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ONTOGENETIC ASPECTS OF MORPHOLOGY, SIZE, STRUCTURE AND PRODUCTION OF SPERMATOPHORES IN OMMASTREPHID SQUIDS: AN OVERVIEW

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ABSTRACT

The ontogenetic trends in morphology and morphometry of spermatophores and spermatophoric glands were studied based on an original methodology in 17 species of all genera of the squid family Ommastrephidae. Seven ontogenetic periods were revealed: 1. embryonic; 2. larval; 3. fry; 4. juvenile; 5. adult maturing; 6. adult, functionally mature, copulating (two substages: 6.1. active spermatophorogenesis continuing, 6.2. residual spermatophorogenesis and its break-down); 7. total exhaustion and death. Morphology, size and number of spermatophores, and the phenomenon of tentative functioning of spermatophoric glands in immature and maturing males with production and release of tentative spermatophores without sperm are described. The minimal ommastrephid male fecundity assessed by a maximum spermatophore number in Needham's sac ranged from 100 (*Hyaloteuthis*) through 600-800 (*Illex*) to 1000-2500 (*Dosidicus*, *Ommastrephes*, *Sthenoteuthis*). The spermatophore production correspondingly followed the changes in the allometric growth patterns of spermatophoric glands in adult squids. There are three male reproductive strategies among ommastrephids: 1) Neritic type (*Illicinae*, *Todaropsinae*) – increase of Needham sac volume and number of periods of formation and accumulation of spermatophores between mates; 2) Intermediate type (*Todarodinae*, *Ornithoteuthinae*, *Eucleoteuthis*, *Hyaloteuthis*) – increase of the volumes of both Needham sac and seminal reservoirs of spermatophores; 3) Oceanic type (*Dosidicus*, *Ommastrephes*, *Sthenoteuthis*) – significant increase of the size of spermatophores and their seminal reservoirs during ontogeny.

Keywords: ommastrephid squids, male reproductive system, spermatophoric glands, morphology, functioning, spermatophores, tentative spermatophores

INTRODUCTION

The phenomenon of spermatophore formation is widely distributed in the Metazoa: it occurs in the different phyla of invertebrates and even in primitive vertebrates. This phenomenon culminates in the Cephalopoda. Males of all species of this class produce spermatophores, and spermatophoric glands and spermatophores are the most complicated structures both morphologically and functionally. The same complexity is observed with respect to the diverse and sophisticated mechanisms of spermatophore transfer

from male to female in cephalopods (Clark 1981, Mann 1984, Mangold 1987, 1989a, b, Sabirov 1989, Hanlon & Messenger 1996, Nesis 1996).

For the first time a spermatophore was discovered in *Sepia* by J. Swammerdam and was described in his «Biblia Naturae» (review: Mann, 1984). Three centuries later there are about 150 publications on cephalopod spermatophores (reviews: Hess 1982, Mann 1984, Sabirov 1989). The data were summarized at different historic stages by Brock (1878), Marchand, (1907, 1913), Drew (1919), Blancquart (1925), Weill (1927), Hess (1982), Mann (1984), Mangold (1987,

1989a, b), Budelmann *et al.* (1997) and Sabirov (1989). For squids of the family Ommastrephidae, there are only scanty and rather superficial literature data on both morphology and mean spermatophore size in 14 species (reviews: Soeda 1956, Roper *et al.* 1969, Hess 1982, Takahama *et al.* 1991).

Thus, the level of recent knowledge on general morphology and partially also on physiology of spermatophores in cephalopods is relatively high. But spermatophore morphology and length-frequency distribution and its changes during ontogeny, as well as male fecundity, i.e. the mechanism of male reproductive system functioning during ontogeny, are not yet well described. Moreover, it is necessary to emphasize that there are no literature data on spermatophore-like products (tentative spermatophores) in squids at immature and maturing stages.

Some new data and generalizations on these ontogenetic problems of spermatophore formation and male reproductive system functioning were revealed during long-term investigations that were carried out in AtlantNIRO and Kazan State University under the direction of Ch.M. Nigmatullin with a group of students and collaborators. These investigations began in 1974. First a methodological approach (Zalygalin 1976, Nigmatullin *et al.* 1981) was developed, based on detailed measurements of different parts of spermatophoric glands and spermatophores in males at all stages of ontogeny. To date, we studied functional morphology of spermatophoric glands and spermatophores, and peculiarities of male reproductive system functioning in different groups of cephalopods: mainly in Ommastrephidae (Zalygalin 1976, Zalygalin *et al.* 1977, 1983, Magaras *et al.* 1983, Nigmatullin *et al.* 1981, 1984, 1999, Nigmatullin & Sabirov 1987, 1995, Laptikhovskiy & Nigmatullin, 1987, 1992, Sabirov & Staroverov 1988, Nigmatullin 1989, Sabirov 1989, 1990, 1995, Zuyev *et al.* 2002), and to a lesser extent in Thysanoteuthidae (Nigmatullin *et al.* 1991, 1995), Gonatidae (Nigmatullin *et al.* 1996), Loliginidae (Sabirov & Ogareva, 1987), Sepiidae (Nigmatullin & Tscherbenedok, unpublished data), and Octopodidae (Bespyatikh *et al.* 2000, Nigmatullin, Laptikhovskiy & Zorikova, unpublished data). During this study a new phenomenon was discovered – a tentative spermatophorogenesis, i.e. production of tentative or quasi-spermatophores without sperm by immature and

maturing males (Laptikhovskiy & Nigmatullin 1987, 1992, Nigmatullin & Sabirov, 1987, 1995). But these papers were published mainly in Russian, and are not easily available for an international readership. The aim of the present paper is to provide a brief overview of the main results of our investigations on morphology, size structure, number and production of spermatophores, peculiarities of the male reproductive system functioning during ontogeny, and male reproductive strategies in most studied ommastrephid squids.

MATERIALS AND METHODS

Squid reproductive systems (1164 males of 17 ommastrephid species) were collected in 1969-1997 by different RVs of the Ministry of Fisheries and Russian and Ukrainian Academy of Sciences in the different regions of the World Ocean from 50°N to 50°S. The studied species represent all ommastrephid genera.

A complete morphometric study of 812 reproductive systems (only the spermatophoric complex of organs = SCO) and 7,865 spermatophores was done, in 122,039 spermatophores the total length was measured within 0.1 mm. The bulk of data refers to *Illex illecebrosus*, *I. argentinus*, *Todarodes pacificus*, *Dosidicus gigas*, *Ommastrephes bartramii*, *Sthenoteuthis pteropus*, *Hyaloteuthis pelagica*, which were used as «model species» (Table 1). The data concerning different intraspecific groups were investigated separately.

A detailed biological analysis was carried out on the male reproductive system. The dorsal mantle length (ML) was measured within 1 mm. The squid body, stomach, digestive gland and reproductive system were weighed. The reproductive systems were preserved either in 4-5% formalin solution or in a formalin-acetic acid mixture.

Maturity was assigned using Nigmatullin's (1989) scale. This scale can be very briefly described as follows. 1. Juveniles: sex is not visually distinguishable; 2. Immature (stages I and II); 3. Physiological maturation: maturation of testis and tentative spermatophorogenesis (stage III-IV); 4. Functional maturation: initial accumulation of normal spermatophores in Needham's (= spermatophoric) sac

Table 1 Data on studied material

Subfamily/Species	Region	MS*	ML	Morphometry (N)	
				SCO	Spermatophores
Illicinae	Northwest Atlantic	I-V	1.3-23.0	79	9264
<i>Illex illecebrosus</i>	Gulf of Mexico	V	21.3-22.8	2	3136
<i>I. argentinus</i>	Southwest Atlantic	I-VII	6.2-29.0	125	21092
<i>I. coindetii</i>	Shelf of Mauritania	V	11.3-20.5	20	7847
	Shelf of Angola	V	12.2-16.0	9	1592
Todaropsinae	East Atlantic. shelf of Senegal	V	11.6-14.0	9	706
<i>Todaropsis eblanae</i>	Indian Ocean	V	14.2-15.0	3	250
Todarodinae	Southwest Atlantic	V	23.3-26.0	2	50
<i>Martialia hyadesi</i>					
<i>Nototodarus hawaiiensis</i>	West Indian Ocean	V	13.1-16.5	4	2692
<i>Todarodes pacificus</i>	Sea of Japan	II-V	19.6-27.3	85	1009
<i>T. angolensis</i>	Southeast Atlantic	V	30.1-32.8	3	190
<i>T. sagittatus</i>	East Atlantic. shelf of Mauritania	V	24.5-24.8	3	178
Ornithoteuthinae	Gulf of Guinea	III-V	4.7-10.1	5	135
<i>Ornithoteuthis antillarum</i>	Southeast Atlantic	VI	19.2	1	55
<i>O. volatilis</i>	Northwest Indian Ocean	V	9.3	1	67
Ommastrephinae	East Pacific:				
<i>Dosidicus gigas</i>	Peruvian and equatorial Region	I-VI	2.7-37.2	167	14383
	Nicaragua waters	V	69.5-72.0	2	1820
	Gulf of California	V	25.2-73.2	133	1330
<i>Ommastrephes bartrami</i>	North Atlantic	V	27.4-39.6	60	2212
	North Pacific	V	33.5-36.4	6	3950
	South Atlantic	V	27.5-40.7	10	2942
	South Indian Ocean	V	27.4-35.5	9	3747
	South Pacific	II-VI	12.9-37.0	75	16869
<i>Sthenoteuthis pteropus</i>	Northeast part of the species range	V	13.5-27.8	117	9733
	Gulf of Guinea	II-VI	10.7-23.2	128	11439
	Southeast part of the species range	V	20.4	1	28
	West-equatorial part of the species range	V	14.0-24.0	21	2802
	Caribbean Sea	V	15.5-19.0	2	8
	Southwest part of the species range	V	15.2-17.5	2	153
<i>S. oualaniensis</i>	Indian Ocean				
dwarf form		V	8.0-9.3	5	357
middle-sized form		V	11.8-16.4	32	1065
<i>Eucleoteuthis luminosa</i>	South Indian Ocean	V	12.4	1	35
<i>Hyaloteuthis pelagica</i>	North Pacific	V	13.5-13.8	2	255
	North Atlantic	V	4.5-5.6	9	54
	South Atlantic	V	5.2-6.5	4	30
	East Pacific	IV-V	6.5-7.7	27	564

MS – maturity stage of reproductive systems after Nigmatullin (1989)

(substage V-1); 5. Functional maturity: active spermatophorogenesis with proper spermatophore accumulation and release at mating (substages V-2 and V-3); 6. Functional maturity with gradual degeneration of testis and decrease of its functioning (stage VI); 7. Spent (stage VII).

An important trait of cephalopod males is the presence of a complex of reproductive accessory organs (= SCO) that determines the division of a sexual maturity period into physiological and functional maturity subperiods. Males become functionally mature and ready to mate only after production of

normal (proper) spermatophores in the spermatophoric glands and their accumulation in Needham's sac in sufficient numbers.

The male reproductive system of squids consists of the testis and the SCO. The latter includes the sperm duct, the system of spermatophoric glands (SG), and Needham's sac (Fig. 1). We elaborated a methodological approach, which was based on detailed measurements of different parts of SCO including mainly SGs, and all spermatophores (Fig. 1a, b) in males of all stages of ontogeny. Measurements of reproductive system include the lengths of testis and

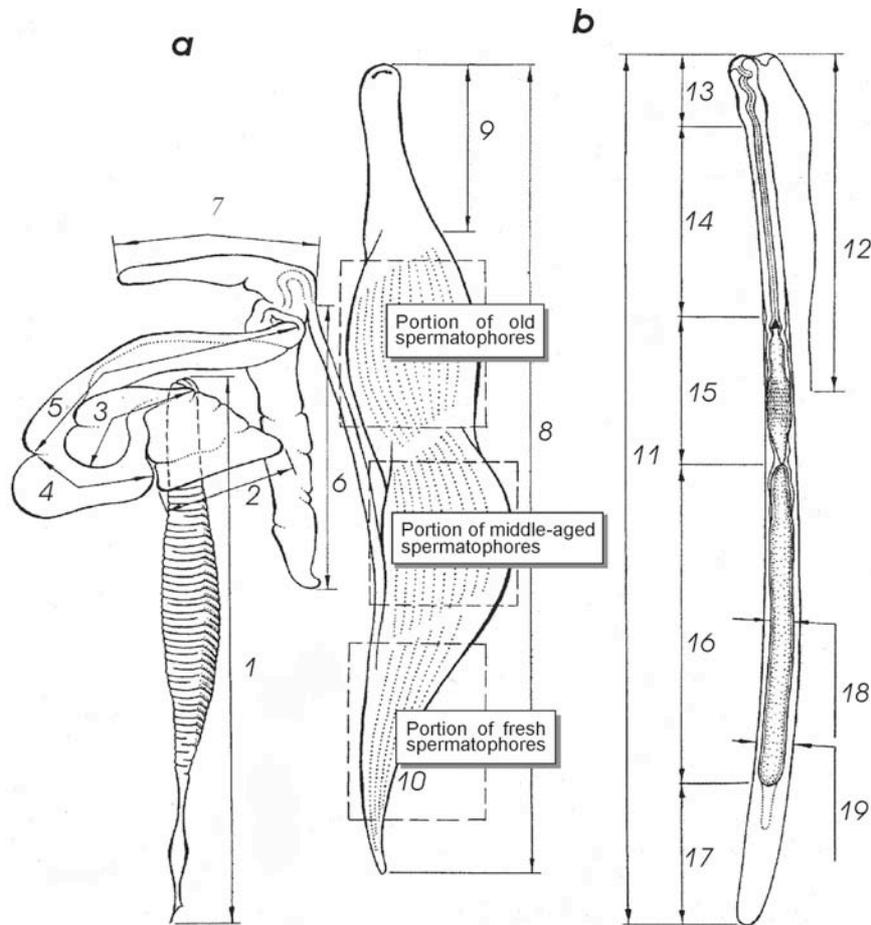


Fig. 1 Scheme of measuring SCO (a) and spermatophore (b) of ommastrephids. Length of: 1 - sperm duct, 2-7 - I-VI spermatophoric gland parts, 8 - spermatophoric sac, 9 - penis, 10 - fundus (not measured), 11 - spermatophore, 12 - tread, 13 - head, 14 - ejaculatory tube, 15 - cement body, 16 - seminal reservoir, 17 - posterior empty part. Width of: 18 - seminal reservoir, 19 - spermatophore

parts of SCO - sperm duct, six parts of SGs and Needham's sac. The positions of limits between SG parts were assumed based on their external and inner anatomical boundaries. All spermatophores were studied and measured that were found in Needham's sac and in the SCO ducts glands of a given male.

To study peculiarities of the ontogenetic aspects of spermatophore production, we investigated all spermatophores taken from the different parts of the spermatophoric sac of immature, maturing and mature males. Those from the deep part or fundus (Fig. 1a) were considered to be the youngest, whereas spermatophores in the penis (Fig. 1a) were supposed to be the oldest. The number of portions depended on the fullness of Needham's sac and spermatophore numbers, it varied from 2 to 9.

There is a methodical difficulty to distinguish pre-mating males from mating ones. To estimate the possible beginning of spermatophore release due to mating the following criteria were used: condition of

the reproductive system (maturity stage), male ML, proportions of the different parts of spermatophoric glands, presence of quasi-spermatophores (most important because it is an indicator of functional maturation before the first mating) in the proximal part of Needham's sac, spermatophore length in the different parts of the spermatophoric sac, relation between sperm reservoir length and posterior empty part of the spermatophore.

The ML was used as a standard measure to estimate the relative dimensions of all the SCO parts and the total spermatophore length; the spermatophore length was used as a standard scale for estimation of relative size of separate parts of spermatophores (Fig. 1b). Volume of the cylindrical sperm reservoir was calculated using the following equation: $v = 0.262 \cdot (3l - d) \cdot d^2$, where v - volume, mm^3 ; l - length of the sperm reservoir, mm ; d - its average width, mm . For statistical processing the program "Statgraphics" was used.

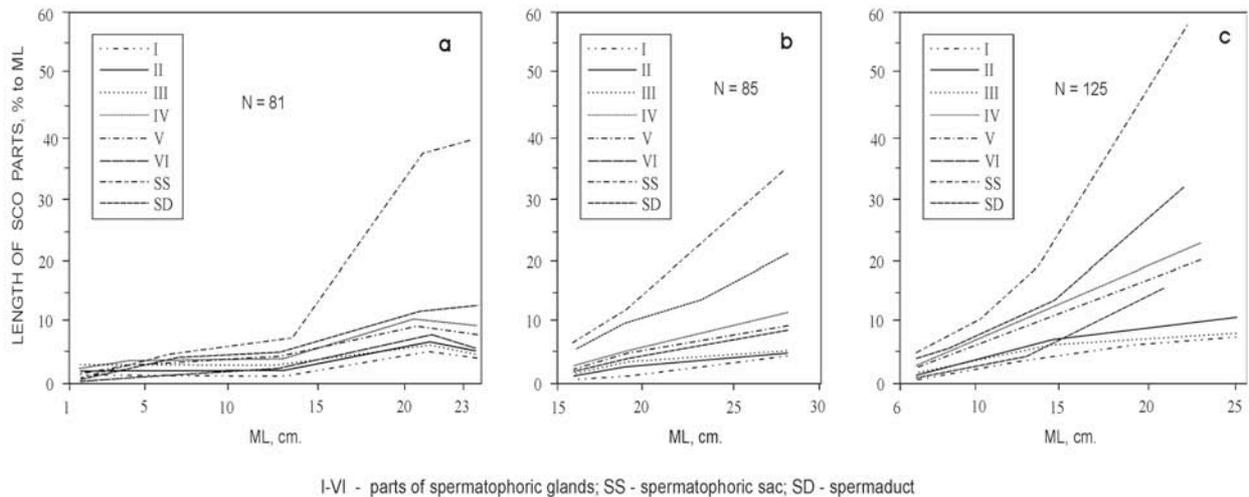


Fig. 2 Growth of the spermatophoric complex of organs: **a** *Illex illecebrosus*, **b** *Todarodes pacificus*, **c** *Sthenoteuthis pteropus*

SCO GENERAL MORPHOLOGY AND THEIR ALLOMETRIC GROWTH

A general SCO morphology (Fig. 1) is recognizable in all the species and there is no directed change (Nigmatullin & Sabirov 1987, 1995, Sabirov 1995) in contrast to the diversity of hectocotylus structures (Roeleveld 1988; our data).

The mature male sperm duct is about 20% ML, and usually is swollen in its middle part. It is oval in cross section and consists of a number (up to 50) of loops. The SG consists of six compactly S-packed parts, successively connected to each other. The SG components are three ducts: intermediate, excretory and spermatophoric. The I and II parts of the SG are sac-shaped, whereas parts III and IV look like long tubes, they are separated by a deep fissure. The sections V and VI are long narrowing sacs (Fig. 1).

There are some differences in relative size of the SG. Specific features of the form and dimensions of spermatophoric gland parts have been found in *Illex* (extraordinarily tiny part IV of the SG, 9-13% of ML, 1.5-2 times shorter than in other species), and also in *T. pacificus* and *H. pelagica* (parts I and II of the SG morphologically are vaguely separated from each other). No distinctions in the SCO morphology among infraspecific groups were found.

Needham's sac are large, attaining up to 60% ML in mature males. Its distal part forms a well-developed penis (Fig. 1). For the first time the inner structure of the spermatophoric sac was studied. In two mature *Ommastrephes bartrami* a complicated and very

specialized system of strong circular and longitudinal-oblique collagen fibre structures was observed in the integument of Needham's sac, guiding longitudinal furrows on its inner surface and two inner transverse membranes with a small "pilot" opening for directed movement of spermatophores along the sac. This system was found for the first time in cephalopods. As a whole this system together with a well-developed muscle system and small glands permits to accumulate and keep the large number of spermatophores in Needham's sac in a well-ordered and compact spiral packed condition. In connection with this discovery it's very important to study the functional morphology of Needham's sacs in different cephalopod groups which differ from each other by male fecundity.

The different parts of the spermatophores are formed by the successively located parts of SG ("principle of conveyor"). Therefore there is a correlation between the size of a given part of SG and the size of a spermatophore or its components. Of great importance is the size of parts I and IV. In the part I the seminal reservoir is formed and in IV the middle and outer tunics of the spermatophore. Correspondingly the length of the normal spermatophore depends on the length of part IV. That is why it is so important to study the peculiarities of allometric growth of different SG parts. In the ommastrephids studied there appeared three types of SG allometric growth during active spermatophorogenesis in the period of functional maturity (Fig. 2). 1) Isometric or with a weak tendency of negative allometry of SG growth (Illicinae, Todaropsinae). 2) A feebly expressed positive

allometry (Todarodinae, Ornithoteuthinae, *Eucleoteuthis*, *Hyaloteuthis*). 3) Positive allometry is clearly expressed and increases during this period. The I and IV SG parts have maximal growth rates (*Dosidicus*, *Ommastrephes*, *Sthenoteuthis*). These differences have significant consequences for the peculiarities of spermatophore formation.

ONTOGENETIC PERIODS OF REPRODUCTIVE SYSTEM DEVELOPMENT AND FUNCTIONING

Seven periods of development and functioning of male reproductive systems in ommastrephid squids were revealed. Generally, they correspond to the ontogenetic stages of this squid family described earlier with regard to the morpho-ecological parameter complex (Nigmatullin 1987, Arkhipkin 1989). The first two of them are based mainly on published information, whereas other periods were characterised from original data.

1. Embryonal. Separation of the non-differentiated sexual rudiment from mesodermal tissue, with large light cells and lining of paired coelomic lumens. The coelomic lumens merge in an unpaired one, and cover the sexual rudiment (Bobretskij 1877, Fausek 1897). But the latter quickly appears to be squeezed between the posterior part of intrinsic yolk and the body wall, taking the form a narrow and long band of cells. Therefore further development of the sexual rudiment occurs in the postembryonic period (O'Dor *et al.* 1982, Boletzky 1989).

2. Larval. Differentiation of the gonad rudiment into a testis or ovary occurs obviously without any hormonal control, by auto-differentiation (Mangold 1987, 1989b). The sex of an animal is determined by development with equal probability of one of two layers in the gonad rudiment - cortical or medullar. SCO appears: its proximal parts (funnel, the ampulla, sperm duct) are formed by mesodermal tissues (walls of the coelomic sac), whereas distal parts (spermatophoric gland, spermatophoric sac) are formed by ectodermal tissue (Livanov 1955, Fioroni 1978, Boletzky 1987, 1989).

3. Fry. There is a proliferation of spermatogonia and spermatocytes I in the testis (Grieb & Beeman

1978, Mangold 1987, 1989a). SCO starting from a non-differentiated feebly curved duct gets its typical shape. There is histogenesis of SG's glandular tissues, but still no secretion.

4. Juvenile. There is formation of spermatocytes II and spermatids in the testis, and glandular secretion occurs in the SG with formation of tentative spermatophores. The latter at first are produced as shreds of an outer tunic without inner contents, and subsequently as curved tubes with shapeless contents (Fig. 6a).

5. Adult maturing. There are two subperiods.

5.1 Physiological maturity, functional immaturity. Spermatogenesis begins in the testis. Glandular secretion increases resulting in the production of false or quasi-spermatophores, which are different from the normal ones whose reservoirs do not contain sperm, and are short and translucent (Fig. 6e). The sense of tentative spermatophorogenesis is to adjust SCO system for optimal working regime before the sperm enters the spermatophoric glands.

5.2. Beginning of functional maturation, but still no mating occurs. With an increase in spermiogenesis intensity the sperm enters the ampulla of the sperm duct, fills in its coils and gets into the SG. From then on false spermatophores with low sperm contents are produced for a while, their sperm reservoirs being translucent and shorter than normal ones (Fig. 6f). Later the production of proper spermatophores begins and quickly increases. The production of tentative spermatophorogenesis (when tentative and false spermatophores are formed) is not stored in the spermatophoric sac but is discarded through the penis. The last false spermatophores with short translucent reservoirs and low sperm contents sometimes are kept close to the penis of the spermatophoric sac and can be used by researchers as markers «no copulation occurred».

6. Adult, functionally mature, copulating. There are two subperiods.

6.1. Active spermiogenesis and spermatophorogenesis continues. The character of the combined growth of SCO parts was investigated on the basis of relative analysis of SCO size variability in squid at the different maturity stages within the limits of one ontogenetic line. It was observed that during male somatic growth (Durward *et al.* 1979, Okutani 1983,

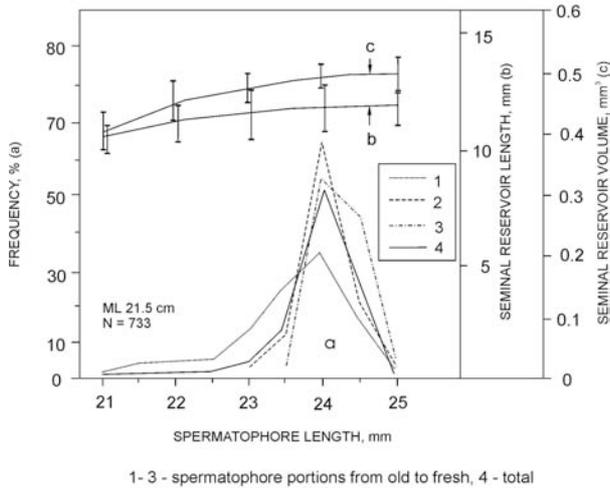


Fig. 3 Ontogenetic variability of spermatophore length, seminal reservoir length and volume in *Illex illecebrosus* from the Northwest Atlantic (ML 21.5 cm, mature male)

Arkhipkin 1989) both at maturation and at maturity, three types of SCO allometric growth in relation to mantle length exist (Nigmatullin & Sabirov 1987, 1995, Sabirov 1995).

1) Heteromorphic linear and weight growth of spermatophoric gland parts during maturation is characterized by a slight positive allometry. At maturity it becomes isometric or, sometimes, shows a weak tendency to a negative allometry. The growth rates of all the SG parts is similar (Todaropsinae, Illicinae) (Fig. 2a). The spermatophore length increases insignificantly (less than 10%) during ontogenesis (Nigmatullin *et al.* 1984, Laptikhovskiy & Nigmatullin 1992), and the proportions of their parts are almost stable (Fig. 3).

2) The growth of all SG parts during morphogenesis, functional maturation and spermatophore production has some features of a feebly expressed positive allometry (Todarodinae, Ornithoteuthinae, *Eucleoteuthis*, *Hyaloteuthis*) (Fig. 2b). The spermatophore length grows also insignificantly up to 10-15% (Fig. 4). There is no substantial growth both in size and capacity of sperm reservoirs (Sabirov 1995).

3) The positive character of allometric growth in the majority of the SG parts increases, attaining a maximum at the stage of active spermatophorogenesis. The growth of IV-VI spermatophoric gland parts (where the spermatophore middle and outer tunics are formed, and spermatophores attain the definitive appearance) is the most intensive (*Dosidicus*,

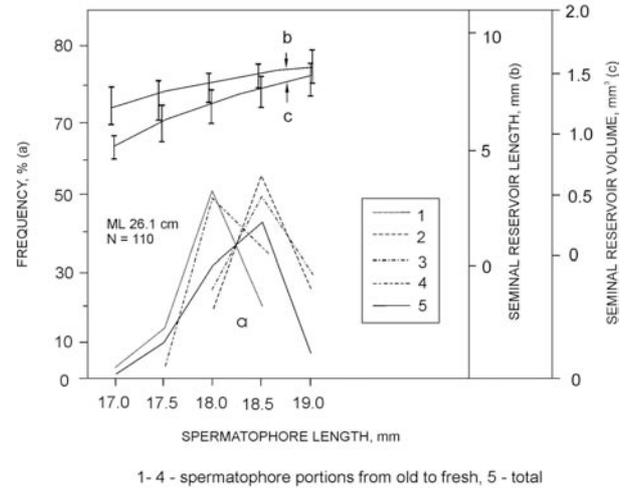


Fig. 4 Ontogenetic variability of spermatophore length, seminal reservoir length and volume in *Todarodes pacificus* from the Sea of Japan (ML 26.1 cm, mature male)

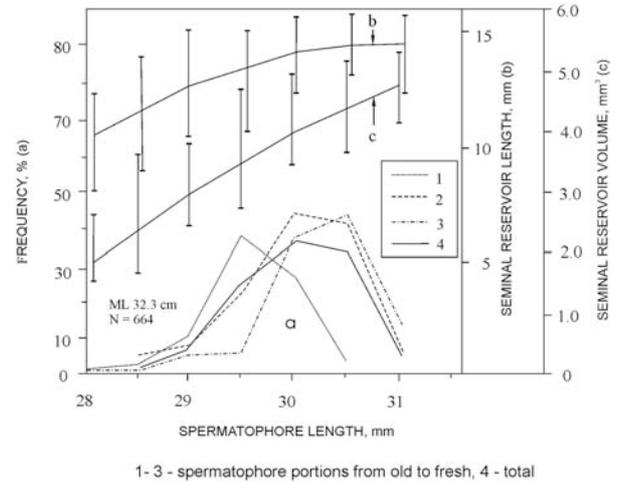


Fig. 5 Ontogenetic variability of spermatophore length, seminal reservoir length and volume in *Dosidicus gigas* from the Peruvian area of the Pacific. (ML 32.3 cm, mature male)

Ommastrephes, *Sthenoteuthis*) (Fig. 2c). There is a substantial increase in spermatophore length during its production, from 10-15 to 30% in this type of the SG parts growth (Zalygalin *et al.* 1977, 1983). Simultaneously there is an increase in both absolute and relative dimensions (in relation to spermatophore length) of sperm reservoirs, and the volume of packed sperm increases too (Fig. 5).

There is a functional maturation of males, with the production and accumulation of proper spermatophores in the Needham's sac before copulation occurs. The rate of spermatophore production reaches its maximum in the middle of this stage and attains a rate of about 5-30 spermatophores per day. The spermatophore length frequencies distribution is unimodal (Fig. 5), whereas

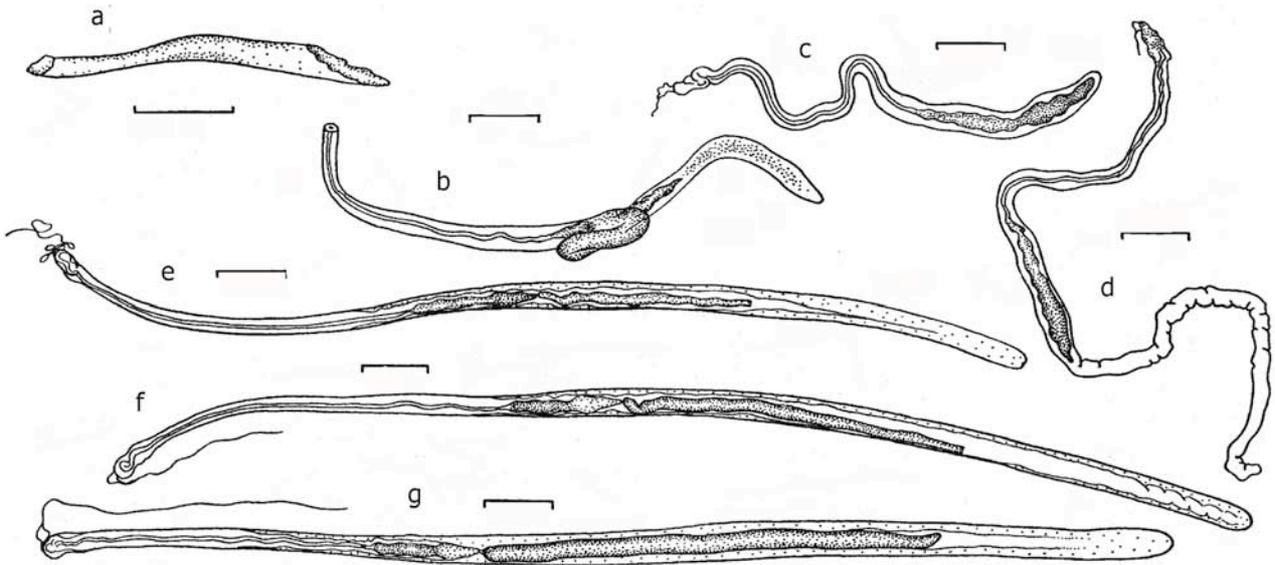


Fig. 6 The production of tentative (a-f) and proper (g) spermatophores in *S. pteropus*: a-d tentative spermatophores, e-f false spermatophores, g proper spermatophores. Scale 1 mm

other types of distribution (Zalygalin *et al.* 1977) occur only rarely. Relative spermatophore size decreases during squid growth. The same size males can produce spermatophores size of which differs by about 10%. Variations of the inner spermatophore elements could be significant as well, attaining up to 30% in the ejaculatory tube. The lowest variability was found in the cement bodies: about 10%.

6.2. Residual spermatophorogenesis and its breakdown. The testis in the process of degeneration (its size decreases significantly) and the rate functioning in the reproductive system is gradually decreased. This is a physiological pre-exhaustion and exhaustion state. There are still enough spermatophores in Needham's sac for a copulation. A residual spermatophorogenesis proceeds in the SG for a while, with formation of smaller spermatophores with reduced size of the sperm reservoir. Their morphology reminds one of false spermatophores (Fig. 6).

7. Full exhaustion (spent) and death. The functioning of the male reproductive system ends. The testis is nearly completely degenerated. In the spermatophoric sac some (usually 1-5) residual spermatophores are found. The SG is in a process of degeneration.

These periods of the reproductive system development and functioning allowed us to create ommastrephid male maturity scales (Nigmatullin *et al.* 1981, 1984, Zuyev *et al.* 1985, Nigmatullin 1989,

Arkhipkin 1992). Each stage diagnosis contains a description of both testis and SCO condition, thus it describes the whole reproductive system. As was shown above, the reproductive system growth and SCO functioning differs within the family. Therefore two separate maturity scales of ommastrephid reproductive systems were suggested for Illicinae (Nigmatullin *et al.* 1984, Nigmatullin 1989) and for Ommastrephinae (Zuev *et al.* 1985).

GENERAL MORPHOLOGY, SIZE AND NUMBER OF PROPER SPERMATOPHORES

Ommastrephid spermatophores are long, elastic tubes, covered by a cap at the proximal end (Figs 1, 6) and they are typical for squids (Hess 1982, Mangold 1987, 1989 b). But they have a cement body with sharp chitinous anterior tip. This is a unique trait as compared to the rest of oegopsid squid groups (Sabirov 1995).

No gradual changes have been revealed in spermatophore morphology in ommastrephid squids, but spermatophores are valuable for systematics (Roper & Mangold 1969, Zalygalin 1976, Nigmatullin & Sabirov 1987, 1995; Sabirov, 1990, 1995). Spermatophores of *Illex* are easily identified by the form of the large and rough tip of the cement body.

Males of *D. gigas* in Peruvian and Equatorial areas produce larger spermatophores than similar-sized squids from the Gulf of Californian. Morphometric spermatophore parameters of large and small males in the Peruvian area differ: the former have a larger cement body and smaller sperm reservoirs (Nigmatullin *et al.* 1999). Proportions of spermatophore parts in *O. bartramii* from the North Atlantic (average length of cement body 9.8%, sperm reservoir 33%, posterior empty part 30.3%) and from other parts of the species range (respectively, 11%, 44.7%, 22%) (Zalygalin *et al.* 1983), of the middle-sized and dwarf forms of *S. oualaniensis* (respectively, 13.2%, 42.8%, 13% and 14.5%, 32.2%, 24.2%) differ essentially. Thus, the difference between spermatophores of *O. bartramii* from North Atlantic and those from other parts of the species range, as well as in the case of *S. oualaniensis* (sympatric small and middle-sized forms), are higher than between genera within the same subfamily.

There is also some variability in cement body morphology. In Todarodinae (excluding *Todarodes pacificus*), Ornithoteuthinae and in the ommastrephin *Hyaloteuthis pelagica* the seminal reservoirs are incompletely divided into two parts by the cross-piece. In the other ommastrephid species the seminal reservoirs are undivided.

On the whole, the identification of spermatophores of Illicinae-Todaropsinae-Todarodinae-Ornithoteuthinae will be carried out mainly on qualitative characters, and Ommastrephinae on quantitative ones (Zalygalin 1976, Sabirov 1990, 1995).

The longest spermatophores were found in *S. pteropus* (mean length 16.4% ML), medium-sized form in *S. oualaniensis* (14.8%), *I. coindetii* (15.6%), the smallest in *O. antillarum* (6.0%), and *T. pacificus* (7.1%) (Table 2). Maximal absolute length of spermatophores has found in North Atlantic *O. bartrami* (till 53 mm) and from other parts of this species range (till 41 mm), *S. pteropus* (till 42 mm), *T. filippovae* (till 40 mm), *I. coindetii* (till 38 mm) (Table 2) and giant form of *D. gigas* (till 49.5 mm) (Markaida 2001). Minimal spermatophore lengths were observed in *H. pelagica* (5 mm) and in the dwarf form of *S. oualaniensis* (8.8 mm).

Generally, the spermatophore length (mm) was correlated positively with male ML, its relative length (%) negatively. The quantitative expression of the

relation between mantle length (L , cm), spermatophore length (l , cm) and spermatophore weight (P , mg) is species-specific. Moreover, it varied between allopatric groups of different species: *O. bartramii* North Atlantic with $l = 0.17 L - 2.06$ ($r = 0.812$), $P = 0.000978 L^{2.75}$ ($r = 0.867$), those from other parts of the species range are $l = 0.128 L - 0.96$ ($r = 0.72$), $P = 0.000132 L^{3.56}$ ($r = 0.840$); *S. pteropus* from the northeast part of the species range with $l = 0.186 L - 0.335$ ($r = 0.898$), those from Gulf of Guinea with $l = 0.186 L - 0.71$ ($r = 0.743$); in sympatric forms of *S. oualaniensis*: the dwarf form with $l = 0.158 L - 0.32$ ($r = 0.687$), and the medium-sized form with $l = 0.186 L - 0.36$ ($r = 0.718$).

The length of a given spermatophore is determined mainly by the length of part IV of the SG where the outer tunic of the spermatophore is formed. Correspondingly, the quantitative expression of relation between mantle length (L , cm), spermatophore length (l , cm) and length of part IV of the SG (M , cm) is also species-specific:

$$dM/dL = a M/l \text{ and } l = c M,$$

where a is an allometry coefficient, c a constant (for instance, for *S. pteropus* $c = 0.83-0.97$).

The minimal male fecundity as assessed by the maximum spermatophore number in Needham's sacs ranged from 100 spermatophores (0.02 cm³ of sperm) in *Hyaloteuthis*, to 600-1800 (0.15-1.4 cm³) in *Illex* and to 1000-2,500 spermatophores (1.5-4 up to 9 cm³ of sperm) in large-sized *Dosidicus*, *Ommastrephes* and *Sthenoteuthis*. Most species have a fecundity in the range of 200-800 spermatophores (Table 2).

TENTATIVE SPERMATOPHOROROGENESIS

The term "tentative spermatophore" means the spermatophore-like production of SG during male immature and maturing periods of ontogenesis (Fig. 6a-f), and it includes both tentative and false spermatophores (as opposed to the proper ones). The tentative spermatophore is devoid of sperm, the false one has sperm in a very small concentration and volume with a short seminal reservoir. These anomalous spermatophores are not accumulated in Needham's sac and they are constantly removed via the

Table 2 Spermatophore length and fecundity parameters in the squid family Ommastrephidae

Subfamily/Species	N	Region	ML, cm	l, mm	l, % ML	N	v, mm ³	V, cm ³
Illicinae								
<i>Illex condeii</i>	29	ECA	11.3-20.5	14.0-38.0 (25.0)	12.5-18.6 (15.6)	1000 (200-400)	0.2-2.8 (1.0)	1.0 (0.2-0.4)
<i>I. illecebrosus</i>	29	NWA	20.8-23.0	18.0-26.0 (23.5)	7.8-11.6 (10.8)	1800 (300-700)	0.3-1.0 (0.5)	0.9 (0.15-0.35)
<i>I. argentinus</i>	73	SWA	16.4-29.0	16.4-36.0 (26.0)	9.8-14.8 (11.5)	1600 (300-600)	0.3-2.4 (0.9)	1.4 (0.27-0.54)
Todaropsinae								
<i>Todaropsis eblanae</i>	12	ECA, WIO	11.6-15.0	15.0-30.0 (22.5)	12.4-21.1 (16.5)	120 (70-90)	2.1-7.8 (5.2)	0.6 (0.4-0.5)
Todarodinae								
<i>Todarodes pacificus</i>	20	NWP	20.9-27.3	14.9-21.2 (18.1)	6.5-7.9 (7.1)	150 (70-100)	0.3-2.4 (1.1)	0.5 (0.2)
<i>T. sagittatus</i>	3	ECA	24.5-24.8	23.0-29.0 (25.0)	9.4-11.8 (10.2)	250 (150-200)	4.0-5.2 (4.5)	1.2
<i>T. angolensis</i>	3	SEA	30.1-32.8	30.0-40.0 (33.4)	9.4-13.2 (10.6)	300 (200-250)	4.3-5.6 (4.8)	1.5
<i>Nototodarus hawaiiensis</i>	9	WIO	13.1-16.5	13.5-22.0 (18.0)	10.7-13.7 (12.7)	1000 (250-400)	1.8-2.4 (2.2)	2.2 (0.7)
<i>Marinolia hyadesi</i>	2	SWA	23.3-26.0	22.5-26.4 (25.0)	9.2-10.1 (9.6)	500 (250-300)	0.84-1.11 (0.97)	0.5 (0.2-0.3)
Ornithoteuthinae								
<i>Ornithoteuthis anillarum</i>	5	CA, SWA	8.6-19.2	8.2-11.2 (9.0)	4.4-8.5 (6.0)	100 (50-70)	0.1-0.25 (0.15)	0.15 (0.1)
<i>O. volantis</i>	1	WIO	9.3	9.2-10.0 (9.6)	10.0-10.8 (10.3)	100 (50-70)	0.07-0.2 (0.1)	0.1 (0.7)
Ommastrephinae								
<i>Dosidicus gigas</i>	73	ECP, SWP	13.0-37.7	17.0-31.0 (25.5)	6.9-13.0 (9.6)	1500 (500-700)	0.7-7.0 (3.0)	9.0 (4.0)
<i>Ommastrephes bartramii</i> forma A*	60	NWA, NEA	27.4-39.6	32.0-53.0 (40.0)	10.3-14.7 (12.3)	800 (400-500)	1.0-12.0 (3.0)	6.0 (3.0)
- " - forma B	47	SWA, SEA, SIO, SP	27.4-40.7	22.0-41.0 (33.0)	7.6-10.7 (9.5)	1700 (500-1000)	0.5-10.0 (3.0)	9.0 (4.0)
<i>Sthenoteuthis pieropus</i>	268	ECA, SEA	10.7-24.0	15.0-42.0 (33.8)	10.6-27.1 (16.4)	500 (200-400)	0.7-5.6 (3.5)	2.5 (1.5)
<i>S. oualaniensis</i> dwarf form	5	WIO, ECP	8.0-9.3	8.8-11.7 (11.0)	9.5-14.9 (12.2)	300 (100-200)	0.4-0.7 (0.5)	0.25 (0.1)
- " - middle-sized form	32	WIO, ECP	11.8-16.4	16.0-32.1 (22.9)	12.7-26.7 (14.8)	250 (100-200)	1.5-4.1 (2.6)	1.2 (0.5)
<i>Euceteuthis hawaiiense</i>	3	SIO, NWP	12.4-13.8	11.2-15.8 (13.0)	8.1-11.7 (10.6)	150 (70-100)	0.5-0.9 (0.7)	0.14 (0.07)
<i>Hyaloteuthis pelagica</i>	40	NEA, SEA, SWP	5.2-7.7	5.0-11.5 (9.5)	9.5-14.3 (13.0)	200 (100-120)	0.1-0.25 (0.15)	0.03 (0.02)

N - number studied mature males, ML - mantle length, l - spermatophore length, N - number (fecundity) of spermatophores, v - volume of seminal reservoirs, V - total sperm reservoirs volume (V = N x v, effective sperm production), modal values are in brackets.

NWA - Northwest Atlantic, NEA - Northeast Atlantic, ECA - Eastern Central Atlantic, SWA - Southwest Atlantic, SEA - Southeast Atlantic, WIO - Western part of Indian Ocean, SIO - Southern part of Indian Ocean, NWP - Northwest Pacific, ECP - Eastern Central Pacific, SWP - Southwest Pacific, SP - South part of Pacific Ocean.

**O. bartramii* forma A is represented by squids from North Atlantic, while squids forma B are from other parts of the species range.

penis (with the exception of the last false quasi-normal spermatophores).

The phenomenon of tentative spermatophore is important for understanding the functioning of the male reproductive system in ontogeny as a whole including immature and maturing periods. Earlier on spermatophorogenesis in cephalopods was studied in mature adult males only (Brock 1878, Drew 1919, Blancquart 1925, Weill 1927, Hess 1982, Mann 1984). It was a static approach however. Our study is based on dynamic ontogenetic approach and shows that the SG functioning in immature males with tentative production is normal for cephalopods. We found this phenomenon in incirrate octopods, sepioids, loliginid and different oegopsid squids (Laptikhovskiy & Nigmatullin 1987, 1992, Nigmatullin & Sabirov 1987, 1995, Nigmatullin *et al.* 1996, Zuyev *et al.* 2002). All types of tentative spermatophores, which gradually became more complicated in immature and maturing stages of male ontogenesis (See: section Ontogenetic periods ... and Fig. 6), were found in all studied ommastrephid species (Nigmatullin & Sabirov 1987, 1995, Sabirov 1995).

Such an early functioning of the SCO with an immature testis and abortive production can only be understood from the point of view of the final goal of the reproductive system and the male as a whole functional system. This goal is the packaging of spermatozoa in spermatophores with a minimal loss and then their transfer to the female (Clark 1981, Mann 1984). Tentative SCO functioning takes place in parallel with testis maturation. In the process of tentative spermatophore formation, more and more SCO parts become involved; precision, reliability and productivity of their operation increase and the mechanism of the SCO «conveyor» and the reproductive system as a whole become adjusted. As a result, the efficiency of the whole reproductive system at the organism level approaches the optimal working condition by the time of complete maturation of testis and the beginning of proper spermatophorogenesis. Hence a delayed development of hectocotylus structure compared to the reproductive system makes sense: its main function (transfer of spermatophores to the female) is carried out at the very last stages of the male reproductive system functioning.

MALE REPRODUCTIVE STRATEGIES

Different ecological groups of ommastrephids show different types of reproductive system growth and SCO functioning (Nigmatullin & Sabirov 1987, 1995, Sabirov 1995).

In neritic-slope Illicinae SCO growth slows at maturity, and the allometric coefficient becomes less of 1. Spermatophore size during their accumulation in Needham's sac in the mature period of ontogeny increases slowly, and modal sizes of spermatophores produced at different times are usually the same. The increase in length and capacity of sperm reservoirs during the individual growth is insignificant (Fig. 3). As a rule males produce relatively smaller, but more numerous spermatophores. The male fecundity depends on the volume of Needham's sac, and on the number of periods of active formation of spermatophores between copulations, which number is higher in larger males. A similar type of reproductive system functioning was found in some Loliginidae (Sabirov & Ogareva 1987) and Gonatidae (Nigmatullin *et al.* 1996).

In the alternative group of the large oceanic Ommastrephinae, mature males produce spermatophores the length of which permanently increases, as does the sperm reservoir capacity. Its background is a permanent male somatic growth, and positive allometry of the SCO growth throughout the entire ontogeny, it attains its maximum at active spermatophorogenesis. The allometric coefficient is particularly high in the functionally most important SCO parts. Spermatophore numbers change insignificantly over male growth. But spermatophore size and sperm reservoir volume increase significantly during their accumulation in Needham's sac in mature period of ontogeny (Fig. 5). Accordingly, the volume of sperm in the sperm reservoirs is higher in larger males because of larger spermatophores. This strategy is peculiar to the opportunistic species dominating among cephalopods of the epipelagic open waters (*Dosidicus*, *Ommastrephes*, *Sthenoteuthis*).

In short, these particular features of the spermatophore production result from the changes in the spermatophoric gland allometric growth patterns in adult squids (Fig. 2-5). In all there are three types of reproductive strategies in ommastrephids, all of them

directed to maximization of **effective sperm production** (ESP – number of sperm packed in proper spermatophores during ontogeny). The concrete mechanisms for attainment of this goal are the following:

1) **Neritic type** (Illicinae, Todaropsinae): an increase of Needham's sac volume and number of periods of formation and accumulation spermatophores between matings;

2) **Intermediate type** (Todarodinae, Ornithoteuthinae, *Eucleoteuthis*, *Hyaloteuthis*): an increase of the volumes of both Needham's sac and seminal reservoirs of spermatophores;

3) **Oceanic type** (*Dosidicus*, *Ommastrephes*, *Sthenoteuthis*): a significant increase during ontogeny of the size of spermatophores and their seminal reservoirs

CONCLUSION

The new data and ideas obtained on spermatophorogenesis in squids (ommastrephid taken as an example) were due to the new methodological ontogenetic approach. It is based on detailed measurements of different parts of the SG and all spermatophores in males at all stages of ontogeny. This methodology offers the possibility for a comparative study of the process of male reproductive system developing and functioning in different groups of cephalopods.

An important result of using this methodology was the discovery of the phenomenon of tentative (or tune-up) spermatophorogenesis. Due to the tentative spermatophorogenesis, the reproductive system as a whole becomes adjusted and up to state by the mature stage. This is the main functional task of this phenomenon. From an evolutionary point of view, the tentative spermatophorogenesis is probably a heterochrony related to the complication of cephalopod spermatophore and SCO structures and to an increase in the cost of producing spermatozoa. In this context, it is important to note that the form of mature spermatophores from Needham's sac in *Nautilus* has a characteristic coiled appearance (Haven 1977, Mann 1984, Tsukahara 1988) like a tentative spermatophore in coleoids. Thus, the coleoid cephalopod in comparison to Nautiloidea is the next stage in

evolution of male reproductive system functioning.

The male reproductive system of ommastrephids is a highly-integrated functional system and its functioning during ontogenesis is regulated precisely by the change in SG allometric growth patterns. On the basis of this mechanism during the adaptive radiation of the family, the main characteristics of spermatophorogenesis were strikingly changed, that appears in the number and size of spermatophores, size of their seminal reservoirs, the volume of packed sperm per spermatophore and correspondingly the ESP values. As a result of family evolution, with the expansion from an initial shelf-slope habitat to the oceanic realm, three male reproductive strategies were formed, and these squids are the representatives of the three main ecological groups (life forms) of ommastrephids (Nigmatullin 1979).

The whole range of the reproductive system functioning in ommastrephid males represents a continuum, which has two extremities with the shelf-slope species at one end, and the eunectonic-oceanic species at the other hand. It is related to the main stream of ommastrephid evolution (Nigmatullin 1979). Females demonstrate the same two main (shelf-slope and oceanic) and intermediate types of reproductive strategy (Nigmatullin & Laptikhovskiy 1994, 1999). It is important to emphasize that the value of effective sperm production in males is correlated with the value of potential and actual fecundity in females. Both the males and the females increased their fecundity (for males the number of spermatophores and ESP value) from neritic *Illex*-like squid to true oceanic *Sthenoteuthis* and *Ommastrephes*-like squids. For females this increase is estimated as a factor of 5-20 (Nigmatullin & Laptikhovskiy 1994, 1999). Same correlation between size and number of spermatophores and number of eggs produced per clutch was described in arthropods - pseudoscorpions (review: Proctor 1998).

Different reproductive strategies that had been evolved in ommastrephids on the basis of monocyclicity and short life cycles provides an optimal reproduction in diverse pelagic habitats of both shelf-slope and oceanic waters.

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