight increase, the follicular placenta of *Anableps* appears to be the most efficient adaptation for maternal-embryonic nutrient transfer in teleost fishes and closely approaches the efficiency ($1.2 \times 10^6\%$) of oophagy and embryonic cannibalism in lamnoid sharks.

FOLLICULAR PLACENTA OF THE VIVIPAROUS FISH, *HETERANDRIA FORMOSA*: II. ULTRASTRUCTURE AND DEVELOPMENT OF THE FOLLICULAR EPITHELIUM

Bryon D. Grove¹, John P. Wourms²

¹Department of Cellular Biology and Anatomy, Louisiana State University Medical Center, Shreveport, Louisiana 71130

²Department of Biological Sciences, Clemson University, Clemson, South Carolina 29634

ABSTRACT

Embryos of the viviparous poeciliid fish, *Heterandria formosa*, develop to term in the ovarian follicle where they undergo a 3,900% increase in embryonic dry weight. Maternal-embryonic nutrient transfer occurs across a follicular placenta that is formed by close apposition of the embryonic surface (i.e., the entire body surface during early gestation and the pericardial amnionserosa during mid-late gestation) to the follicular epithelium. To complement our recent study of the embryonic component of the follicular placenta, we now describe the development and fine structure of the maternal component of the follicular placenta. Transmission electron microscopy reveals that the ultrastructure of the egg envelope and the follicular epithelium that invests vitellogenic oocytes is typical of that described for teleosts. The egg envelope is a dense matrix, penetrated by microvilli of the oocyte. The follicular epithelium consists of a single layer of cuboidal cells that lack apical microvilli, basal surface specializations, and junctional complexes. Follicle cells investing the youngest embryonic stage examined (Tavolga's and Rugh's stage 5-7 for *Xiphophorus maculatus*) also lack apical microvilli and basal specializations, but possess junctional complexes. In contrast, follicle cells that invest embryos at stage 10 and later display ultrastructural features characteristic of transporting epithelial cells. Apical microvilli and surface invaginations are present. The basal surface is extensively folded. Apical and basal coated pits are present. The cytoplasm contains a rough endoplasmic reticulum, Golgi complexes, and dense staining vesicles that appear to be lysosomes. The presence of numerous apically located electron-lucent vesicles that appear to be derived from the apical surface further suggests that these follicle cells may absorb and process follicular fluid. The egg envelope, which remains intact throughout gestation and lacks perforations, becomes progressively thinner and less dense as gestation proceeds. We postulate that these ultrastructural features, which are not present in the follicles of the lecithotrophic poeciliid, *Poecilia reticulata*, are specializations for maternal-embryonic nutrient transfer and that the egg envelope, follicular epithelium, and underlying capillary network form the maternal component of the follicular placenta. © 1994 Wiley-Liss, Inc.

REPRODUCTION AND DEVELOPMENT OF *SEBASTES* IN THE CONTEXT OF THE EVOLUTION OF PISCINE VIVIPARITY

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John P. Wourms

Department of Biological Sciences, Clemson University, 29634-1903 Clemson, SC, U.S.A.

Synopsis: Selected aspects of the reproduction and development of *Sebastes* and other rockfishes are reviewed in the context of piscine viviparity. Among the eight subfamilies of the Scorpaenidae, viviparity is confined to the subfamily Sebastinae; gestation is lumenal and the embryos usually develop to term within the egg envelope. Transitional states from oviparity to viviparity are evident in different species within the family. A scenario for the evolutionary origin of viviparity in rockfishes is derived from an analysis of scorpaeniform reproductive biology. Although viviparity is best developed in the genus *Sebastes*, it is still in a primitive, unspecialized state. Rockfish viviparity is essentially lecithotrophic, i.e. embryonic nutrition is dependent on the energy reserves laid down during oogenesis. In other groups of viviparous fishes, lecithotrophy has been shown to be better suited energetically to seasonally unpredictable habitats, whereas matrotrophy requires a predictable food supply. During the evolution of an essentially primitive form of lecithotrophic viviparity in rockfishes, the advantages of high fecundity associated with oviparity were retained while an enormous increase in the survival rate of the developing embryos was acquired. The basic lecithotrophic pattern of oviparous development was not changed since it offered selective advantages both in terms of energetics and as a basis for retaining a large brood size.

Key words Rockfish - Embryonic nutrition - Teleost - Maternal-fetal relationship - Scorpaenidae