INVERTEBRATE REPRODUCTION

K.K. NAYAR
University of Kerala
Karyavattam, India

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Preface

This book has been written to bring together an account of the biology of reproduction in invertebrates. Protozoa and some of the smaller groups of invertebrates have been omitted in this survey. The different problems of reproduction have been dealt with by several authors, but those accounts have been presented from the topic of their interest like taxonomy, embryology, entomology or endocrinology and lie scattered in various journals and monographs. In this book the biological aspects of the methods of reproduction have been presented and I believe that this is the first attempt to present it in such a way. A general background in invertebrate biology is expected of the person using this volume. The account is given as an introduction to the study of invertebrate reproduction which may prove useful to the postgraduate and research students especially of Asian countries.

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Karyavattam, India K.K. NAYAR

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1. Introduction

THE phenomenon of producing young ones is the subject matter of reproduction. In invertebrates, reproduction occurs by sexual or asexual means. Various methods are employed in both. Production of buds, fragments or special bodies like statoblasts comprise asexual methods. In addition, parthenogenesis or reproduction without meiosis and fertilisation (ameiotic), and production of multiple embryos from the same zygote (Polyembryony) are also observed in the asexual reproduction of several invertebrates. Fission also is not unknown.

The sexual method is by far the most extensive method in reproduction. Here, the germ cells that bring about the production of the zygote and the future young, are products of meiosis and this facilitates a means of genetic recombination. Parthenogenesis also is a means of sexual reproduction. Especially in those large number of instances in invertebrates which exhibit ameiotic diploid, and haploid parthenogenesis, occur modifications in egg production; these also are therefore described along with sexual methods.

The gametes are the final products of the two sexes, male and female. The male gamete is the sperm and the female one is the ovum. Their union brings about the formation of a zygote. This single cell gives rise to the next generation individual by its development. The production of gametes is by gametogenesis. The process of gametogenesis involves mobilization of nourishment, multiplication and differentiation of cells, gamete accumulation and discharge. Gametogenesis occurs in the well defined reproductive system of Bilateria. The system comprises the sex glands called gonads, their ducts (gono or genital) and various accessory organs. The male gonad is the testis, and the ovary is that of the female. Usually they occur in separate individuals or sexes, when it is described as dioeciousness or gonochorism. When the two gonads occur in the same individual, the animal is called a hermaphrodite. In such cases,

very often the testis becomes functional first (protandry). Rarely the ovary becomes active first (protogyny). Neoteny is the condition where the gonads become functional in the larval or the juvenile period of the animal's life.

The gonads arise from the mesoderm. Mesenchyme cells or cells lining the epithelium of the coelom have been claimed to give rise to the gonad. Some evidence for this view has been adduced in the starfish *Asterias*. In a large number of animals sex cells have been traced early to form a gonad which gets connected to the coelom. This has been specially investigated in forms which show determinate cleavage. In many arthropods this development has not been confirmed, but in nematodes this has been followed up from early cleavage stages (Boveri, 1899) and in *Sagitta* as early as in the blastomere stage (Eplatevskii, 1910 cited in Beklemishev, 1969).

In many invertebrates reproduction occurs in a breeding season. It is at this time that the gametes which are mature are liberated. When the release of the gametes occurs in the surrounding water, the condition is described as spawning. The fertilised eggs in many examples grow into the young without any period of arrestation of development. In other cases the zygotes will be retained within folds or parts of the body; this condition of brooding is widespread in several instances like *Lamellidens*, *Balanus* etc. Certain forms retain the eggs in specific parts and even nourish the embryos which develop, this being called viviparity.

Sperms are released into the genital tract or other parts of the body (this latter being so in cephalopods) during mating or copulation.

The zygote develops into the embryo, which hatches out as a free-living form called the larva, or miniature adult called the juvenile. The larva may have several morphs during the larval life; and in many examples there will be a prolonged period of free existence.

Various endogenous and exogenous factors operate in the phenomenon of reproduction, which will be dealt with in subsequent chapters.

A brief survey of the reproductive system is given below.

THE MALE REPRODUCTIVE SYSTEM

The testis is the male gonad. It is built up of tubules or vesicles and spermatozoa develop within them. A spermatic duct or vas

deferens arises from the testis. The testis occurs as single, paired (plural, testes) or multiple organs, and the vasa deferentia are mostly paired. They lead to the formation of a short, common duct which wholly or terminally passes through the copulatory organ, where it is differentiated as the ejaculatory duct. Mature sperms will be retained in a pouch or sac or dilated portion of the duct itself, which forms the seminal vesicle. The duct terminates at the genital pore. The pore most often lies at the tip of the copulatory organ called the cirrus or penis. The penis is muscular and protrusible. A smaller, protrusible, temporary projection of the ejaculatory duct is the region which is described as a cirrus. The penial region is often glandular. The entire set of organs which comprise the mating structures, which in certain cases are rather complex as in Pulmonata, is generally designated as the copulatory apparatus.

Variations in the organisation of the reproductive system are seen in the different groups of invertebrates and even in the different genera of the same group. A survey of the system in the different groups is given below, as adapted from Hyman (Hyman, 1940, 1951, 1955, 1959).

Platyhelminthes

Only two forms of Turbellaria show separate sexes. Both are marine triclads, *Sabussowia dioica* and *Cercyra teissieri*. The other turbellarians are hermaphroditic. Trematodes are also hermaphroditic except Didymozoonidae and Schistosomidae which have the sexes separate. This gonochorism has been attributed to the loss of organs of one sex. The animal assumes the characteristic shape of the sex corresponding to the gonad retained, and sexual dimorphism becomes manifested. *Wedlia* is an example showing a well defined separation of the two sexes; the female is large and rounded and the hind end of the smaller male gets lodged in a depressed region of the female. The male has paired testes at the hind end of its body which is lodged in the depression on the female. The large female has a single, large ovary, which is coiled and built up of tubular glands (yolk glands), seminal receptacles and uterus along the course of the duct.

The blood flukes (Schistosomatidae) occurring in vertebrates have the sexes separate with no part of the other represented in the body of one sex. The generally broader male has on its ventral surface a shallow groove—gynaecophoral canal—within which the female

is permanently housed. The male shows a number of globose testes and a genital duct which leads to the outside posterior to the acetabulum. The duct has a seminal vesicle associated with it. Cestodes are hermaphroditic with the exception of *Dioecocestus*, which shows sexual separation or dimorphism, the male being shorter and more slender than the female. The male has the proglottides which are slender, each provided with a pair of testes, the ducts opening laterally and the terminal regions traversed by cirri.

Rhynchocoela

Among the Rhynchocoela the sexes are separate except in some genera of Hoplonemertini (e.g. *Geonemertes*, protandric hermaphrodite *Prostoma*). Gonads are rounded, paired, scattered bodies. The testes lie in the anterior part of the body. Sexually mature animals often exhibit colour differences due to the colour differences of the cells of the gonads which could be seen through the body-wall. The ovary is situated behind the level of the testes. The gonad leads into a gonoduct as the animal becomes mature, and laterally opens out through the genital pore; however, the position of this pore is variable being dorsal, ventral or dorsolateral. The male pore is on a papilla in the male in a few examples like *Phallonemertes.*

Acanthocephala

The males have elongated or round testes lying in the ligament sac supported by its strands. Each leads to a sperm duct, which is compartmentalised into a sperm vesicle and a duct. Unicellular, rounded or vesicle-like cement glands, numbering six to eight with individual ducts, enter the sperm ducts. *Eoacanthocephala* have these cement glands syncytial. It shows a duct with a reservoir from which a connection to the genital duct is formed. A muscular tube called the genital sheath encloses the sperm duct and the cement duct, leading on to a bursa. The bursa is eversible and capped and works by fluid pressure from a sac called the Saefftigen's pouch (Yamaguti, 1935). The bursa contains a grasping penis which is eversible and used to hold the female during mating.

Aschelminthes

Rotifers exhibit marked sexual dimorphism, the females being larger. Bdelloidea have no males. Large, single, saccular testis has

a ciliated sperm duct running to the genital pore. Paired "prostate glands" also are present. The terminal wall of the duct bears an eversible cirrus. In Seisonacea, however, testes are paired, and the genital ducts form a syncytium, traversed by ciliated swellings within which spermotophores are bundled. No specialised copulatory organ is seen in them.

The male system is degenerate in the chaetonotid Gastrotricha, except in *Xenotrichula*. In the others, the male system has paired testes and ducts which terminate at the male genital pore on a small penis. When only one testis is present, it represents that of the right side. Kinorhyncha have the female and male as separate individuals but they are not externally distinguishable. Testes are paired and the ducts terminate at the genital pore; there are penial spines or spicules. In Priapulida, a pair of urinogenital organs is present in both sexes. Each gonad is tubular, forming a network, on one side of which lie the excretory solenocytes. The urinogenital canals spring from these and lead out by separate pores at the hind end.

Nematodes possess separate sexes. The testis is single, long and convoluted, nearly filling up the body; it may occur as paired organs as in *Heterodera*—these represent the monorchic and diorchic conditions respectively. The testis is followed by a vas deferens which distends into a seminal vesicle. It runs on as the ejaculatory duct and terminates close to the anus. The ejaculatory duct receives openings of the duct from a number of prostate glands. Lodged in special pouches of the cloaca are a number of copulatory spicules of various sizes and shapes. The cloaca is muscular. An accessory piece called the gubernaculum and sometimes an additional telamon, guide the spicules in copulatory moves; these lie within the cloaca. The spicules are sclerotised and curved, and show variations of taxonomic value. The hind end of the body of the male has special muscles which are useful in manipulating the spicules in copulation. In Trichuroid nematodes, the cloaca is long and lined with spines forming an eversible cirrus, which may coexist with spicules also. In Nematomorpha the organisation of the reproductive system is poorly known. The parasitic juveniles have been examined by Feyel (1936); in *Nectonema* the male has a single testis with a duct that leads to the genital opening, while in Gordioids paired pores are represented. In the Gordioids the terminal end of the body is lobed and armed with bristles.

Entoprocta

Loxosomatid Entoprocta are apparently dioecious as also are Pedicellinids. Gonads are paired sacs; the sperm ducts unite, and with a seminal vesicle the duct ends at the genital pore. The single genital opening lies close to the nephridiopore, on a specialised patch. In *Urnatella* one species has been reported to be with sexes separate.

Lophophorate phyla

Phoronida and Ectoprocta show hermaphroditism though some cases of dioecious organisation have been cited in literature. In the colonial Gymnolaemata the "gonochorism" could be considered as instances of protandry (*Alcyonidium duplex*) or different sexes may be represented by different zooids as in Cheilostomes. Germ cells are packed to form the gonads and genital ducts are wanting. In Brachiopods, the sexes are separate except in *Argyrotheca*. Four lobes, each multilobed, form the gonads. The gametes are discharged into the coelom and get out of the body through the nephridiopores. Here also the genoducts are absent.

Sipunculida

The sexes of Sipunculids are separate. The testes are clusters of cells on the coelomic wall of the retractor muscles, and the genital ducts are not developed. The germ cells are released from the gonads at an immature stage and while in the coelom they grow into the sperms over a period of several months. Nephridia function as genital ducts. How the cells get into nephrostome is not known. Sperms themselves become active only on discharge into the sea water in examples like *Golfingia* and the cloud of sperms stimulates the ejection of eggs from the females (Gerould, 1906).

Echinodermata

With some exceptions represented in all classes of the phylum, all other echinoderms have the two sexes separate. Masses of sex cells around the coelomic ephithelium in the form of a double structure composed of cortical envelope and a medullary axis or rachis (genital cord) form the gonads. They lie in the arms or in the genital pinnules, as in the crinoids. The sperms escape by the rupture of the wall of the pinnule. Most holothuroids are dioecious, but *Cucumaria laevigata, Mesothuria intestinalis* and some synaptids are hermaphroditic. The gonad is single, lying interradially (CD)

and anteriorly and leads on to the genital pore at or on the madreporite. The gonad here is not a mere collection of cells but is branched and tubular. The duct leads on to the opening close to a small cirrus. Asteroids also have the sexes separate but sometimes dioecious species may exhibit hermaphroditism as in *Asterias rubens*, *Asterina batheri* etc. A pair of saccular, lobular gonads are present in each arm and the gonad narrows into a gonoduct proximally, opening out through the genital pore. Sometimes as in *Leptychaster*, the testes show paired genital pores in a serial manner in each arm. Echinoids have five gonads generally fused and suspended by strands of mesentery from the interambulacra. Mounted on small papillae, are short ducts which open to the outside. Ophiuroids exhibit separate sexes: the testes are loose sacs with germ cells within; some ophiuroids are hermaphroditic. The number of gonads is highly variable: in *Gorgonocephalus* several thousands of sacs build up the testes. Four species exhibit very tiny males—in *Amphilycus androphorus* the small male clings on to the oral end of the female with the arms alternating; in *Ophiosphaera insignis* and *Ophiodaphne materna* the dwarf males and the females cling mouth to mouth and in *Astrochlamys bruneus* the small male sits astride the large female on her aboral side.

Mollusca

Separate sexes are seen only in Chaetodermatidae among Solenogastres. Single or paired, dorsal testes with lateral diverticula, a slender gonopericardial canal from each testis with seminal vesicular swellings, and a common duct opening to the exterior form the male reproductive system. Except *Trachydermon*, Polyplacophora are all dioecious. A sex dimorphism is sometimes distinct: in *Cryptoconchus porosus* the male has an orange coloured mantle and the female has it coloured olive green. The lobed testis lies anterior and dorsal to the pericardium from which emerge paired gonoducts opening laterally in the pallial groove. A coloured, so called seminal vesicle (not known whether sperm storage occurs) lies in association with each duct. *Neopilina* of the Monoplacophora, is dioecious, with two pairs of lobed testes lying ventral to the intestine and their short ducts open into the second and third pairs of nephridia.

The reproductive system of gastropods show a wide variety of differences in organisation. Many prosobranchs show separate sexes, and opisthobranchs and Pulmonates hermaphroditism. Sexual diffe-

rences in prosobranchs may be manifested by the differences in sizes of the shell (larger shells in females) or variations in the copulatory organs. In Viviparidae, the right tentacle is a sexual tentacle, fused with the penis. The testis is single often embedded in the visceral mass, but differently coloured. The simple condition of the male genital duct is seen in some prosobranchs where it runs as a canal to near the anus. In many forms, however, the genital duct leaving the testis becomes distended and convoluted to form seminal vesicles, into which region opens the prostatic gland also. The genital duct narrows terminally and proceeds to the base of the muscular penis after traversing the floor of the mantle as a tube or a ciliated groove. The penis (verge) is on the right side of the head or the neck in Monotocardia, the tubular genital duct runs through it, and may extend beyond as a terminal filament. In the Viviparidae the right tentacle acts as a penis. Special glands may be associated with the penis as in Littorinidae. An accessory copulatory organ may also be present, which may be provided with its own set of accessory glands as in *Bythinella*. In Heteropods this has a role as a hold fast organ. In Turritellidae, Janthinidae and some other groups a penis is wanting.

A peculiar condition of the sexes has been reported in *Crepidula* and other Calyptraeidae. Males are smaller and a piling up of settling animals of *Crepidula* occurs in such a way that the lower and larger forms are females, upper smaller ones are males and the intermediate ones show phases of transformation to females from above downwards in the pile. The males lie in the piled up mass in such a way that the penis could be inserted into the gonopore of the female below. Sex reversals of other prosobranchs are also known. Scaphopoda have the sexes separate. Extending up to the hind end of the animal is an elongated testis. From its anterior region arises the genital duct which gets connected to the right nephridium.

Bivalves are mostly dioecious with the males possessing paired testes with short genital ducts joining the nephridia on each side. In eulamellibranchs and filibranchs, the genital ducts have no relation to the nephridia and the gonopore is a separate opening near the nephridiopore. The pore is carried on a papilla in forms like *Mercenaria*.

Cephalopods have the sexes separate and the males are characterised by comparatively smaller size and the possession of special-

ized arms. Sexual dimorphism is also exhibited by the shell in the female as a receptacle for eggs as in *Argonauta* and during the breeding period variations occur in the colour of the male. The testis is sac-like, situated in the posterior part of the body and has an internal cavity of coelomic origin. A coiled vas deferens leaves the testis, part of it being a seminal vesicle with grooved lining internally and bearing glands and cilia, it is in this region that spermatophores get produced. Needham's sac, for storing spermatophores, forms a reservoir which opens into the mantle cavity on the left side. In *Octopus* the male duct is differentiated into a vas deferens, a seminal vesicle, prostate, distal vas deferens, Needham's sac and spermatophoric duct (Mann *et al.*, 1970). The seminal vesicle and the prostate contribute to the material of the spermatophore and the distal vas deferens produces the seminal plasma and a cement. The genital ducts are paired in *Nautilus*. One of the circumoral arms is modified in most cephalopods to function as a copulatory limb of the male, this is the hectocotylised arm. This is maximally developed in *Argonauta*. The arm becomes flattened, and cup bearing; this collects spermatophores from the tip of the Needham's sac. Terminally the arm becomes slender in the breeding male and could be broken off into the mantle cavity of the females to release spermatophores picked up by it. In *Nautilus* four arms are thus modified, but the modification is not so prominent.

Annelida

Chaetopoda exhibit separate sexes only in Polychaeta. Most polychaets have their gonads as cellular masses arising from the coelomic epithelium and may lie in several segments of the body. In forms like *Arenicola* gonads are restricted to six reproductive segments and in *Tomopteris* they are confined to one segment. The ripe spermatogonia escape into the body cavity and finally to the exterior through the nephridia. Separate genital ducts are seen in a few forms like Capitellids. In tube dwelling forms, a ventral, median ciliated groove functions as a channel for the passage of sperms released from the nephridiopores. In eunicids, the sperms escape by the dehiscence of the body wall and usually after the escape of the gametes the spawning part of the worms die. Copulatory setae have been reported in *Micronereis* and here internal fertilisation occurs. The male of *Platyneries megalops* ejects sperms through its anus and the entwined male inserts its hind end into the mouth of the

female. The gut of the female is atrophied and the sperms could fertilise the eggs in the coelom. Zygotes are shed through the openings of the bodywall of the female.

Epitoky is a phenomenon exhibited by some polychaets like nereids, syllids, and eunicids, where the body undergoes secondary modifications involving sense organs, size of the segments, parapodia, muscles, etc. The palolo worm *Eunice viridis* shows an anterior, unmodified region and a posterior epitokal region which is a long, many segmented part, and each segment bearing eye spots. Such animals are very active swimmers, and a number of females swimming about in water perhaps attract the males which later then shed the sperms. This activity elicits egg laying by the female. The female is said to elicit this sequence of activity by the release of a fertilizin (not the fertilizin of the eggs).

Some Hesionids and Sabellids are hermaphroditic polychaets.

Echiurida

Echiurids have the two sexes separate and in the male the testis are mesenteric specialisations. Sperms are released into the coelom before maturity, and ripe sperms escape through the nephridia. *Bonellia* shows reduced males clinging to the proboscis of the large female; later it moves into her body to the nephridia through the mouth and dwells as an internal parasite. Isolated larva grows always into a female. In *Haemingia* the fertilised egg is retained in the nephridia where it grows into a male.

Tardigrada

Sometimes tardigrades are grouped along with arthropods. The two sexes are separate, the females predominate and sometimes males may be unrepresented. A supraintestinal testis is present with paired vasa deferentia. These pass around the rectum and open out by a ventral common pore. The relative scarcity of males has also suggested a possibility of parthenogenesis and two types of eggs are sometimes seen.

Arthropoda

The arthropod reproductive system is well organized. The gonadic chamber is a coelomic derivative (Chilopoda, Onychophora) or a schizocoelic pouch or may be a new structure. (Beklemishew, 1969). The genital cells however originate from the coelomic epith-

elium. A variety of organisational differences is exhibited in this group. The testis may be median (Xiphosura), paired (insects, crustaceans), multiserial (Chilopoda, Diplopoda), with three lobes with interconnecting tubules (Scorpions), or with extensions into the limbs (Pycnogonids). Paired or single ducts from the testis run to the exterior through single or paired genital pores or the pores may be even repeated metamerically as in Pantopoda. Seminal vesicles and accessory glands may be represented as simple or complex tubes or sacs (mostly in insects). Specialized androgenic glands (see later) are present in several crustacea (Amphipoda, Decapoda) and some insects (certain beetles). Specialized and often elaborate terminal copulatory parts are seen and show their highly complex development in insects. A penis is developed in cirripedes at the hind end of the abdomen and in the isopod *Priapion* on the seventh thoracic segment. Appendages which are helpful in copulation are also seen, like the modified elements of the aedeagus of insects, the copulatory limbs of millipedes, the thoracic pincers of copepods, the first pleopods of Macrura or the hemipenis in hermit crab and the paired penes in crabs. Organs for sperm or spermatophore transfer are developed in scorpions and mites (pectiniform organs); in mites the organ has been serving a penial function. The genital pore region (atrium) grows into an elongated penis in some harvestmen. The third pair of walking legs in Ricinulei function as male gonopods; such gonopods are seen in Diplopoda also. The male *Peripatus* thrusts the spermatophore on to the cuticle of the female to effect an insemination through the integument (hypodermic). In pterygote insects the ejaculatory duct traverses a phallus with a base and devices like lateral parameres and clasping harpes constitute prehensile parts of the genitalia.

THE FEMALE REPRODUCTIVE SYSTEM

The female gonad or the ovary has a duct, the oviduct, the paired or multiple ducts unite and a common oviduct specializes into a distended, muscular, often ciliated uterus. The uterus may be sac like or tubular. Specialised sacs receiving sperms during mating form the seminal receptacles (or spermathecae) which sometimes remain distinct from the oviduct. A particular portion of the terminal part of the oviduct will receive the sperms when mating, this is spoken of as the bursa copulatrix. The common oviduct is the

antrum and is formed by the union of two oviducts when such an arrangement is present. A short or long vagina is the terminal region of the oviduct which opens to the outside through the female genital pore. The tracts may often be ciliated and muscular and may be partly or completely lined by the coelomic epithelium in coelomates, and with ciliated coelomic funnels (gonostomes), separate from or connected to the nephridia. It may mix with the nephridium to form a nephromixium. In pseudo-coelomate animals, the genital ducts are continuous with the gonads.

Platyhelminthes

The female part of the reproductive system is well known in hermaphroditic flatworms. The isolated examples of dioecious forms have been studied only in a few scattered investigations. A parthenogenetic mode of reproduction has been indicated here.

Rhynchocoela

External sexual differentiation is afforded by cirri in the males. Ovaries are limited to the intestinal zone of the body and lie as paired bodies in between the diverticula of the gut. In forms without gut lobes, an arrangement simulating rows is maintained. Each ovary is saccular, without muscles, and having thin walls. The oocytes differentiate and get laden with yolk from yolk-forming cells which get incorporated into them. Temporary oviducts, appearing at the time of maturation, open out by dorsolateral or lateral pores. Each ovary of *Hoplonemertes* has large eggs at intervals. Eggs may be fertilised while within the ovary. Sometimes the zygotes will be retained in the body in examples like *Geonemertes*, *Lineus* and others which are spoken of as viviparous. Pyriform capsules are produced by secretions from the walls of the ovary, for lodging the eggs, or, as in *Prostoma*, the capsule may be gelatinous and string like, secreted by the integumentary glands.

Acanthocephala

The female has an original single or paired ovary which subsequently breaks up into several ovarian balls. Ovaries lie on the dorsal ligament sac, in the pseudocoel. A central syncytium giving rise to the oogonia is seen in each ovarian ball. The cells move towards the periphery of the ovarian ball during which period the egg becomes fully formed. The oviduct has an initial region called the