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Fetal Maintenance and its Evolutionary Significance in the Amphibia: Gymnophiona

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ABSTRACT—The oviducts of several species of caecilians are modified for maintenance of fetal development through metamorphosis. Nutrition is provided by secretions from epithelial cells of the duct. Nutritional demands on the parent are great. It is concluded that the species-specific fetal dentition is functional in obtaining nutrition in the oviduct, in contrast to previous suggestions. This mode of viviparity is found in members of three of the four families of caecilians.

* * *

Several species of amphibians are known to retain developing young in their oviducts and to give birth to fully metamorphosed juveniles. The majority of such amphibian species belong to the order Gymnophiona—the blind, limbless, elongate caecilians of the tropics. Several aspects of the reproductive biology of caecilians are correlated with the ability to bear living young. Members of all caecilian species practice internal fertilization and have a number of morphological and behavioral modifications to facilitate it (Barrio, 1969; Wake, 1968, 1970, 1972); females produce relatively few, but large and yolky eggs (Wake, 1968); oviducts are capable of great distention and of secretory activity (Wake, 1970). Study of the morphology of oviducts of pregnant and non-pregnant adult females and the way developing young are maintained in the oviducts, as well as analysis of the developmental morphology of the fetuses, has produced some new ideas about the mechanism of viviparity in caecilians. In addition, it has necessitated review of previous ideas about caecilian fetal growth and nutrition.

Morphology of the Oviduct.—The gross morphology of the oviduct of several species, both viviparous and oviparous, has been described (Parker, 1956; Wake, 1970). A specimen of *Dermophis mexicanus* has more extensive epithelial proliferation than seen in other species. Three 'columns' of epithelium, one ventral, two lateral, fill the lumen of the duct, except for the space occupied by fetuses. The six 25 mm fetuses have gills, but yolk appears to be resorbed, or nearly so.

General comments about the microanatomy of the ducts of two viviparous species, *Gymnopsis multiplicata* and *Scolecophorus kirkii* were also presented by Wake (1970). Material is now available representing the non-pregnant *Gymnopsis multiplicata* oviduct, pregnant and non-pregnant *Dermophis*, and the pregnant and non-pregnant ducts of *Typhlonectes compressicauda*. These agree in general with the descriptions by Parker (1956) and Wake (1970). In non-pregnant females of both species the duct is slender, 1-3 mm in external diameter. Projections of connective tissue and capillaries covered with epithelium fill the lumen of the duct. The histology of the oviduct has been examined in more detail in order to consider the characteristics of the epithelium, especially the secretory cells of pregnant females. The epithelium is a single cell layer thick, and virtually all cells are ciliated. Nuclei are large; the

surrounding cytoplasm appears stromatous but not granular. With pregnancy, the oviduct dilates and the luminal projections ramify. The epithelial layer proliferates, and as the connective tissue-capillary projections ramify, they "enclose" thick beds of epithelium so that glands as described by Parker (1956) are formed. These are deep multicellular pockets with 'necks' to the lumen of the oviduct. The cells comprising the glands are not ciliated, nuclei are less deeply stained, and the cytoplasm is granular.

It is not unusual for oviducal epithelia in mammals to undergo changes from non-secretory to secretory states in a cyclic manner, and the cytological modifications noted above are characteristic for such states (Bloom and Fawcett, 1968:744-745). Bloom and Fawcett also state that there are no true glands in the mammalian oviduct and that true glands form by invagination of epithelia into the basal connective tissue. It appears that the 'glands' of caecilians are epithelial beds enclosed by connective tissue ramifications. Thus caecilians, and perhaps other lower vertebrates, lack true glands in the oviducts according to Bloom and Fawcett's definition of glands.

As noted previously (Wake, 1970), the oviducal epithelium of females carrying small (less than 50 mm total length) fetuses is intact, and the 'glands,' which I shall refer to as secretory beds, are extensive. In females carrying larger fetuses, the epithelium is no longer present lining the lumen in areas around the fetuses, and capillaries and connective tissue comprise the luminal surface. However, the epithelium is intact well anterior and posterior to the fetuses. The secretory beds of the oviduct in the vicinity of the fetuses are elongate and deep. In the most dilated, thinnest-walled oviducts (of female *Gymnopsis* and *Typhlonectes* carrying several fetuses of over 100 mm total length), the secretory beds are several millimeters long. They are disposed parallel to the long axis of the duct, and are often only a single secretory cell layer deep.

These secretory beds are of particular significance in viviparous forms, for they secrete a nutritive substance that is ingested by the fetuses (Parker, 1936, 1956). The glandular secretion, or 'uterine milk,' was characterized by Parker as "a thick white creamy material consisting mainly of an emulsion of fat droplets, together with disorganized cellular material" when seen in the stomachs of freshly killed fetuses. Parker also states that many of the fetuses that he examined had full stomachs, containing (in preservation) "an amorphous non-cellular mass, but often containing a considerable amount of cellular debris and sometimes some recognizable erythrocytes." My observations on mouth and stomach contents of fetuses of several species corroborate his.

I suggest, then, that 1) the epithelium proliferates and becomes secretory at the time fetuses reach 25-50 mm in length and have nearly resorbed their yolk; 2) that the entire oviducal epithelium is potentially secretory; 3) that the connective tissue of the inner oviducal wall ramifies and nearly encloses beds of proliferated secretory epithelium; 4) that as oviducal dilation occurs and epithelium is stripped, the secretory beds remain intact so that sufficient nutrient substance is secreted to meet fetal nutritional requirements. Histochemical studies are in progress to determine the nature of the cellular changes, and to determine the components of the secretion.

Fetal development.—Information on numbers of fetuses in the oviducts of members of the seven known viviparous genera is scattered. Parker and Dunn (1964) report 2-7 in *Schistometopum thomense*, Barrio (1969) reports 6-10 in *Chthonerpeton indistinctum*; my own dissections show 1-9 in *Typhlonectes compressicauda*, 3-4 in *Geotrypetes seraphini*, 1-12 in *Dermophis mexicanus* and 2-8 in *Gymnopsis multiplicata*. Fetuses are usually disposed in nearly equal numbers in each of the two oviducts. In general, large (6 × 4 × 3 mm) yolky eggs are taken into the oviducts. Embryos are contained in the egg membrane until much of the yolk is resorbed, gills are developed, and coordinated movement is possible. The embryos emerge from the egg membrane at about 10-12 mm in *Gymnopsis* (my data), and 25 mm in *Geotrypetes* (Parker, 1956). The fetuses then uncoil and align themselves lengthwise, or with the posterior one third of the body curved toward the head. My dissections show that small fetuses are nearly equally spaced in the oviduct and that larger ones do overlap, but their heads are not in

close association. The embryos and fetuses of *Gymnopsis*, *Typhlonectes*, and *Dermophis* have gills during most of their oviducal existence. The gills of *Schistometopum* and *Geotrypetes* are resorbed shortly after emerging from the egg membrane (Parker and Dunn, 1964). All terrestrial species have a pair of triramous fimbriated gills; the aquatic typhlonectids have paired sac-like gills. Both forms of gills are supplied by three aortic vessels. There is some indirect evidence that gills may be used in gaseous exchange in association with the oviducal epithelium. Preserved *Gymnopsis* (Wake, 1967, 1969) and *Dermophis* fetuses frequently are found with one gill extending above the head and the other along the body and appressed to the oviduct wall. In *Typhlonectes* fetuses often have one sac-like gill extended above the head and one down cloaking the body. The gills are some two-thirds of the length of the fetus, and when the sac structure of the gill is flattened, it is a highly vascularized plate lining much of the circumference of the oviduct. The oviduct, too, is highly vascularized, so gaseous exchange is possible. This gill positioning occurred in 24 of 35 fetuses observed in six pregnant female *Typhlonectes*. This suggests that it is a common, perhaps efficient functional arrangement. Parker and Dunn (1964) suggest that cutaneous exchange may be important, especially for species whose gills are resorbed early. Gills are resorbed before birth in all forms.

The fetal dentition may be resorbed before birth, or shortly afterward. The adult dentition is usually acquired after birth, but may develop *in utero* (Parker, [1956] reported a 145 mm fetus of *Dermophis* that has an adult dentition, and *in utero* acquisition is possible in *Chthonerpeton* [Parker and Dunn, 1964]). According to Parker (1956) newborn *Geotrypetes* retain the fetal dentition, as do some *Gymnopsis multiplicata* (Taylor, 1955). Parker and Dunn (1964) note that small (126-161 mm) juveniles of *Caecilia tentaculata* and *C. subnigricans* have a fetal or mixed fetal-adult dentition. This is of significance for it is not known whether members of the genus are oviparous or live-bearers. Dunn (1942) states that *Caecilia* probably lays eggs (for reasons not mentioned other than the 1845 specimen). Gill slits are present in *Ichthyophis* larvae after hatching and gill resorption (Sarasin and Sarasin, 1887-90), but I have not seen open gill slits in any oviducal embryos. Tschudi (1845) reported a free-swimming 'larva' of *C. tentaculata* that had open gill slits, but no gills. It is difficult to determine just what Tschudi was looking at; it is possible that he observed the 'collar' annuli which are often incomplete. It is also possible that the species is viviparous, because of the presence of a fetal dentition. The presence of a fetal dentition in two species and the complete absence of any but adult-type teeth in all of the known oviparous species allow the inference that the genus *Caecilia* may include at least two viviparous species.

There is substantial variation in size of fetus at birth. Parker and Dunn (1964) report birth in *Geotrypetes* at 73-77 mm fetal total length; Heinroth (1915) records birth at 190-210 mm in *Typhlonectes compressicauda*. Based on Parker and Dunn's data, birth in *Dermophis mexicanus* occurs at approximately 150 mm, and Taylor's (1955) data and my information indicate that birth takes place at 110-130 mm in *Gymnopsis multiplicata*. There appears to be some gross correlation of fetal size with maternal size; adult *Geotrypetes* are from 235 to 400 mm, the majority of pregnant specimens from 270 to 320 mm; adult *Typhlonectes* from 250 to 625 mm, with most (75%) of the pregnant females that I have examined being 330 to 500 mm; mature *Gymnopsis* are 250-500 mm, with pregnant females of *Gymnopsis* of different sizes show little correlation of size of fetus with size of female within a species. A maximum fetal size (and state of development) of 110-130 mm was found in females of 283, 341, and 392 mm, so it would appear that fetuses reach that size before birth no matter what the size of the maternal female.

The demands upon the female for nutrition are very great. Yolk is resorbed in *Geotrypetes seraphini* at 25-40 mm (Parker, 1956); *Geotrypetes angeli*, 38 mm; *Schistometopum thomense*, 32-36 mm (Parker and Dunn, 1964); *Typhlonectes compressicauda*, 29-40 mm; and *Gymnopsis multiplicata*, 24-38 mm (the latter two species from my data). *Geotrypetes* young of 77 mm may be born of a 235 mm female (each fetus is 32% total length of the maternal female) (Parker and Dunn, 1964). One hundred twelve mm young of *Schistometopum* are 57% the length of the mother, 125 mm young may be born of a 250 mm *Gymnopsis* (50% maternal

length), and 200 mm *Typhlonectes* of 330 mm females (60% maternal length). All measurements are from museum specimens. These percentages may reflect extremes in which 'normal-sized' young are born of small females, and the percentages are reduced for larger females (for example, a 200 mm young born of a 500 mm *Typhlonectes* is 40% of the maternal total length), but these ratios are still significant. A female *Typhlonectes* may bear as many as nine young. The embryos resorb their yolk at approximately 30 mm; they are born at approximately 200 mm, having increased their lengths 6.6 times during the period of maternal nutrition. Nine fetuses, *each* increasing 6.6 times in size, and each 60% of the female's total length at birth, present great nutritional demands on the maternal female. My data do not indicate that females carrying large numbers of young have smaller young than females of the same size with fewer young, nor that females with large numbers of young give birth any earlier than females with fewer young. However, smaller females may have fewer young. My samples are small, however, and concrete data consisting of X-rays of females before birth to check fetal number and growth with records of live births or significant samples of preserved pregnant females are needed to adequately consider these aspects of reproductive biology.

The mode of fetal nutrition and its evolutionary significance.—Parker (1956) said that fetuses ingest the 'uterine milk' by mouth, but did not say how. He also stated that the fetal teeth of *Geotrypetes* were used *after* birth to scrape algae from rocks and leaves of the watery substrate where the animals were found. He suggested that the fetal teeth of *Geotrypetes* might function as a rasping organ during early post-partum life (1936, not 1956 as Taylor [1968] states). He has since (1956, and Parker and Dunn, 1964) steadfastly denied that the fetal dentition is functional at all. It is interesting that the general conception has been that the fetal teeth are used to scrape the oviducal wall (Goin and Goin, 1971; Porter, 1972; Salthe and Mecham, 1974; Taylor, 1968) even though Parker, the only modern worker who has examined the teeth, has denied their use in that manner. Some (Porter, 1972; Taylor, 1968) have attributed to Parker the conclusion that teeth were so used.

I propose to substantiate the conclusion that the fetal dentition is functional, and that it is used to obtain nutrition while fetuses are developing in the oviduct. Parker (1956) stated that the "special foetal dentition can scarcely be an adaptation for . . . a special foetal mode of nutrition." He stated that 1) the teeth are apparently unsuitable for the ingestion of milk, 2) that such an adaptation could not credibly have arisen more than once, and that if it has so arisen, all the viviparous species would be a close phyletic assemblage, which he pointed out they are not.

As to the assertion that the teeth are unsuitable for the ingestion of "milk," one must consider the mechanisms by which it is ingested. If milk were simply sucked into the mouth, or the fetus were passive as milk somehow flowed into its open mouth, teeth would not be necessary. However, I have found epithelial cells and smooth muscle fibers in 'uterine milk' in the mouth and gut embryos; I have reported the apparent stripping of the epithelium of the oviduct in the vicinity of the heads of larger fetuses (Wake, 1970). It appears that the teeth are used to scrape the oviduct lining, stimulating secretion of the 'milk' (as Salthe and Mecham [1974] also suggested), and helping to gather the milky secretion. The teeth also bite areas of the proliferated epithelium, probably effecting more secretion by irritating the secretory cells. The shapes and arrangements of teeth facilitate these actions (Wake, 1976). In addition, an out-group comparison with fetuses of *Salamandra* which use a similar method implies function. Further, Norris and Prescott (1959) concluded that the flexible jointed teeth in adult *Girella nigricans* are adapted for scraping. They postulate that such teeth are able to scrape a greater surface area of subtidal rocks to obtain algae.

Fetuses are prevented from eating through the dilated oviduct in several ways. The teeth are flexible and very tiny with a rather weak joint at the crown-pedicel junction (Wake, 1976). This suggests that they are used for holding tissue, not incising through it. The soft proliferated epithelial tissues could be torn if held by the teeth as the head is turned, but the tissue association in the oviduct seems to be one that allows epithelium to tear away from the connective tissue without serious damage. If the mouth were to open sufficiently widely to

place the teeth on the concave surface of the duct, the tension of the wall would cause it to maintain position so the mouth could not close on it in order to effect a bite. In addition, fetuses of many species begin resorption of teeth before birth, beginning with the outer rows, thus further lessening the possibility of biting the oviducal wall at the time of greatest duct dilation. Condition of the duct epithelium suggests that as the fetuses stimulate secretion by scraping, they also ingest areas of proliferated tissue as well as their secretions, then move in the oviduct to an adjacent, un-ingested area. Secretory cell proliferation continues in these adjacent areas, and in the secretory beds encased in connective tissue, so a supply of nutrient material is assured.

Parker's (1956) and Parker and Dunn's (1964) conclusions about the evolutionary history of fetal and adult dentitions can also be challenged.

Parker and Parker and Dunn's arguments about evolutionary relationships are based on the presence of polystichy (multiple rows of teeth) in fishes, in some extinct orders of reptiles and amphibians, and in certain extant salamander families. They note that polystichy is frequently restricted to palatal and pharyngeal bones, (ignoring the facts that those specimens are adults, and the teeth are functional in those specimens). They did point out that the extinct amphibians and reptiles are not known to change either tooth morphology or number of rows of teeth, again ignoring the implication of functionality. They cited examples from various salamander genera whose larvae lose patches of teeth at metamorphosis, but *do not replace* them at all as adults, and also cite instances in salamanders in which a mixed polystichous-monostichous (single-rowed) condition exists on particular elements. They note that a *change* to a totally monostichous condition as in adult caecilians is doubtful (their term) among most salamanders, but state that such a change does occur in *Salamandra atra* and *S. salamandra*. The adults of these species do, indeed, have a monostichous dentition following a polystichous one. Parker and Dunn failed to note that these are two of the exceedingly few species of salamanders known to be live bearers, and omitted the significance of that fact relative to the question of the function of the caecilian fetal dentition. In fact, it is well known that oviducal young of *Salamandra* ingest the oviducal wall, maternal red blood cells, and even their siblings (Amoroso, 1952)—probably using their polystichous dentition. Parker and Dunn point out that several salamanders shift from a monocuspid to a bicuspid tooth morphology at metamorphosis; this is indeed a shift, though not as radical a one as that in viviparous caecilians.

They explained the multiple-rowed fetal dentition in terms of Edmund's Zahreihen theory (1960), apparently accepting travelling stimuli as real. Their interpretation according to replacement theory of the acquisition of multiple rows is sound, for it merely involves retention of generations of replacement teeth. Further, their analysis of the acquisition of several cusps on the fetal teeth points out that this may merely involve elaboration of the two cusps of adults, which, as Kerr (1960) stated, are parallel crescent-shaped ridges. They consider that delay in replacement series to produce the polystichous fetal dentition, with acquisition by adults of a genetic restriction to monostichy, is a reasonable mechanism to explain the change, but that it does not account for change in tooth form and change in site and arrangement of teeth. Fetal tooth development and replacement are analyzed by Wake (1976).

Some of Parker's assumptions about caecilian phylogeny are faulty; for example, he stated that gills in American genera are single and plate-like, while the African forms have triaxial gills. Triaxial gills occur in all of the American forms except typhlonectids. It is true that viviparity is not evidence of close phylogenetic relationship, for it occurs in three of the four families of caecilians.

Parker contended that the fetal dentition is a primitive ancestral character retained as a result of *lack* of function. He concluded that free-living larvae and adults of all species, as predaceous carnivores, suppressed many-rowed, hinged, multicusped teeth in order to have more functional single rows of rigid teeth. He postulated an ancestral amphibian with many rows of hinged teeth on all of its dentigerous elements, and commented that previous workers considered a rasping dentition as 'ichthyic' and suggests that the dentition might be associated with a vegetarian diet. In that context, he considered caecilians the most primitive order of

amphibians. I believe that caecilians are derived amphibians. Among the characters that I consider derived is the fact that all caecilians apparently practice internal fertilization. This is a necessary precursor of viviparity, and a far greater number of caecilian species than of those of other amphibian orders are viviparous. Parker and Dunn are concerned that polystichy cannot have arisen more than once. It is generally conceded that oviparity is the primitive condition. Parker and Dunn do not seem concerned that viviparity must have arisen more than once, since it is only the derived viviparous forms that have the fetal dentition. Though at the time that Parker made his analysis all caecilians were included in a single family, he must have been aware that viviparity occurs in a mosaic of genera, and that these genera were not the ones considered primitive on the basis of other characters. Viviparity is now known to occur in three of the

TABLE 1. Viviparous species of caecilians.*

Family Caeciliidae
<i>Caecilia subnigricans</i>
<i>Caecilia tentaculata</i>
<i>Dermophis mexicanus</i>
<i>Caecilia oaxaca</i>
<i>Caecilia parviceps</i>
<i>Geotrypetes angeli</i>
<i>Geotrypetes seraphini</i>
<i>Gymnopsis multiplicata</i>
<i>Schistometopum thomense</i>
Family Scolecomorphidae
<i>Scolecormorphus uluguruensis</i>
Family Typhlonectidae
<i>Chthonerpeton indistinctum</i>
<i>Chthonerpeton viviparum</i>
<i>Nectocaecilia petersi</i>
<i>Nectocaecilia ladigesi</i>
<i>Typhlonectes compressicauda</i>
<i>Typhlonectes natans</i>
<i>Typhlonectes obesus</i>

*Oviducal embryos or newborns with fetal dentitions are known for these species. Additional species in the above and other genera are suspected to be viviparous.

four currently recognized caecilian families (Caeciliidae of both New and Old World, the New World Typhlonectidae, and the east African Scolecomorphidae). The Caeciliidae comprise both egg-laying and live-bearing species; several species of typhlonectids are known to be viviparous and none to be oviparous, and it is likely that all species of these aquatic genera are live-bearing. One species of *Scolecormorphus* of the monogeneric Scolecomorphidae is known to be viviparous, and nothing is known of other species in the genus. Table 1 lists the known viviparous species of caecilians. It is possible that a single caeciliid stock gave rise to viviparous caeciliids in Central and South America and East and West Africa and that the typhlonectids and scolecomorphids were subsequently separately derived from viviparous forms in South America and east Africa, respectively. There are no dates to support times of derivation of these stocks, nor any information about their reproductive states in evolutionary time. However, one need not argue so conservative an origin, for viviparity is thought to evolve as fertilized eggs are retained in the oviducts for periods of time, and any mechanism for maternal nutrition is present. No one argues that viviparity in teleost fishes or in reptiles arose only once, and there is substantial evidence for its multiple origin in these groups.

Another point that Parker clearly appreciated, but ignored in his evaluation of the evolution and function of the fetal dentition, is that of the distinct differences in morphology of the fetal dentition among species. Not only are they very different from the adult-type developing teeth of embryos of egg-laying species, but there are real differences among viviparous species. These differences are discussed in detail by Wake (1976). Parker does not account for those differences at all. I suggest that the most plausible explanation for those differences in external tooth structure among fetal dentitions is that selection has produced an effective dentition in each species. This is not to say that the dentition arose *de novo* in related species. As an adaptive radiation of caecilian species took (and takes) place, selective factors influencing the fetal dentition, as well as other characters, operated according to the discrete species substrate available, resulting in species-specific modifications of the dental pattern in fetuses. The tooth morphology of fetuses in each viviparous species is well adapted for use as a scraping device. If the fetal teeth are of adaptive significance, as implied by the production of morphological change through evolution, they likely are functional. Several pieces of evidence, especially the distinctive morphology and arrangement of the fetal teeth and the presence of

maternal cells in the gut of the fetus, cause me to conclude that the fetal dentition is functional, and used to stimulate secretory cells of the oviducal epithelium, and to gather and ingest the 'uterine milk' and components of the oviducal wall. This is a highly derived mode of viviparity, seen among vertebrates in some elasmobranchs, in live-bearing caecilians, and two species of salamanders. While placentation is not involved, maternal nutrition of oviducal young occurs, and gaseous exchange across fetal skin and gills to oviducal capillaries may also take place. I conclude that viviparity, and with it the fetal dentition, has arisen in caecilians following the retention of developing eggs by members of several lineages.

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