

Evolution of viviparity in the genus *Ophryotrocha* (Polychaeta, Dorvilleidae)

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ABSTRACT

Brooding is a common feature in the genus *Ophryotrocha*. Viviparity, the most extreme type of parental care, is represented by only one species, *O. vivipara*, but tendencies towards viviparity have also been reported from gonochoric as well as hermaphroditic species. Except for the viviparous species, all species studied deposit their eggs in a gelatinous matrix. The surface of the egg mass may remain soft and sticky, but in two distinct species groups the surface hardens to a solid membrane that encloses gel and eggs. In both groups newly spawned egg masses may occasionally contain a few young larvae. Such larvae never occur in a young female's first egg mass. The larvae are interpreted as originating from fertilized eggs that have been trapped in the coelom of the female during a previous spawning. They develop inside the female at a retarded rate.

In *O. socialis* not only larvae at an early stage of development are released but also larvae/juveniles at more advanced stages. Usually they are released together with a normal spawn, but they may also appear single. Juveniles with up to 12 setigerous segments have been observed. During the normal course of development, the 12-setiger stage is attained after about 80 days. At that age they have already developing oocytes in the coelom whereas the viviparous progeny with the same number of segments have not.

Observations of incipient viviparity in three species groups call for a reevaluation of some previous reports on self-fertilization and on viable larvae obtained in crosses between species that are otherwise reproductively isolated.

RÉSUMÉ

Évolution de la viviparité dans le genre *Ophryotrocha* (Polychaeta, Dorvilleidae)

C'est un trait fréquent du genre *Ophryotrocha* d'incuber ses oeufs. La viviparité, le type le plus extrême du soin parental, est représentée chez une espèce, *O. vivipara*, mais des tendances vers la viviparité ont aussi été rapportées chez des espèces gonochoriques aussi bien que chez des espèces hermaphrodites. Exception faite des espèces vivipares, toutes les espèces étudiées déposent leurs oeufs dans une matrice gélatineuse. La surface de la masse d'oeufs peut rester molle et collante, mais dans deux groupes d'espèces distincts, cette surface durcit en une membrane solide qui renferme le gel et les oeufs. Dans les deux groupes, des masses d'oeufs récemment déposées peuvent contenir, de temps en temps, quelques rares larves/juveniles. De telles larves n'apparaissent jamais dans la première masse d'oeufs d'une jeune femelle. Les larves proviennent probablement d'oeufs fécondés antérieurement qui sont restés dans le coelome de la femelle où ils se sont développés lentement.

Chez *O. socialis* des individus larve/juvenile, à un stade avancé sont relâchés en même temps que des larves en début de développement. Habituellement elles sont émises en même temps qu'une ponte normale, mais elles peuvent aussi apparaître

seules. De tels juvéniles ayant jusqu'à 12 segments sétigères ont été observés. Au cours d'un développement normal ce stade 12 sétigères n'est atteint qu'après environ 80 jours. Ces larves/juvéniles ont alors déjà développé des ovocytes dans le coelome tandis qu'il n'y a pas d'ovocytes dans les juvéniles issus d'un développement vivipare au même stade de développement. Les observations faites sur cette tendance à la viviparité dans les 3 groupes d'espèces nous conduisent à une révision des résultats antérieurs traitant de l'autofécondation et aussi des larves viables qui en réalité n'ont pas été obtenues dans des croisements entre espèces différentes.

INTRODUCTION

Brood protection has evolved many times among both invertebrates and vertebrates (HOGARTH, 1976; CLUTTON-BROCK, 1991). The same applies also to viviparity, the most extreme form of brood protection. Evidence from most groups indicates that viviparity has evolved from oviparous ancestors and that internal fertilization has been a preadaptation for the evolution of viviparity. In transition stages fertilized eggs have been retained for progressively longer periods of time. They do not receive any nutrients from the female and this holds true also for species with ovoviviparity, the least advanced form of viviparity. In more advanced viviparous forms, the female continues to provide the embryos with nutrients. Often a kind of placenta analogue develops or the embryo/larva receives nutrients from surrounding body fluids of the female.

For the evolution of viviparity from oviparous ancestors to occur, transition stages must also be selected. The continuing discussion has been widened to involve other aspects of brood protection and its relation to egg size. SHINE (1978) suggested the "safe harbor" hypothesis according to which optimal offspring size is determined by relative mortality rates of egg stages and free-living juveniles. Selective forces tend to maximize the time spent in the safest stages of development. In brooders eggs are safer than juveniles which should account for the positive correlation often seen between brood protection and large egg size (SHINE, 1989; CLUTTON-BROCK, 1991).

According to HOGARTH (1976), evolution towards viviparity is favoured in species that already produce a restricted number of eggs. Retention and viviparity protect the progeny against both predators and harsh environmental conditions such as cold climate, desiccation or, for marine animals, suboptimal salinity levels.

Viviparity has been reported from several polychaete families and SCHROEDER & HERMANS (1975) have listed 19 species. However, for 9 of these the original reports on viviparity have not been verified in later studies. Many older reports on viviparity were analyzed by SMITH (1950) who provided evidence that some of them were erroneous. Some embryos or larvae from inside the body of polychaetes were either developmental stages of parasitic polychaetes or turbellarians.

The purpose of this paper is to describe a possible line of evolution towards viviparity in the genus *Ophryotrocha* of the family Dorvilleidae. Dorvilleid polychaetes are generally small and many of the smallest, nonparasitic species belong to the genus *Ophryotrocha*. Only three species exceed a length of 10 mm. Two of these are commensals in the gill chamber of crabs (MARTIN *et al.*, 1991), the third one is found near geothermal vents (BLAKE, 1985). The smallest of all *Ophryotrocha* species, *O. vivipara* Barse, 1963, is only 0.8-1 mm long. BANSE's description was based on two specimens from the vicinity of Friday Harbor, Washington. This was the only record until I collected about 50 specimens in the aquarium of the Tjärnö marinbiologiska laboratorium located about 200 km north of Gothenburg. *Ophryotrocha vivipara* is one of the few species that I have failed to maintain as a laboratory culture; nonetheless BANSE's observation of a truly viviparous species could be confirmed. The juveniles have two or three setigerous segments when released from the posterior end of the female. In contrast to a uniform adult morphology in most species, reproduction is remarkably variable. In addition to the traits listed in Table 1, species or species groups may also vary in other reproductive adaptations such as clutch size and time between consecutive spawnings, sex ratio in gonochoric species and amount of energy allocated to individual eggs (ÅKESSON, 1973).

Mating behaviour is equally variable. SELLA (1985, 1988) analyzed pair formation and egg trading in the simultaneous hermaphrodite *O. diadema*. A behaviour has evolved that safeguards against non-reciprocating partners. In gonochoric species, females often discriminate against males from other geographic populations and they certainly do so in interspecific crosses (ÅKESSON, 1972a, 1977b, 1978, 1984). In the protandrous hermaphrodite *O. puerilis*, sex reversal may occur several times in the same individual. In pair cultures with females, the result of fights over sex will be that the winner remains female and the loser changes to male. BERGLUND (1991) has shown that females prefer small males. If a female mates with a large male, she is at risk of being challenged to change sex when she is weakened after spawning.

TABLE 1. — Reproductive traits in the genus *Ophryotrocha*.

	KEY REFERENCES
Germ cells are not shed freely into the water. Pseudocopulation ensures fertilization	REMANE, 1952; SWEDMARK, 1964
No pelagic larvae (but demersal, lecithotrophic larvae in <i>O. maculata</i>)	ÅKESSON, 1973
Short generation length	
Semicontinuous reproduction	ÅKESSON, 1982, 1984
Gonochoric species: (A) with sexual dimorphism, (B) with 'inducible hermaphroditism', (C) with facultative hermaphroditism and self fertilization, (D) with environmental sex determination	(A) ÅKESSON, 1972b; ZAVARZINA & TZETLIN, 1986, 1991; OUG, 1990. (B) BACCI <i>et al.</i> , 1979, (C) PARENTI, 1960; ÅKESSON, 1984. (D) ROLANDO, 1982, 1984; SELLA & RAMELLA, pers. com.
Uneven allocation to male and female function in simultaneous hermaphrodites	SELLA, 1990; OCKELMANN & ÅKESSON, 1989
Egg trading	SELLA, 1985, 1988
Both sequential and simultaneous hermaphrodites; in one species age (size)-related change from hermaphrodite to female	ÅKESSON, 1984; PARENTI, 1964
Cross fertilization the rule, but selfing possible in some hermaphrodites	PARENTI, 1960; ÅKESSON, 1984; OCKELMANN & ÅKESSON, 1989
Brooding of (A) large gelatinous egg masses with sticky surface, (B) egg masses with hard surface, (C) egg masses deposited in tubes made by the parents	ÅKESSON, 1984; OUG, 1990
Incipient viviparity in two species groups, viviparity in one species	BANSE, 1963; this paper

Incipient viviparity has been reported from the simultaneous hermaphrodite *O. diadema* (ÅKESSON, 1973, 1976). Occasionally one or two larvae appear in newly spawned egg masses, but never in a female's first brood. The fusiform egg masses of *O. diadema* are surrounded by a tough wall and larvae cannot enter an egg mass from the outside.

As in all other known *Ophryotrocha* species, fertilization in *O. diadema* is preceded by a kind of pseudocopulation similar to that described by Westheide from *O. gracilis* (WESTHEIDE, 1984, fig. 3). Selfing has not been observed. Eggs and spermatozoa are shed into a gelatinous matrix and mingle there. The egg mass is molded to its final shape and usually attached to a substratum. Then the surface of the mucus hardens to form the tough outer wall.

The explanation suggested for the presence of larvae in newly spawned egg masses is that a few eggs have been trapped in the female part of the coelom during a previous spawning. They have been fertilized by entering spermatozoa, developed inside the body, and then released together with the next spawn (ÅKESSON, 1976).

The same type of incipient viviparity as in *O. diadema* has also been observed in several members of the labronica group, a group of related gonochoric species within the genus (ÅKESSON, 1973). Members of that group produce a different kind of egg mass that is tube-shaped and contains smaller, but more numerous eggs than that of *O. diadema*. Enclosed larvae inside newly spawned egg masses have been observed in *O. labronica*, *O. notoglandulata*, and *O. macrovifera*, and they may occur in all members of the labronica group.

Ophryotrocha socialis, another simultaneous hermaphrodite, was recently described by OCKELMANN & ÅKESSON (1989). The gelatinous matrix around the eggs is sparse in this species but there is enough to attach the eggs to each other forming tubular or irregular egg masses. As in *O. diadema* fertilization takes place after pseudocopulation. Isolated individuals may self-fertilize but such self-fertilization is external.

In a still ongoing life table study that began with fertilized eggs, 0-setiger larvae occasionally appeared in the bowls when the experiment had continued for about 6 months. The larvae were at the stage of development that is normally obtained in 3 weeks (OCKELMANN & ÅKESSON, 1989, Fig. 10). Since the adult worms were transferred to clean bowls once a week, these larvae could not be the result of a previous spawn. Eventually more advanced larvae could also be collected, i.e., larvae with 1-2 or more setigerous segments. The peak production of such larvae was observed when the adults were 10 months old and had 19-20 setigerous segments. In one week 40 adults had produced 11 0-setiger larvae

and 17 juveniles with 7-12 setigers (mean 9.9 ± 0.4). In addition, the adults had spawned 919 eggs during the same week.

After a normal spawning, the progeny develops into functional males with 6 setigers after about 50 days. The first spawning was observed at an age of 60 days in worms with 10 setigers. Only few worms spawn before the 11-setiger stage (OCKELMANN & ÅKESSON, 1989). Not even the largest viviparous progeny had any visible oocytes in the coelom. They were more slender than larvae with the same number of setigers that develop after normal spawning. It has not been possible to determine the age of the viviparous progeny when released from the coelom.

REEVALUATION OF SOME PREVIOUS REPORTS

The observations of incipient viviparity in two species groups as well as mixed oviparity and viviparity in *O. socialis* may justify a reevaluation of some previous reports on self-fertilization and on results of crossing experiments.

HARTMANN (1943) and BACCI (1978) reported on rare instances of self-fertilization in *O. puerilis*. In some crosses between the Atlantic and Mediterranean subspecies of *O. puerilis*, a very low percentage of spawned eggs were reported to develop into viable larvae (ÅKESSON, 1973). The possibility should be considered that these reports concern incipient viviparity of the same kind as in *O. diadema* and the labronica group. However, it is evident that some species may reproduce by both cross-fertilization and self-fertilization. This is true of *O. labronica* (but note the discussion about identity of species in ÅKESSON, 1984), *O. socialis*, and a not yet described species from Florida (LA GRECA & BACCI, 1962; PARENTI, 1960; ZUNARELLI, 1962; ZUNARELLI-VANDINI, 1967; ÅKESSON, 1984; OCKELMANN & ÅKESSON, 1989).

In the light of these findings, the previous report on partial success in crosses between the Pacific species *O. notoglandulata* and *O. labronica pacifica* should be reevaluated. ÅKESSON (1984) reported that occasionally a few (< 10) viable hybrids were obtained in crosses between female *O. notoglandulata* and male *O. l. pacifica*. These supposed hybrids were all female and therefore F₂ hybrid breakdown could not be tested. No progeny was obtained in backcross with *O. l. labronica* males except for a few larvae. As in the first cross, the number of larvae per egg mass was always below 10. In backcross with *O. notoglandulata* many egg masses were produced, usually with almost 100 % development.

A return to the original data sheets revealed that in the interspecific cross only 5 "hybrids" developed into normal, mature females. They were first used in backcross with male *O. notoglandulata* and then with *O. l. labronica*. Previous and subsequent crosses between *O. labronica* (both subspecies) and *O. notoglandulata* proved to be intersterile. More than 100 egg masses in each reciprocal cross have been observed. Moreover, the "hybrid" progeny reported by ÅKESSON (1984) was all female. The same was true of all viviparous progeny observed so far in the three gonochoric species where incipient viviparity has been recorded. A very likely explanation of the crossing results (ÅKESSON, 1984) is that the few larvae obtained were an expression of incipient viviparity.

In recent experiments with both inter- and intraspecific crosses, individual egg masses have been analyzed for enclosed larvae. Such larvae are found in less than 5 % of the egg masses and only in egg masses produced by females that have spawned previously. The fact that such larvae were produced in two subsequent generations in the crosses reported by ÅKESSON (1984) may indicate a heritability of the trait, but recent selection experiments with viviparous progeny has not yet proved this.

DISCUSSION

For the evolution of viviparity in the genus *Ophryotrocha*, transition stages between oviparity and viviparity should have a selective advantage. One such advantage may be that those embryos that are retained in the female's body have better chances of survival than the siblings which are fertilized and spawned at the same time. A brooding worm presumably has better chance of escaping a predator than embryos enclosed in an immobile egg mass that the female will desert when attacked.

Internal fertilization as a prerequisite for viviparity is not fulfilled in *Ophryotrocha*, but functionally the kind of pseudocopulation found in the genus comes close to internal fertilization (WESTHEIDE, 1984). The final stage, obligate viviparity, is found in the smallest known *Ophryotrocha* species only. This may be an indication that the evolution of viviparity is one of many adaptations to 'the problem of being small'. As has been repeatedly discussed for meiofauna species (SWEDMARK, 1964; WESTHEIDE, 1984), smaller size is correlated with changes in

reproductive traits compared to related larger species. WESTHEIDE (1987) demonstrated how progenetic (neotenic) evolution has been one of the major forces behind adaptation to the interstitial habitat. The morphology of an adult *Ophryotrocha* is very similar to the larval morphology of larger eunicid polychaetes, e.g., to the larvae of *Dorvillea rudolphi* (RICHARDS, 1967). The evolution of progenesis is also demonstrated in WESTHEIDE's (1987) series of increasingly juvenile characters in dorvilleid genera where the endpoint is the dinophilid genus *Dinophilus*. It has been shown that dinophilids are closely related to eunicids (HERMANS, 1969; ÅKESSON, 1977a; WESTHEIDE, 1985).

Reproduction in the genus *Ophryotrocha* is more variable than in any other polychaete taxon of similar size. Energetic constraints related to small size may be one reason; opportunistic life histories with often sparse populations may be another. The most important of those reproductive traits are listed in Table 1.

WESTHEIDE's (1987) series of successive embryonization in the family Dorvilleidae indicates that small species have evolved from larger ones. ---"these small interstitial species must then form the end-point of an evolutionary line which originates in larger benthic species" (WESTHEIDE, 1984, p 266). For the genus *Ophryotrocha* it has also been suggested that the atrochal, demersal larvae found in *O. maculata* occurred in the larger ancestors (ZAVARZINA & TZETLIN, 1991). Obviously the progenetic evolution has been very successful and has triggered an adaptive radiation.

The egg diameter varies between 240-320 µm in *O. cosmetandra* (OUG, 1990) and 56.5 µm in *O. paralabidon* (HILBIG & BLAKE, 1991). At the end of the brooding period, the progeny of some species is released as polytrochous larvae with no setigerous segments, whereas other species release juveniles with up to 5 setigers. In *O. vivipara* the progeny has only 2-3 setigers when released, but the largest recorded viviparous progeny of *O. socialis* had 12 setigers.

In summary, the variability in reproductive traits in the genus *Ophryotrocha* makes it an extremely valuable study material, a kind of marine *Drosophila*. "This genus may be very important for sex allocation studies, since it contains all three of the basic forms of sexuality found in animals" (CHARNOV, 1982, p 201).

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