

STUDIES ON THE REPRODUCTIVE BIOLOGY OF  
THE WARM WATER SQUID *LOLIGO DUVAUCELI* D'ORBIGNY

1. FUNCTIONAL MORPHOLOGY OF MALE REPRODUCTIVE SYSTEM

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ABSTRACT

Male reproductive system of *Loligo duvauceli* resembles in general with those of other squids. This system includes the median testis, the vasdeferens (AVD) the complex spermatophoric organ, the vas efferens (MVD) and the Needham's sac which continues as the posterior vasdeferens (PVD). The whole system is unpaired and shifted to the left side of the mantle cavity except the testis which is median in the apex of the mantle. The system differs from those of other squids in possessing a compact three lobed spermatophoric gland, the extension of the Needham's sac into a narrow long PVD which is flattened at the terminal part, the absence of the muscular penis and the presence of a hectocotyliised arm which is differentiated at the terminal region.

INTRODUCTION

VERY little is known about the biology and reproduction of the Indian cephalopods. Though Hornell (1917, 1922) has given a general account of the fishery of Palk Bay squids and octopus, Rao's (1954) work deals with the biology and fishery of the squid *Sepioteuthis arcipinnis*. Practically nothing is known about the reproductive biology of *Loligo duvauceli*. Even the basic anatomy of the male reproductive system has not been reported so far.

MATERIAL AND METHODS

The squid *Loligo duvauceli* was mostly collected from mechanised boats which reach Royapuram Fishing Harbour (Lat. 13°06'N, Long. 80°18' E) of North Madras (South east coast of India). Live squids collections were also obtained from the mechanised trawlers operated by the Central Institute of Fisheries Nautical and Engineering Training, Madras, Survey-cum-Inshore Fishing Centre of Tamil Nadu Fisheries, Madras and Marine Biological Station of Zoological Survey of India, Madras.

The squids were invariably packed in ice and brought immediately to the laboratory, situated at a distance of about 5 km for analysis. Squids of different sizes were dissected to reveal the growth pattern of the different components of the male reproductive system. Care was taken to separate the highly coiled distal portion of the anterior vasdeferens, the spermatophoric gland which is in the form of a lump, the completely hidden vasdeferens, the large Needham's sac and the long posterior vasdeferens.

RESULTS

Arnold and Arnold (1977) have divided the male reproductive system of decapod cephalopods into five major portions: The median testis, the vas deferens, the complex spermatophoric organ, the vas efferens and the Needham's sac or spermatophoric sac which continues into the muscular penis. However, various workers use different terminology for the same organs. The terminology used by different authors is compared in Table 1. In decapod cephalopods the mature testis is pure white

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median in the apex of the mantle and flattened up by the ciliated funnel of the vasdeferens against the pen. From its central lumen, it (Arnold and Arnold, 1977).

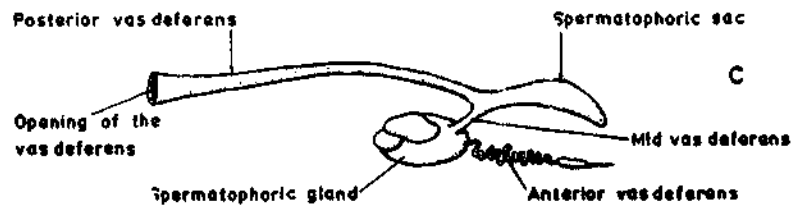
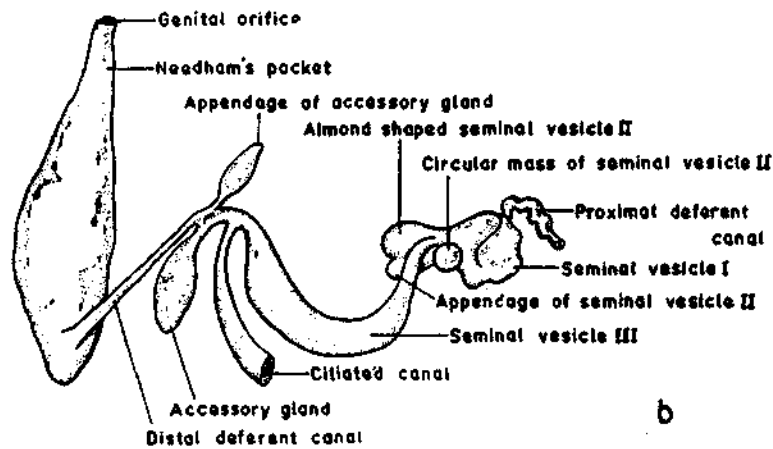
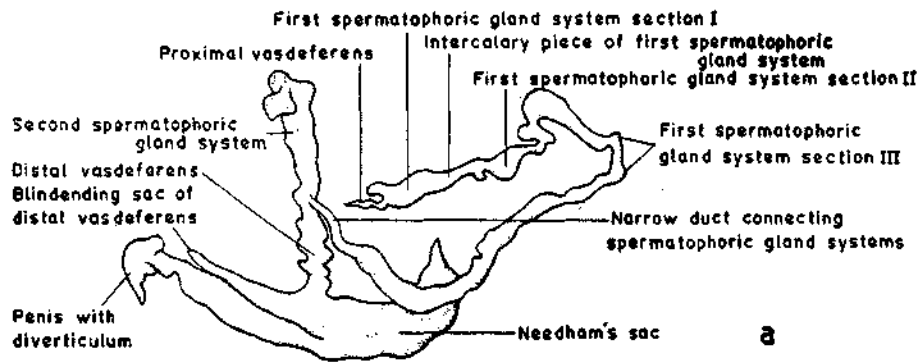


Fig. 1 a. Spermatophore forming organ after removal of the connective tissue capsule of *Octopus vulgaris*, b. Dorsal view of the male genital duct of *Sepia officinalis* - the component parts of which have been separated and c. Dorsal view of the male genital tract of *Loligo*.

empties the mature sperm into the space surrounding it where they are immediately picked

The single spermiduct is a greatly convoluted tube which leads from the cavity of the capsule

TABLE 1. Comparison of the terms used by various authors for the different parts of the male reproductive tract of decapods

Blancquaert (1925) in <i>Sepia</i> based on Tompsett, 1939	Blancquaert (1925) in <i>Sepia</i> reproduction of marine invertebrates Volume IV based on Giese & Pearse (1977)	Arnold and Arnold (1977) in decapods	Ramadan <i>et al.</i> (1981) in <i>Sepia officinalis</i>	<i>Loligo duvauceli</i> (present study)
Proximal deferent canal	Vas deferens	Vas deferens	Proximal vas deferens	Anterior vas deferens (AVD)
Reniform seminal vesicle I Seminal vesicle II Seminal vesicle III	Tripartite spermatophoric organ	Complex spermatophoric organ	Spherical glandular region (with 4 parts embracing and overlapping one another)	Complex tripartite spermatophoric gland
Accessory gland (Prostate gland)	Accessory gland			
Appendage of the Accessory gland	Appendix of Accessory gland			
Distal deferent canal	Vas deferens	Vas deferens	Distal vas deferens with distal gland (Enlarged portion of the wall of the distal vas deferens which is previously called prostate gland)	Mid vas deferens (MVD)
Needham's pocket	Spermatophoric sac	Spermatophoric sac or Needham's sac	Needham's organ	Needham's sac
—	Penis	Muscular penis	—	Posterior vas deferens (PVD)

towards the left. In *Loligo pealei* the vas deferens gradually increases in diameter all the way to its end while in *L. opalescens* it first increases in diameter, then decreases as it joins the spermatophoric organ (Arnold and Arnold, 1977). In *S. officinalis* however, the genital duct commences on the ventral wall of the posterior part of the coelom. The opening in the coelom leads into a slender tube, the proximal deferens canal which varies in length from 5-10 cm according to the size of the animal. This tube is very much convoluted and packed into a tangled mass. Further this does not lie in the genital sac, but is bound to the wall of the coelom by a membrane (Tompsett, 1939).

In cephalopods, the single spermiduct opens into an elongated vesicula seminalis, to which is appended a glandular body, the prostate. In the interior of the vesicula seminalis, the sperms are rolled up by the action of a system of grooves and ridges into long narrow bundles of about 2 cm in length (Parker and Haswell, 1954). In *Sepia officinalis* the proximal canal at its distal end opens into a reniform seminal vesicle I (Fig. 1). This leads to seminal vesicle II, which consists of 3 parts, one of them spherical on the outside, another almond shaped, while the third consists of a cecilla shaped appendage of the almond shaped part. Seminal vesicle III is a large structure, the canal of which is crescent shaped in cross-section though most of the cavity being occupied by a projection from the side of its wall.

The next part was called the prostate by earlier authors, but has been renamed as the accessory gland. It has thick glandular walls enclosing a large cavity. The accessory gland is entered from seminal vesicle III by a very narrow passage. A slender canal called ciliated canal is given off from this passage and opens by a funnel-like expansion into the genital sac. The duct which leads on of the accessory gland travels into a structure of complicated internal form called the appendage of the accessory gland, the latter leads by a slender tube, the

distal deferent canal, to the posterior end of Needham's pocket, at the end of which the genital orifice is situated (Tompsett, 1939).

In *Loligo* vas deferens ends in the spermatophoric organ which is a complex array of glandular tissue and lumina and empty into a central canal or sperm tract. In passage through this organ, the sperms are formed into a spiral mass and coated with the various membranes and tunics of the spermatophores.

The vas efferens takes the fully mature spermatophores and transfer them one at a time into the spermatophoric sac or Needham's sac for storage till copulation. The penis lies to the left of the anus as a muscular extension of the spermatophore reservoir or Needham's sac through which small bunches of spermatophores are passed during copulation.

In all the decapods described, the entire male reproductive tract with exception of the testis is on the left side of the middle line (Arnold and Arnold, 1977). Like the other decapods, the warm water squid *Loligo duvauceli* has the entire reproductive system pushed to the left side of the mantle cavity except for the median testis. In order to understand the growth pattern of the different parts of the reproductive system the squids are categorised into three size groups, in the present study.

Group I : Less than 5 cm dorsal mantle length

Group II : About 7 cm dorsal mantle length

Group III: About 9 cm dorsal mantle length

Group I squids are considered to be immature as they do not possess spermatophores in the Needham's sac. Group II squids on the other hand are considered to be just mature as a few spermatophores appear in the Needham's sac. Whereas, the group III squids are ripe in as much as the Needham's sac is always packed with the spermatophores (Haley, 1973).

TABLE 2. Length of the testis, anterior vas deferens, spermatophoric gland, Needham's sac and posterior vas deferens of immature, mature and fully mature *Loligo duvauceli*

Dorsal mantle length in cm	Stage of maturity	Length of the anterior vas deferens in cms	Length of the spermatophoric gland in cm	Length of the Needham's sac in cm	Length of the posterior vas deferens in cm	Length of the testis in cm	No. of spermatophores
5.0 and below	Immature	0.4-0.5	0.3-0.5	0.2-0.3	0.5-1.0	0.2-0.7	Nil
57.0	mature	1.0-1.3	0.8-1.0	0.4-1.0	1.0-2.4	0.8-1.9	Few
9.0	Fully mature	1.5-2.5	1.0-1.5	0.9-1.2	2.4-3.3	1.7-3.3	Plenty

On the basis of anatomical and histological analyses, the male reproductive system of *L. duvauceli* is divisible into the median testis, anterior vasdeferens (AVD), the complex spermatophoric gland, the mid vasdeferens (MVD), the spermatophoric sac or Needham's sac which ends within the mantle cavity by the genital orifice through the posterior vasdeferens (PVD), but not by a muscular penis.

#### Testis

The immature testis measures 0.2-0.7 cm in length and 0.1-0.2 cm in width. It is whitish in colour and enclosed in a capsule and suspended in the coelom by a mesentery. The testis is ovoid and not much flattened.

The testis of the just mature squid is more whitish in colour and flattened in the apex of the mantle, measuring about 2.0 cm in length and 0.4 cm in width. However, the ripe testis of a squid with 9 cm dorsal mantle length is pure white and more flattened and measures about 2.5 cm in length and 0.5 cm in width. There appears to be a progressive increase in size and flattening of the testis against the pen along with the increased whiteness in colour.

#### Anterior vas deferens

The AVD, called by different names in different cephalopods (Table 1) is a highly convoluted tube in *L. duvauceli* enclosed in a transparent covering. The entire vas deferens in fact packed into a mass within the covering and found attached to the hind end of the spermatophoric gland, which is clearly seen only under a binocular dissection microscope. Though the AVD is divisible into proximal and distal regions which have distinct histological and functional differences, externally there is no marked difference between the two except the distal vas deferens has a slightly increased width with a round lumen against the slightly thinner proximal portion of the AVD with compressed lumen.

The measurements of anterior vasdeferens of squids with the dorsal mantle length of 5 cm, 7 cm and 9 cm are provided in Table 2.

#### *Spermatophoric gland*

This is the most prominent portion of the entire male reproductive system not excluding the testis and Needham's sac. The spermatophoric gland is named differently by various authors as is evident from Table 1. In *L. duvauceli* it measures differently in different size groups (Table 2). It consists of a closely placed three lobes which are evident when the outer covering is removed. For convenience they are named as 'A', 'B' and 'C'. Lobe 'A' the largest of the three is lower in position, flat and elongated with a longitudinal wedge at the centre. The coiled AVD runs over the upper lobe 'C' and enters lobe 'A' by making a 180° turn. Almost in the same location of lobe 'A' the MVD emerges out. 'B' is the smallest pear shaped lobe situated behind. On the contrary, lobe 'C' is of medium size while oblong shaped.

#### *Mid vasdeferens*

This is a more obscure portion revealed only in serial sections. Because it is very short even in the ripe condition it is not prominent and sandwiched between the enormously grown spermatophoric gland and the Needham's sac. Added to this, it is thin walled and transparent eventhough wide.

#### *Needham's sac*

The so called spermatophoric sac or Needham's sac, named after John Tubervill Needham (1745) who in his 'New microscopical discoveries' gave the first detailed description of both the milt sac and the 'milt vessel' of 'Calamary.' It is a crescent shaped sac in *L. duvauceli* with the apex of the crescent pointing outwards leading gradually to a tubular posterior vasdeferens. The dimensions of the Needham's sac of immature, mature and

ripe animals are also provided in Table 2. There appears to be not much difference in the shape and colour of this organ in squids of different sizes.

#### *Posterior vasdeferens*

This is the terminal portion in *L. duvauceli* is a simple tubular structure varying in length and diameter in different size groups (Table 2) ending in a wide opening into the mantle cavity. It is observed that the terminal portion of the posterior vasdeferens is enlarged before ending in the orifice, in the case of the mature and ripe animals. The absence of any muscular penis is yet another unique feature of this species.

#### *Hectocotylised arm*

It is well known that the absence of an intromittent organ in cephalopods is compensated by a hectocotylised arm which involves modification of one or more of the arms in the males. The arm or arms modified are said to be hectocotylised. It is interesting to note that in *Philonexis* and *Argonauta*, this modified arm is charged with spermatozoa and then inserted into the mantle cavity of the female where it is detached. This detached arm was wrongly described by early observers as a parasitic worm and named it *Hectocotylus* (Borra-daile and Potts, 1958).

The hectocotylised arm characteristic of most cephalopods is hard to be distinguished in *Loligo* (Arnold and Arnold, 1977). However in the case of *L. duvauceli*, though it resembles the other arms in general, the suckers are greatly reduced in number. The distal half of the hectocotylised arm is not only devoid of suckers, but also much flat and broad with serrated margin. A new observation made on the hectocotylised arm of *L. duvauceli* is its flat and thin outer extension, which is more clearly seen in the cross section (Fig. 2). A comparison of the measurements of the extension of the

hectocotylied arm with that of normal arm is also provided in the same figure. In this squid, it is the fourth arm on the left side which is modified, as in the case of the other species of *Loligo*.

#### DISCUSSION

The anatomical study of the organs of reproduction of male *L. duvauceli* reveals a basic similarity to those of the other squids, especially in having the five major portions namely the median testis, the vas deferens (AVD) the complex spermatophoric organ, the vas efferens (MVD) and the Needham's sac which continues into the posterior vas deferens (PVD) (Arnold and Arnold, 1977). The unpaired duct system finally leads to open into the left side of the mantle cavity. While the colour, shape and location of the testis are very similar to those of the other squids, the AVD first increases in diameter and then decreases as it enters the spermatophoric organ. In this regard it shows similarity to *L. opalescens* while differing from *L. peali* (Arnold and Arnold, 1977) in which the vasdeferens gradually increases in its diameter all the way to its end. The spermatophoric organ has been described by Arnold and Arnold (1977) as a complex array of glandular tissue and luminal which empty into the central canal or 'sperm tract'. By the present study on *L. duvauceli* it is revealed that the spermatophoric organ consists of three lobes of which the lower one 'A' is large and flat into which the AVD enters and from which the MVD departs. The 'sperm tract' or the central canal runs only inside this lobe of the gland.

The spermatophore forming organ of *Octopus vulgaris* and *Sepia officinalis* contrast with the situation in *L. duvauceli* in which it is compact and enclosed in a sac of the gonocoele. In *Octopus* this system includes the first and second spermatophoric gland system which is a blind ending tube with thick glandular wall (Arnold and Arnold, 1977). In *S. officinalis* the system

includes the seminal vesicle I, seminal vesicle II which consists of three parts, one of them spherical on the outside, another almond shaped and the cedilla shaped appendage of the almond shaped part, seminal vesicle III, accessory gland and appendage of the accessory gland (Tompsett, 1939). A comparison of the reproductive system of these cephalopods is attempted in Fig. 1.

The mid vasdeferens of *L. duvauceli* is an obscure portion of the reproductive system by being short and thin walled while wide. It ought to play a role in the transfer of spermatophores formed in the spermatophoric gland to the Needham's sac. The squids of the colder waters possess a corresponding portion often called vas efferens which takes the fully mature spermatophores and transfers them one at a time into the Needham's sac for storage till copulation. The angle of the attachment of the vas efferens is such (backward and upward) that the spermatophores are aligned in parallel arrays with their aboral (non opening) end pointed distally (Arnold and Arnold, 1977). In *S. officinalis*, this portion is called distal deferent canal (Tompsett, 1939), which is a slender and long tube leading to the Needham's pocket. A recent study of the structure of the male reproductive system of *S. officinalis* by Mohamood *et al.* (1981 a) describes this portion as distal vas deferens and records that it is originating at the same point of the accessory duct. It does not appear as a natural continuation of the main region, but a complex structure embedded in a gelatinous mass found above the main vasdeferens and extends backwards forming a loop over the surface of Needham's sac, where it merges into its cavity posteriorly. In *O. bimaculoides* the distal vasdeferens appears to be a short and wide tube leading to Needham's sac (Peterson, 1959).

The next portion of the reproductive system is the Needham's sac, which is crescent shaped and thick walled leading to the PVD. In *S. officinalis* also the Needham's organ is a cres-

cent-shaped tube-like organ, but twisted and differentiated into a spacious sac with a terminal contractile tube. The sac is broadest at the middle, furnishing a suitable lodge for most of the vasdeferens (Mohamood *et al.*, 1981 a). In *O. bimaculoides*, the Needham's

The final portion of the male reproductive system of *L. duvauceli* is a long tubular PVD which is narrow to begin with gradually widens and terminates in a wide male genital opening within the mantle cavity. The terminal portion of the PVD is flat though contains spermatophores.

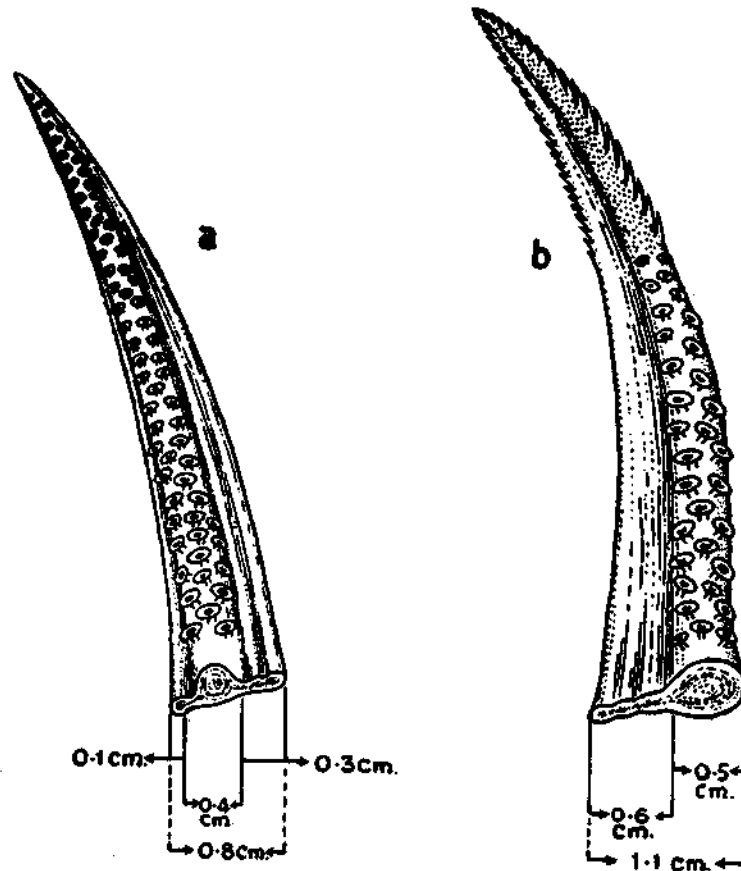


Fig. 2. [Arms of *Loligo duvauceli* : a. normal arm and b. hectocotylised arm.

sac is a blind tube where a general finishing and hardening of spermatophores occur (Peterson, 1959). Of all the octopods and decapods studied, *L. duvauceli* appears to possess a simple spermatophoric sac which is thick walled and probably functions mainly as storage organ for the spermatophores.

phores. However, in *L. pealei* and *L. opalescens* the penis lies to the left of the anus as a muscular extension of the spermatophoric sac through which small bunches of spermatophores are passed during copulation (Arnold and Arnold, 1977). The muscular penis noted in the other squids is conspicuously absent in



*L. duvauceli*. In *S. officinalis*, a genital orifice is situated at the narrow end of the Needham's pocket resulting in the absence of both PVD as well as penis. A penis with diverticulum occurs in *O. bimaculoides* which is called the terminal organ (Peterson, 1959) and the diverticulum of the terminal organ (Peterson, 1959) and the diverticulum of the terminal spermatophoric duct by Mann *et al.* (1970) in *O. dofleini martini*.

In most cephalopods, hectocotylus is a characteristic feature which is hard to distinguish in *Loligo*. But it is prominent in other species as a modification, reduction or loss of the suckers on an arm or frequently as a modification by reduction or shape change of one whole arm on one side. This is species specific and is used as a taxonomic characteristic (Arnold and Arnold, 1977). It is known that in the squids the fourth arm on the left side is modified for hectocotylisation. This arm in *L. duvauceli* though not conspicuously

different from other arms, is devoid of suckers at the distal region where it is flat and broad with a serrated margin. In the male of *S. officinalis*, the proximal half of the fourth arm on the left side is modified. The suckers are greatly reduced except at the base of the sucker-bearing surface where there are a few normal ones (Tompsett, 1939). It is the third arm on the right side that becomes the hectocotylus of octopus where the tip is spoon-like (Nayar, 1977).

Thus the male reproductive system of the warm water squid *L. duvauceli* has a basic similarity to that of the other squids. However, the presence of a compact three lobed spermatophoric gland, the extension of the Needham's sac into a narrow and long PVD which is flattened at the terminal region, the absence of the muscular penis and the presence of distally modified hectocotylised arm are notable features of this squid which may reflect some significant role in the reproductive process.

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