LARVAE OF MARINE BIVALVES AND ECHINODERMS

V.L. KASYANOV ▪ G.A. KRYUCHKOVA
V.A. KULIKOVA ▪ L.A. MEDVEDEVA

Scientific Editor
David L. Pawson

LARVAE OF MARINE BIVALVES AND ECHINODERMS

V.L. KASYANOV, G.A. KRYUCHKOVA,
V.A. KULIKOVA AND L. A. MEDVEDEVA

Scientific Editor

David L. Pawson

SMITHSONIAN INSTITUTION LIBRARIES
Washington, D.C.
1998

Smin B87-101

Lichinki morskikh dvustvorchatykh
mollyuskov i iglokozhikh

Akademiya Nauk SSSR
Dal'nevostochnyi Nauchnyi Tsentr
Institut Biologii Morya

Nauka Publishers,
Moscow, 1983 (Revised 1990)

Translated from the Russian

Library of Congress Cataloging-in-Publication Data

Lichinki morskikh dvustvorchatykh molliuskov i iglokozhikh. English Larvae of marine bivalves and echinoderms/V.L. Kasyanov . . . [et al.]; scientific editor David L. Pawson.

p. cm.

Includes bibliographical references.

1. Bivalvia — Larvae — Classification. 2. Echinodermata — Larvae — Classification. 3. Mollusks — Larvae — Classification. 4. Bivalvia — Larvae. 5. Echinodermata — Larvae. 6. Mollusks — Larvae.

I. Kas'ianov, V.L. II. Pawson, David L. (David Leo), 1938-III. Title.

QL430.6.L5313 1997 96-49571

594'.4139'0916454 — dc21 CIP

Translated and published under an agreement, for the Smithsonian Institution Libraries, Washington, D.C., by Amerind Publishing Co. Pvt. Ltd., 66 Janpath, New Delhi 110001

Printed at Baba Barkha Nath Printers, 26/7, Najafgarh Road Industrial Area, New Delhi – 110 015.

UDC 591.3

This book describes larvae of bivalves and echinoderms, living in the Sea of Japan, which are or may be economically important, and where adult forms are dominant in benthic communities. Descriptions of 18 species of bivalves and 10 species of echinoderms are given, and keys are provided for the identification of planktotrophic larvae of bivalves and echinoderms to the family level. Information on identified species is preceded by a description of the morphology, physiology, and behavior of larvae of the given classes.

The book is addressed to marine biologists, embryologists, zoologists, and specialists engaged in fisheries.

FOREWORD TO THE ENGLISH EDITION

The Smithsonian Institution Libraries, in cooperation with the National Science Foundation, has sponsored the translation into English of this and hundreds of other scientific and scholarly studies since 1960. The program, funded with Special Foreign Currency under the provisions of Public Law 480, represents an investment in the dissemination of knowledge to which the Smithsonian Institution is dedicated.

In this volume, the authors review and summarize many aspects of the early life history of the marine bivalve mollusks and echinoderms that are common in the Sea of Japan. Several of the species covered are of commercial value, and the scientific information given here will be very useful in planning successful exploitation and management. Many of these species have a wide distribution in the Northern Hemisphere, and thus the book is of broad regional interest.

For many readers, this English-language translation presents for the first time a review of Russian research on mollusks and echinoderms that would be otherwise inaccessible. It updates a 1980 book (in Russian) by V.L. Kasyanov, L.A. Medvedeva, Y.M. Yakovlev and S.N. Yakovlev, and it includes relevant literature references up to, and including, the year 1990. The editors have taken great care to ensure that this translation accurately reflects the original text. However, some scientific names and parts of the classification, especially in the Echinodermata section, have been changed to reflect current thinking, and to make the data more readily accessible.

This work is a significant addition to the literature on embryology and larval development of mollusks and echinoderms, and it should prove to be important and useful to fishery biologists, embryologists and marine biologists.

DAVID L. PAWSON
National Museum of Natural History
Smithsonian Institution
Washington, D.C.

CONTENTS

INTRODUCTION

The life cycles of commercially exploited and cultured mollusks and echinoderms comprise, in most cases, a prolonged benthic period and a brief pelagic period. In the benthic period the animal feeds, grows, attains sexual maturity, produces gametes, and participates in reproduction. The production of gametes (gametogenesis) and their subsequent release and fertilization by mollusks and echinoderms inhabiting temperate waters usually occurs every year. The annual reproductive processes in bivalves and echinoderms inhabiting the Sea of Japan were described earlier by researchers in the Laboratory of Embryology, Institute of Marine Biology [Razmnozhenie iglokozhikh i dvustvorchatykh mollyuskov (Reproduction of Echinoderms and Bivalves), Kasyanov *et al.*, 1980]. The present book is a continuation of the 1980 publication. Here we describe the larvae of bivalves, sea stars, sea urchins, brittle stars, and sea cucumbers of the Sea of Japan, which are economically important or abundant forms in benthic communities. The larvae of these species are planktonic, feed on phytoplankton, grow, and are carried out to sea by currents. Then they migrate from the surface to the bottom, settle there, and metamorphose, thus completing the pelagic period of their life cycle. This period is less known and understood than the benthic, even though many papers and books deal with the subject. Among such works, mention should be made of those by Thorson (1936, 1946, 1950), Mortensen (1921, 1937, 1938), Mileikovskii (1977, 1981), and Jagersten (1972). The structure of the larvae discussed here have been examined by O.M. Ivanova-Kazas in her two-volume work on the embryology of mollusks and echinoderms (Ivanova-Kazas, 1977, 1978).

Particular attention is paid in the present book to those characters which make possible the determination of the species affinities of larvae. Thus 18 species of bivalves and 10 species of echinoderms are described in detail, and keys are provided to enable identification to family level of planktotrophic larvae of bivalves and echinoderms from Peter the Great Bay. The descriptions of the larvae are preceded by descriptions of the morphology, physiology, and

behavior of the larvae of individual classes, based on published and original material. Larvae are examined not so much from an embryological point of view (as a developmental stage of a definitive animal), but from a zoological viewpoint (as an organism endowed with all the systems required for a viable existence in the plankton). The general description of the larvae studied begins with a brief report on early development (up to the stage of trochophore or dipleurula). Cytoembryological aspects of early development are not described because extensive literature is available on this topic. The description concludes with a summary of the process of metamorphosis and a brief characterization of lecithotrophic larvae. Ecological aspects of the pelagic life of larvae and their settling to the bottom are not described due to space constraints of this book.

Plankton samples were collected mainly in Vostok Bay, which is situated in the eastern part of Peter the Great Bay of the Sea of Japan. To obtain the required stage of larval development, artificial fertilization with subsequent culturing of larvae was done, in addition to selection of larvae from plankton samples and subsequent culturing. This work was carried out under the guidance of V.L. Kasyanov, assisted by S.Sh. Dautov, who described the larvae of the sea star *Asterias amurensis* and compiled Table 5 (Types of Development of Sea Stars).

The authors are grateful to V.A. Sveshnikov, the editor-in-chief of this volume, to V.V. Malakhov and V.G. Chavtur for excellent advice, and to O.M. Korn, T.I. Ponurovskaya, T.N. Chernenko, and the staff in the photographic laboratory of the Institute of Marine Biology who assisted in manuscript preparation. We thank the corresponding member of the Academy of Sciences, USSR, A.V. Zhirmunskii, the entire staff of the Laboratory of Embryology, Mrs. Irina Barsegova and Mrs. Tatiana Kotnova for their support during this endeavor. Collection of material and its analysis was partially financed by TINRO MRKh* of the USSR. The authors are grateful to Mr. Gulab Primlani and Oxonian Press for translating their book into English.

In the new edition we have introduced corrections and additions. The list of species described in the book has been enlarged, new illustrations have been added, and species sections have been rewritten. It is hoped that through this English language edition the book will reach a new circle of readers.

V. Kasyanov

---

* Pacific Scientific Research Institute of Fisheries and Oceanography, Ministry of Fisheries—General Editor.

CHAPTER 1

LARVAE OF MARINE BIVALVES (MORPHOLOGY, PHYSIOLOGY, AND BEHAVIOR)

EARLY DEVELOPMENT

The development of bivalves has been best studied in *Dreissena polymorpha*, a species inhabiting fresh and brackish waters and exhibiting a development typical for marine bivalves (Meisenheimer, 1901); in Unionidae—freshwater mollusks endowed as larvae, at the glochidium stage, with an adaptation to temporary parasitism (Lillie, 1895); and in *Crassostrea gigas* — a marine bivalve in which the larva is a typical veliger (Fujita, 1929).

Egg

The eggs of bivalves contain relatively little yolk, which is uniformly distributed throughout the egg cell. The position of an animal pole is indicated by the extrusion of polar bodies in the egg cell. Bivalve eggs have a diameter of 40–360 μm. Like the eggs of other Bilateria with external fertilization, they are surrounded by a vitelline and a jellylike membrane. The thickness of the vitelline membrane is 1–2 μm; the thickness of the jellylike membrane may be more than 10 μm. The jellylike membrane is generally transparent, delicate, and is poorly defined after fixation (Drozdov and Kasyanov, 1985b). The eggs have a jellylike membrane in addition to the vitelline one (Allen, 1953, 1961).

Fertilization: Eggs and spermatozoa are released in water where fertilization and subsequent development take place. In species that brood the embryo and larva in the mantle cavity or gills, sperms in the water pass through the incurrent siphon of the maternal organism into the mantle cavity or oviduct where fertilization occurs. In *Mysella tumida* spermatozoa fall in the gill chambers of the female and the transported sperms become attached to the gill

filaments by microvilli issuing from the sperm acrosome. The sperm may remain so attached for several months, until fertilization (O'Foighil, 1985). In *Crassostrea virginica* (Longwell and Stiles, 1969), *Ostrea rivularis* (Hamada, 1927), and *Mytilus edulis* (Longo and Anderson, 1969), fertilization takes place at the stage of metaphase I division of the maturing oocyte. Contrarily, in *Ostrea circumpicta* and *Spisula solidissima*, the oocytes retain the germinal vesicle until the time of fertilization (Hamada, 1927; Schechter, 1941; Sachs, 1971). According to observations by Vasetskii (1973) and Ginzburg (1974), in *Crassostrea gigas*, *Spisula sachalinensis* and *Mactra chinensis*, fertilization may take place at any stage of the process of maturation up to metaphase II. According to Hylander and Summers (1977), upon activation of the sperm during fertilization, the axial rod of the acrosome surrounded by the membrane of the acrosomal vesicle is transformed into an acrosomal process making contact with the plasmic membrane of the microvilli of the egg.

Cleavage : The eggs of bivalves are subject to spiral heteroquadrant cleavage. The cleavage plane of the first division divides the egg into two unequal blastomeres: the smaller *AB* and the larger *CD*. After the second division, a four-celled embryo is formed in which blastomere *D* is much larger than the remaining blastomeres (Figures 1 and 2). In many species, during division by cleavage, a polar lobe forms; this is a large cytoplasmic process at the vegetal pole which, during division by cleavage, merges with blastomere *CD* and in the second division, with blastomere *D* (Figure 3). Cleavage in bivalves loses its synchrony early. Blastomere *D* and its daughter cells divide faster than the other blastomeres of the embryo. Among the daughter cells of blastomere *D* of the main quartet, blastomeres 2*d* and 4*d* are distinguishable, which are the first and second somatoblasts. In species with a polar lobe, its material first merges with blastomere 1*D* and then with blastomeres 2*d* and 4*d*.

Cleavage in bivalves is characterized by a strict order of sequence of dexitropic and laeotropic divisions. However, in many cases (for example, in *Crassostrea*), this order is disturbed (Fujita, 1929).

Blastomere 2*d*, after four small cells have separated from it, splits uniformly into the right cell *Xd* and the left *Xs*. Blastomere 4*d* divides into two equal cells, *Md* and *Ms* (Figure 4, A).

As a result of cleavage, a ciliated sterro- or coeloblastula is formed; this is the first larval stage of bivalve mollusks which is provided with cilia. A sterroblastula is characteristic of marine bivalves and a coeloblastula of brackish and freshwater mollusks (Malakhov and Medvedeva, 1986). The sterroblastular cavity is occupied by a large cell, 2*d* or its daughter cells (Figure 4, B). In the fresh- and brackish-water mollusk *Dreissena polymorpha*, on the other hand, the blastocoel, which performs an osmoregulatory function, is formed very early (Meisenheimer, 1901). The primordium of the shell gland

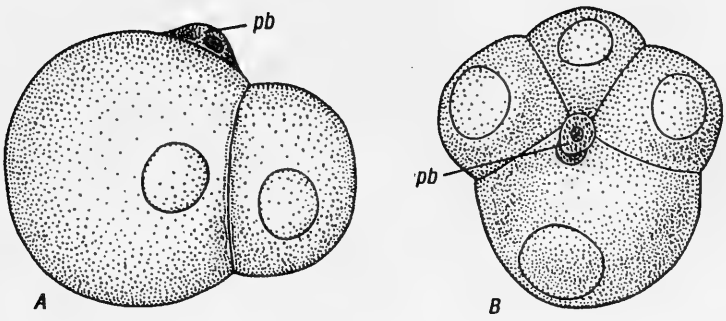


Figure 1: Cleavage in *Dreissena polymorpha* Pall. (from Meisenheimer, 1901).
A— stage with two blastomeres; B — with four blastomeres; pb— polar body.

is formed as a result of multiplications of *Xd* and *Xs* cells (Figure 5). In marine bivalves the primordium of the shell gland is invaginated in the embryo from the very beginning. In freshwater forms it initially lies in the blastula wall and then invaginates in the embryo (Lillie, 1895; Meisenheimer, 1901).

Cells *Md* and *Ms* each produce one entodermal cell (enteroblast) and then transform into mesodermal teloblasts from which the transitory mesodermal band originates later. Some part of the mesenchyme probably originates from the ectodermal cells (Meisenheimer, 1901). A notable contribution to the study of the early development of bivalves is the paper by Gustafson and Reid (1986). They have described the development of a primitive protobranch bivalve, *Solemya reidi*. Cleavage of the large (270 μm in diameter) eggs of this species is to date the only example, possibly, for bivalve mollusks of an initial homoquadratic spiral cleavage with equal-sized blastomeres.

Incomplete division has not been observed in bivalves.

Gastrulation : Gastrulation occurs through the invagination of the entoderm near the vegetal pole of the embryo. After eversion of the shell gland, the blastopore shifts far forward on the ventral side of the embryo.

Trochophore

In marine bivalves already in the blastula (sterroblastula) stage, one or several circlets of cilia appear and at the animal pole—cilia of the aboral organ. Thus, in marine bivalves the blastula stage is a transition to free living. Free living is also possible for stages with an everted rudimentary shell gland and a well-formed blastopore. After eversion of the rudimentary shell gland, a trochophorelike larva forms (Figure 6). In the fresh- and brackish-water

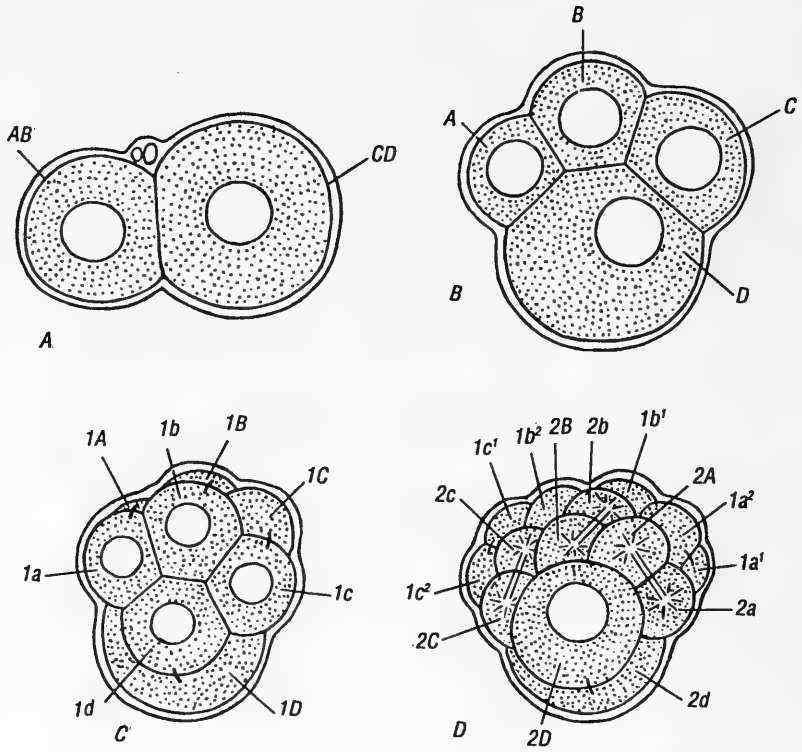


Figure 2: Cleavage in *Mactra chinensis* (from Medvedeva and Malakhov, 1983).
A — stage with 2 blastomeres, lateral view; B — stage with 8 blastomeres, view from animal pole; C — stage with 8 blastomeres, view from animal pole; D — stage with 16 blastomeres, view from vegetal pole. Legend given in text.

bivalve *D. polymorpha*, only trochophore larvae are free living (Meisenheimer, 1901; see Figure 5).

The prototroch—a broad ciliary circlet—is the main organ of locomotion of the trochophore larva. On the animal pole of the trochophore an apical tuft of cilia appears, under which lies a thickening of the ectoderm (aboral organ). The mouth is situated under the prototroch and leads to blind gut. The terminal part of the gut adjoins the ventral wall of the trochophore where, later, the hind gut and anus form.

Veliger

The trochophore transforms into a veliger, which has a more complex structure (Figures 7 and 8). The animal pole of the trochophore develops into

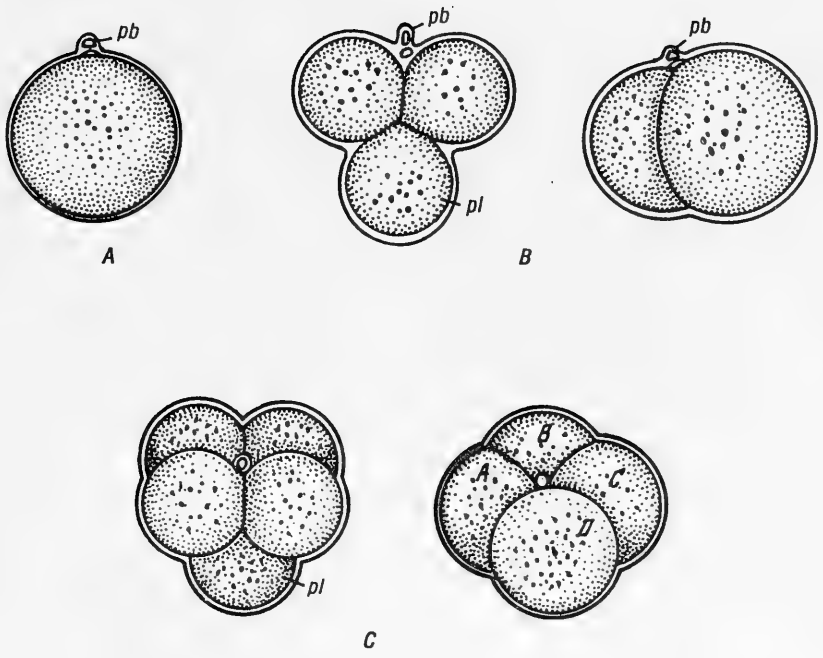


Figure 3: Cleavage in *Pinctada maxima* (Jameson) (from Wada, 1941).
A — zygote; B — with two blastomeres; C — with four blastomeres; pb — polar body; pl — polar lobe.

a sail or velum—a disk fringed with cilia that serves as a swimming organ. An apical tuft of sensory cilia is located in the center of the velum. The rest of the larval body is covered with a translucent shell through which the internal organs are visible.

The description of the internal structure of the veliger is based largely on Meisenheimer's (1901) classical description of the development of *Dreissena polymorpha.*

Feeding : The digestive system consists of the ectodermal foregut, entodermal midgut, and ectodermal hind gut. Capture of food and its transfer to the oral opening is accomplished by means of the ciliary band of the velum (Figure 9). The velum is thus important in feeding as well as in locomotion. According to Yonge (1926), the food particles from the long cilia of the preoral outer band are passed to the adoral band. The distance between them in the veliger of *O. edulis* is several microns. The length of the cilia of the adoral band is about 8 µm and the width of the band about 20 µm. Food particles are encased in mucus as they move along the adoral band toward the

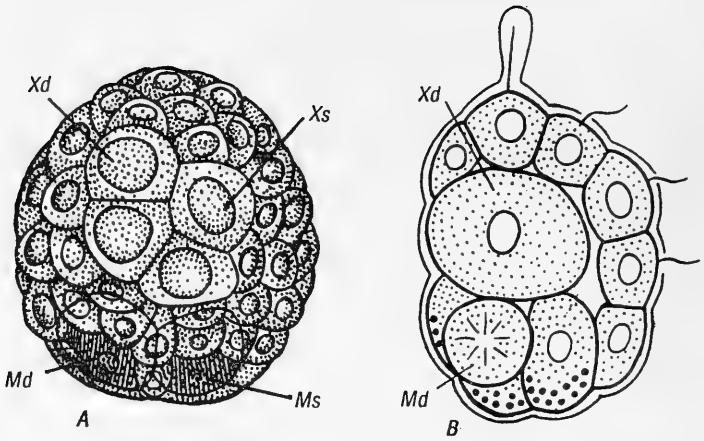


Figure 4: Blastula of *Dreissena polymorpha* Pall. (A) (from Meisenheimer, 1901) and *Mactra chinensis* (B) (from Medvedeva and Malakhov, 1983). Legend given in the text.

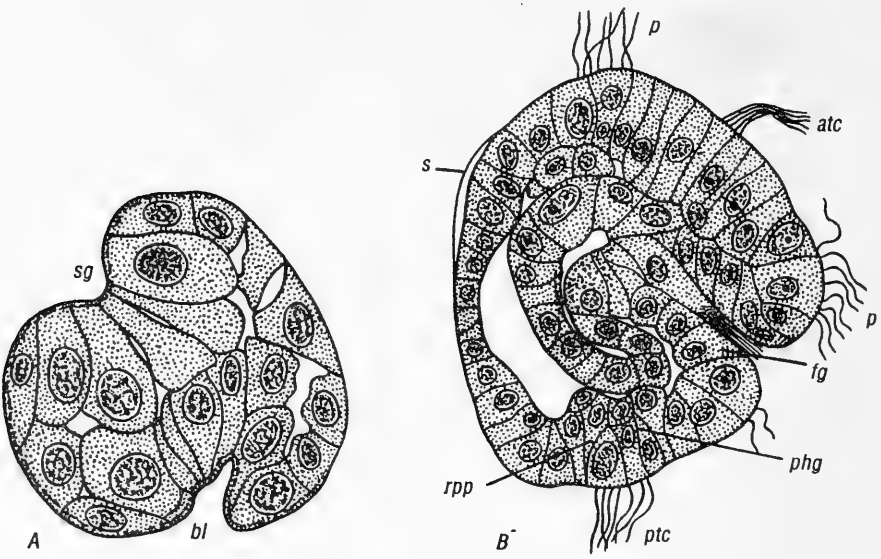


Figure 5: Gastrula (A) and trochophore (B) of *Dreissena polymorpha* Pall. in sagittal section (from Meisenheimer, 1901).

atc — apical tuft of cilia; bl — blastopore; fg — foregut; p — prototroch; phg — primordium of hind gut; ptc — postanal tuft of cilia; rpp — renopericardiac primordium; s — shell; sg — shell gland.

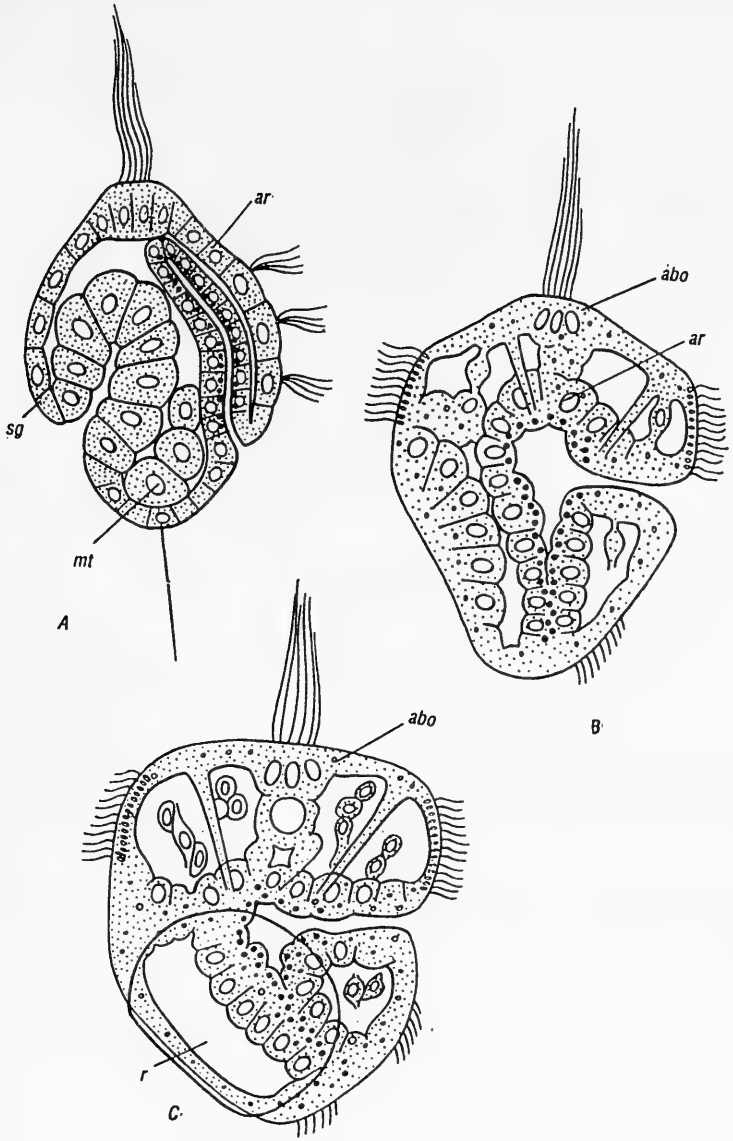


Figure 6: Early larval development in *Mactra chinensis* (from Medvedeva and Malakhov, 1983).

A — larva with everted shell gland and blastopore, lateral view; B — trochophore; C — commencement of shell formation.

abo — aboral organ; ar — archenteron; mt — mesodermal teloblasts; r — rudiment of shell; sg — shell gland.

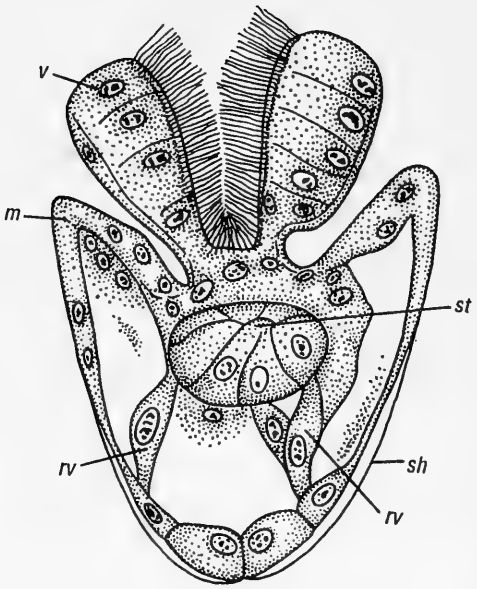


Figure 7: Early veliger of *Cardium edule* L. (from Creek, 1960).
m — mantle; rv — retractor of velum; sh — shell; st — stomach; v — velum.

oral opening. Below the adoral band, under the oral opening, there is a postoral ciliary band comprising one row of complex 15–20 µm long cilia. The coordination of the beating cilia of the pre- and postoral ciliary bands ensures, according to Strathmann and his colleagues (1972), concentration of food particles from the water by the ciliary band. The larger the cilia of the preoral band, the greater the rate (and the lower the efficiency) of filtration of particles (Strathmann and Leise, 1979).

The rate of filtration of food particles (flagellate algae at a concentration of 1.5–5.5 × 10^3 cells/ml water) in *M. edulis* larvae is 11.4 µl/hr per larva (Riisgard *et al.*, 1980). At a concentration of food particles exceeding 200 µl, the rate of feeding decreases (Bayne, 1976). Walne (1965) showed that larvae of *O. edulis* efficiently capture particles from 3.0 to 8.0–9.0 µm in size. The larvae of *M. edulis* cannot efficiently capture particles less than 1.0 µm or more than 8.0–9.0 µm in size (Riisgard *et al.*, 1980). Colloidal substances in suspension are not suitable for feeding; they form lumps which entangle the larvae of *M. edulis*. At the same time, frozen or lyophilized algae and granulated food from macrophytes and detritus are better assimilated (Mason, 1972). The larvae of *Crassostrea virginica* and *Mercenaria mercenaria* do not use organic debris and pure bacterial cells as food (Loosanoff, 1969).

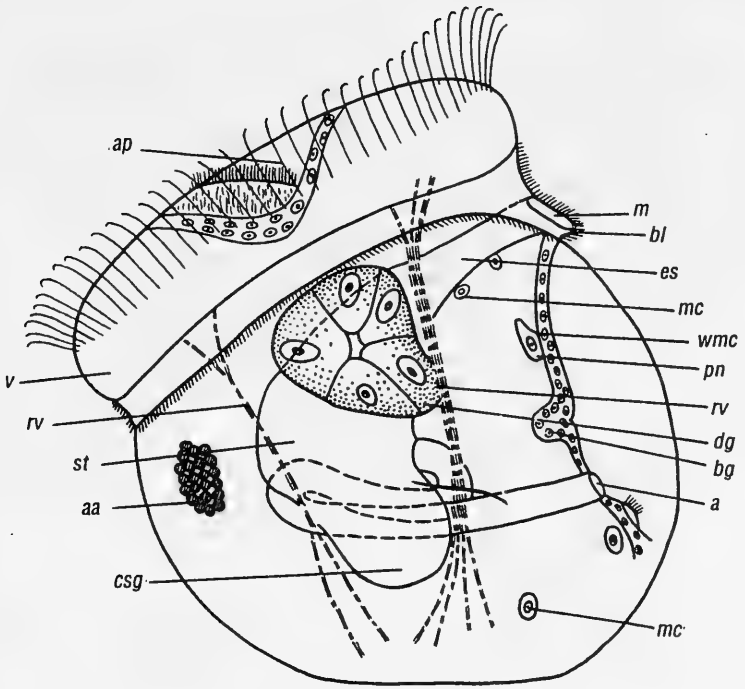


Figure 8: Veliger of *Ostrea edulis* L. (from Erdmann, 1935).
a — anus; aa — anterior adductor; ap — apical plate; bg — byssus gland; bl — buccal lobe (plate); csg — gland of crystalline style; dg — digestive gland; es — esophagus; m — mouth; mc — mesenchymal cells; pn — protonephridium; rv — retractor of velum; st — stomach; v — velum; wmc — wall of mantle cavity.

A positive relationship has been established between rate of larval growth and number of cells caught by the larva. Flagellate algae, such as *Monochrysis* and *Isochrysis*, devoid of a cell wall and forming no toxic substances, constitute a better food for larvae (Ukeles, 1969, 1975). At a low concentration of food particles, the rate of filtration and its efficiency increase.

The postoral tuft of cilia lies in the buccal region and is formed by the postoral ciliary band. According to Waller (1981), these cilia may have a sensory function or facilitate expulsion of excess mucus and excess food from the mouth.

The oral opening, situated at the edge of the lower part of the velum, leads to the esophagus. Cells of the esophagus contain vacuoles and bear powerful cilia that fill the lumen of the esophagus and project exteriorly through the oral opening. The next section of the digestive tract is the stomach. The gastric cells contain vacuoles; cilia are absent. The digestive gland or liver consists

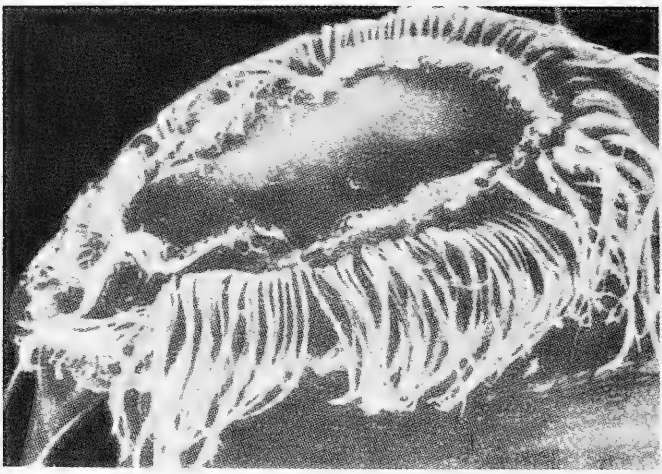


Figure 9: Velum of the veliger of *Ostrea edulis* L. (from Waller, 1981).

of two pouches (lobes) arising from the stomach (see Figure 8). The cells of the liver vacuolize later. The right lobe of the liver is larger than the left and shifted backward. Cells of the digestive gland are marked by larger size and sometimes by color—greenish or reddish-brown depending on food. Accumulated granules of food matter are visible in them. Neutral lipids, and not glycogen as in adult mollusks, are the principal energy reserve of larvae (Holland and Spencer, 1973; Holland, 1978). A changeover to the new reserve nutrients takes place in three- to five-month-old spat (Holland and Hannant, 1974). The large liver allows us to suggest a storage function for this organ; a large part of the reserve nutrients is consumed during metamorphosis and in the initial period after settling on the bottom, during which the larva does not feed (Holland and Spencer, 1973). It may be that together with such large cells, the larval liver contains small undifferentiated cells of the future definitive liver.

The gland of the crystalline style forms on the right side of the posterior part of the stomach. It is lined with cilia. At the end of larval life, or after the larva settles to the bottom, the cells of this gland secrete the crystalline style containing digestive enzymes. Behind the stomach lies the small intestine, which forms a loop, and in the larvae of *M. edulis* the blind gut (Bayne,1971). In the early veliger the gut may lack a lumen and resemble a cylinder of closely packed cells (La Barbera, 1975). The gut epithelium is simple, flattened, and bears cilia. The small intestine passes into the short hind gut—the proctodeum—with vacuolated cells. The proctodeum opens exteriorly through the anus; cilia are visible in its lumen.

The gut wall lacks muscles and the movement of food in the gut is accomplished by cilia. In the larvae of some species, behind the anal opening, which is surrounded by short cilia, there is a postanal tuft of dense 15 µm long cilia (Figure 10). The postanal tuft facilitates removal of fecal matter from the mantle cavity.

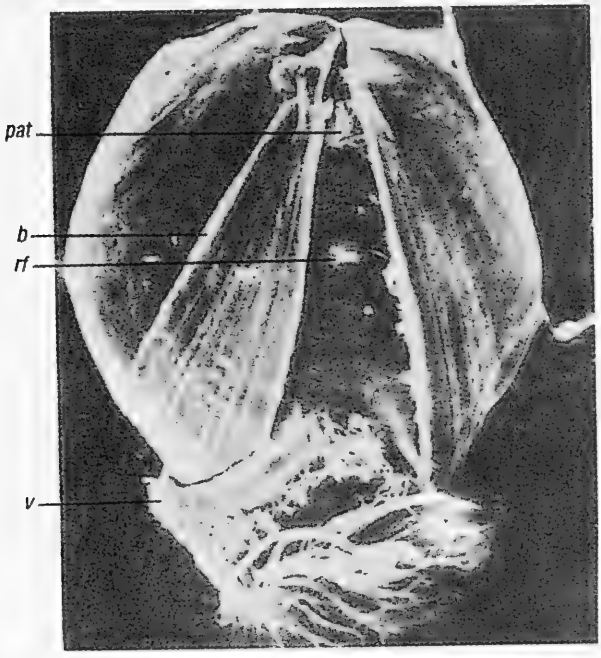


Figure 10: Veliger of *Ostrea edulis* L. (from Waller, 1981).
Posterior view: b — border between prodissoconch I and II; pat — postanal tuft of cilia; rf — rudiment of foot; v — velum.

Respiration : A specialized respiratory apparatus is absent in the larvae of bivalves. Oxygen is supplied and carbon dioxide eliminated through diffusion. Since diffusion is facilitated by a flow of water, the various locomotory hydrokinetic structures of the larvae, in addition to other functions, also accomplish respiration. These are, the pre- and postoral ciliary tufts, and also the ciliary tracts of the esophagus and gut. Respiration is further assisted by cilia situated along the margin of the mantle cavity, including the region of future gill formation.

Transport of substances : The larvae of bivalves lack a circulatory system. Nor do they possess a branched gastrovascular system, which could replace a circulatory system. The transport of substances from one organ to the other and

particularly that of nutrients from the digestive system to other parts of the body, occurs through the extensive body cavity. Transport of various substances in the cavities is accomplished by means of flexion and extension of muscles.

The body cavity of larvae of *Crassostrea virginica* and *C. gigas* contains two main types of coelomocytes:

(1) phagocytes participating in the processes of excretion, and
(2) coelomocytes with smooth endoplasmic reticulum that do not participate in the process of phagocytosis, but evidently process and transport the soluble nutrients secreted by the cells of the digestive system (Elston,1980).

Excretion : In the larvae of some bivalves, unlike other mollusks (except pulmonate gastropods), the excretory system is represented by larval protonephridia. These have been described in *Dreissena polymorpha, Teredo navalis, Ostrea edulis*, and *Codakia orbicularis* (Hatschek, 1980; Meisencheimer, 1901; Waller, 1981; Alatalo *et al.*, 1984). Protonephridia originate from the ectoderm and are arranged on both sides of the body under the epithelium, extending from the esophagus to the base of the foot (Figure 11). A protonephridium is composed of two to three cells. Along the sides of the esophagus in the body cavity lie ciliated cells—one for each protonephridium. These cells are usually conical, often with a vacuole, and bear a tuft of very long cilia lying in the protonephridial canal and extending to its excretory pore. The canal is formed by a second cell. In transverse section, it is possible to see the covering of this intracellular canal, isolated from the cytoplasm of the canal-forming cell (Figure 12). The main mass of cytoplasm and the nucleus are situated in the distal part of the cell; in the proximal part, firmly attached to the ciliated cell, the wall of the canal becomes very thin. A third, sometimes poorly discernible cell, delimits the excretory pore of the protonephridium. The pores of the protonephridia are scarcely visible as they lie deep in the mantle cavity (Figure 13).

In veligers of other mollusks—*Pandora inequivalvis, Cardium edule* (Creek, 1960; Allen, 1961), and others—neither protonephridia nor other excretory organs are seen. Possibly this function is taken up by the coelomocytes scattered in the body cavity. Elston (1980) has described the diapedesis—passage of coelomocytes loaded with processed substances from the body cavity through the velum tissue into the mantle cavity.

Locomotion : In the veliger, swimming consists of a vertical rise followed by a passive sinking. The veliger moves by beating the cilia of the ciliary band along the margin of the velum. The velum in bivalve larvae is usually oval. A remarkable large bilobate velum (Figure 14) is found in transoceanic and deepwater species. Such is the velum of the transoceanic larva *Planktomya*

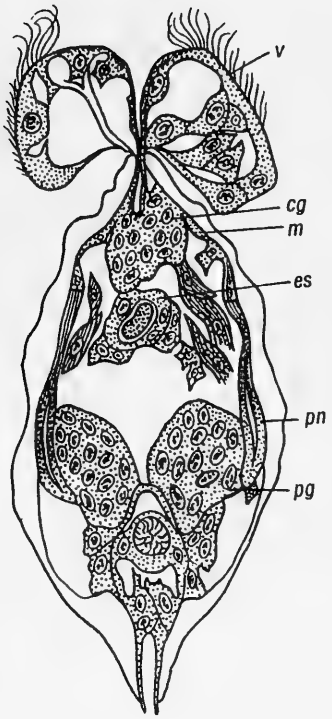


Figure 11: Frontal section through the veliger of *Dreissena polymorpha* Pall. at level of protonephridia (from Meisenheimer, 1901).
cg — cerebral ganglion; es — esophagus; m — mantle; pg — pedal ganglion; pn — protonephridium; v — velum.

henseni belonging to an unidentified species (Allen and Scheltema, 1972). A larger velum facilitates larval migration to greater distances and efficient collection of food particles (which are rare in open seas) since an increase in velum size means an increase in number of ciliary bands. For example, in the deepwater pholadid *Xylophaga atlantica*, the larva has no less than six ciliary bands (Culliney and Turner, 1976).

Beating of the cilia produces the upward and somewhat forward movement of the veliger, during which the velum is slightly inclined forward relative to the axis of movement. While swimming, the veliger resembles a flying helicopter. The principal locomotor organ is the outer preoral ciliary band of the velum, consisting of a double row of ciliated cells. In the veliger of *O. edulis*, 20–80 long cilia (50–70 μm in length) originate from each cell. The cilia are in contact almost throughout their length and together form a

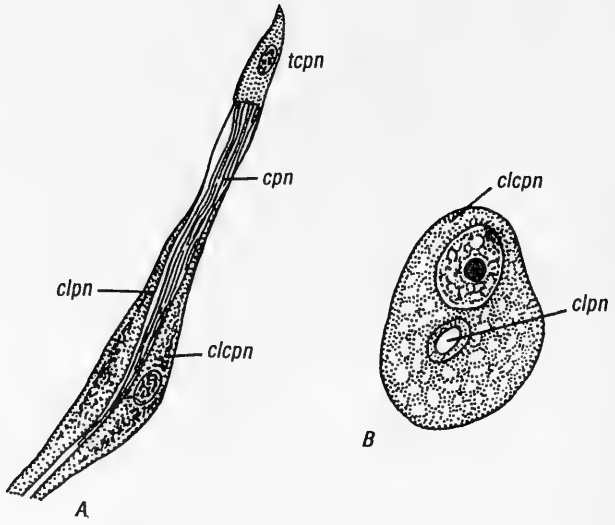


Figure 12: Protonephridium of the veliger of *Dreissena polymorpha* Pall. in longitudinal (A) and transverse (B) section (from Meisenheimer, 1901).
clcpn — canalicular cell of protonephridium; clpn — canaliculus of protonephridium; cpn — cilia of protonephridium; tcpn — terminal cell of protonephridium.

"complex cilium". The orientation of cilia in the complex cilium, parallel or perpendicular to the plane of beating, ensures a thrust of maximum force, moving the veliger upward. The efficient beating of straight cilia is directed downward and coordinated by the wave of beating by the entire band (Figure 15). The reverse upward motion of cilia is accomplished in a bent condition. If the wave passes at a right angle to the plane of beating of an individual complex cilium, then the veliger, moving upward, will rotate in the direction opposite to that of the wave. Inhibition of this rotation is ensured by beating cilia that are inclined relative to the beating ciliary band and relative to the velar margin.

The postoral ciliary band of the velum also plays some role in the locomotion of the veliger. It is a single row of complex cilia 15–20 μm long. Each complex cilium consists of four to five simple cilia. Their beating is effectively directed upward and counteracts the beating of the cilia of the preoral ciliary band (pcb) (Waller, 1981).

At an average speed, the veliger expends nearly 10% of its energy for locomotion. Locomotion at higher speeds increases this expenditure up to 50% (Zeuthen,1947).

The veliger moves upward with a fully extended velum and intensive cilial beating. As the intensity of cilial beating decreases, the veliger slowly sinks.

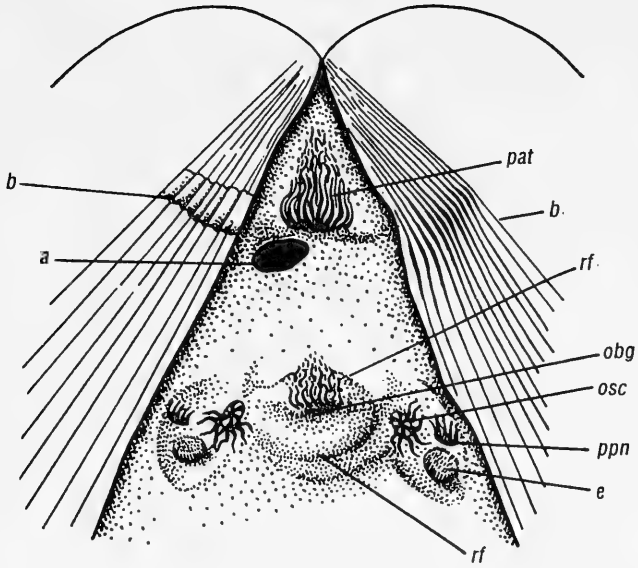


Figure 13: Disposition of organs at base of mantle cavity of the pediveliger of *Ostrea edulis* L. (from Waller, 1981).

Posterior view: a — anus; b — border between prodissoconch I and II; e — eye; obg — opening of byssus gland; osc — opening of statocyst canal; pat — postanal tuft of cilia; ppn — pore of protonephridium; rf — rudiment of foot.

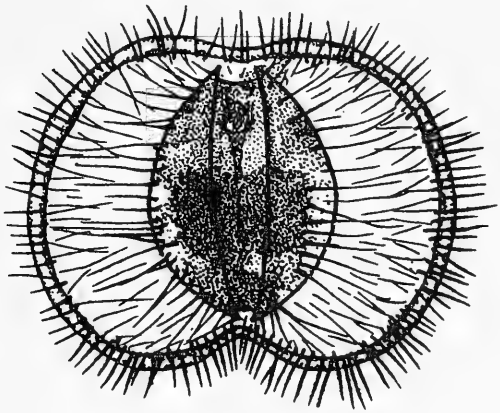


Figure 14: Stretched velum of the deepwater woodboring pholadid *Xylophaga atlantica* Richards (from Culliney and Turner, 1976).

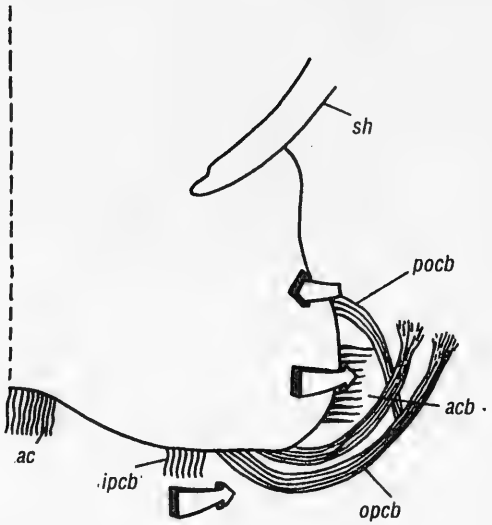


Figure 15: Schematic presentation of beating of the cilia of the velum of the veliger of *Ostrea edulis* L. (from Waller, 1981).

ac — apical cilia; acb — aderal ciliary band; ipcb — internal preoral ciliary band; opcb — outer preoral ciliary band; pocb — postoral ciliary band; sh — shell. Arrows show the direction of beating of the waves of cilia.

The speed of sinking increases when the cilia of the velum stop beating. The speed of sinking is greatest when the velum is rolled and the valves of the shell closed. Rolling of the velum is affected by two or three pairs of larval muscles, the velum retractors. They originate from the shell in the region of the posterior part of the hinge line. In *Dreissena polymorpha* the dorsal retractor passes along the dorsal side of the larva and supplies muscle fibers in the dorsal region of the velum, which are attached to the velum integument. The medial retractor proceeds forward from the place of its insertion to the ventral and medial regions of the velum. One muscle is attached to the apical plate, while the remaining fascicles are attached to various areas of the anterior part of the velum (Meisenheimer, 1901). In *Cardium edule* there are individual retractors for the medial and ventral regions of the velum (Creek, 1960). During rolling of the velum first the apical plate withdraws into the shell, then the lateral parts of the velum apparently roll up and the valves of the shell close. During withdrawal of the velum under the shell, the stomach and esophagus are shifted backward. Opening of the valves, slackening of the muscles, and filling of the fluid in the extensive cavity of the velum, ensure its extension.

The ascent of the veliger usually follows a spiral pattern; this type of veliger locomotion is seen in *Ostrea edulis, Mercenaria mercenaria, Dreissena polymorpha*, and others. In other species the veliger ascends in a vertical line,

rotating in the process like a flying cannonball; the veliger of *Argopecten irradians* exemplifies this type of locomotion. The nature and speed of veliger locomotion depend on change in salinity, temperature, and pressure (Mileikovsky, 1973; Cragg and Gruffydd, 1975; Hidu and Haskin, 1978; Cragg,1980).

The veliger of *Mercenaria mercenaria* ascends at a speed of 7–80 cm/min (Turner and George, 1955; Carriker, 1961), the late veliger of *Crassostrea virginica* at a maximum speed of 60 cm/min (Wood and Hargin, 1971), and the veliger of *Lyrodus pedicellatus* at a speed of 45 cm/min (Isham and Tierney, 1953, cited by Mileikovsky, 1973).

Nervous System : Under the apical plate of the velum lies the cerebral ganglion connected with the anterior part of the plate. Initially, the cerebral ganglion is a single structure that later becomes bilobate. Numerous nuclei and nerve cell fibers are visible in sections. In the middle part of the ventral side there are two large pedal ganglia, which later join through connectives with the cerebral ganglion (Figure 16). Development of the pedal ganglia precede that of the foot (Meisenheimer, 1901; Cranfield, 1973).

Sense organs : Considerable development of the nervous system and diversity and degree of development of the sense organs are associated with the high locomotor activity of the veliger. The most noteworthy sense organ of the veliger is the apical plate, which may be drawn in, forming an apical pit. The diameter of the pit in *O. edulis* is 10–15 μm. In its anterior part lie 20–100 cilia, 6–8 μm long, which perform a sensory function (Waller, 1981). In *Teredo navalis* the apical plate bears only three complex cilia. As the apical plate grows, the cilia shift to its posterior half (Culliney, 1975). A sensory function is also performed, evidently, by the cilia of the internal preoral band. These are small cilia, about 20 μm long, arranged irregularly. In the veliger ciliary bands and the ciliated field generally function in locomotion and reception.

Integument : Protection of the veliger from unfavorable external influences is done by the cells of the outer epithelium; a firm contact between them ensures some protection of the larva. According to Waller (1981), the cells of the outer epithelium are covered with mucus; apparently, the secretion produced by these epithelial cells also has a protective function. However, these adaptations are accessory in character relative to the prime protective structure—the shell. Like other organs of the larva, the shell simultaneously performs several functions: protective, supportive for muscle attachment, and jet-directing; however, the primary, and often basic function is protection. The shell, as already mentioned, is a product of the activity of secretory cells of the shell gland. The peripheral cells of the shell gland located along its narrow opening secrete the primary unpaired organic periostracum (Kniprath, 1979),

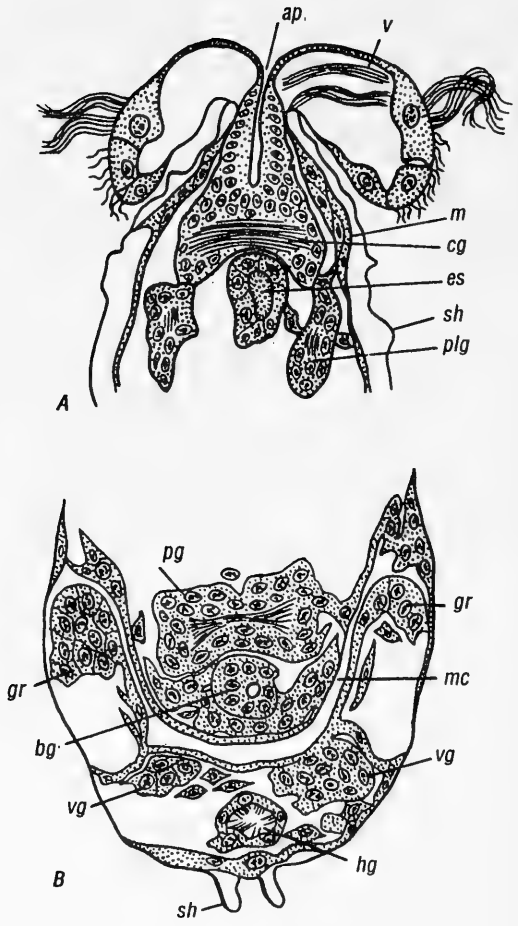


Figure 16: Cerebral, pleural (A) and pedal, visceral (B) ganglia of the pediveliger of *Dreissena polymorpha* Pall. (from Meisenheimer, 1901).

ap — apical pit; bg — byssus gland; cg — cerebral ganglion; es — esophagus; gr — gill rudiment; hg — hind gut; m — mantle; mc — mantle cavity; pg — pedal ganglion; plg — pleural ganglion; sh — shell; v — velum; vg — visceral ganglion.

which initiates shell formation of a veliger, i.e., the prodissoconch I. The shell gland evaginates and soon a mantle forms consisting of a single row of cells. The growing margins of the mantle envelop the larval body from the sides. The shell bends along the mediodorsal line and becomes bivalved.

The precise moment of initiation of calcification of the shell in bivalves is not known. Evidently, this process begins after eversion of the shell gland, as in gastropods. Due to the activity of the margins of the growing mantle, the

size of the shell increases rapidly and already in the early veliger stage it entirely covers the larval body. When this happens, the formation of the prodissoconch I is completed. The outer surface of each valve in ostreids has a punctate-stellate appearance; a small punctate zone occurs in the center and an extensive stellate-radial zone along the periphery (Figure 17). Possibly, the punctate zone is formed as a result of the activity of the cells of the shell gland and the stellate zone because of the activity of the mantle cells after eversion of the shell gland (Waller, 1981). The valves of the prodissoconch I are usually similar in size; they are calcified and transparent. However, there is no calcification on the dorsal side of their place of attachment; this area of the shell is replaced by the thickened periostracum. The hinge margin is straight and usually (except in mytilids) nondentate. The valve is D-shaped.

The cells of the free margin of the external mantle fold and the thickened

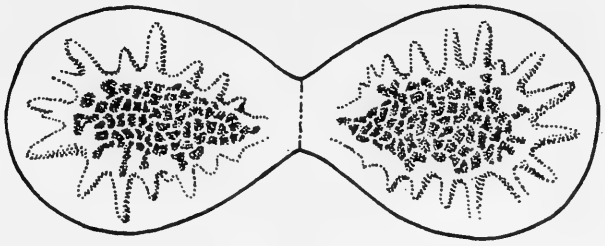


Figure 17: Early prodissoconch I of *Ostrea edulis* soon after eversion of the shell gland and before bending along the hinge line (from Waller, 1981).
Dots — two centers of calcification.

margin of the mantle under the hinge continue to discharge a secretion from which a new area of the larval shell is formed—the prodissoconch II. It differs from the prodissoconch I in hinge development, appearance of lines on the shell surface (repeating the outline of the mantle margin), and a change in shell shape. The most significant change in shell shape is the appearance of a prominence (umbo) on both valves.

The umbones are arranged dorsal to the hinge margin. Like the prodissoconch I, the prodissoconch II is also calcified; one exception is the prodissoconch II of *Planktomya henseni* (Allen and Scheltema, 1972).

In *Perumytilus purpuratus*, umbones do not develop and, at the time of metamorphosis, the shell is mainly represented by the prodissoconch I and is D-shaped (Ramorino and Campos, 1979).

Structural features of the larval hinge (Figure 18) and size and shape of the shell valves make it possible to identify the species of different larvae. These will be discussed in detail later. The central straight part of the larval hinge — the provinculum — consists of different cardinal teeth along the hinge

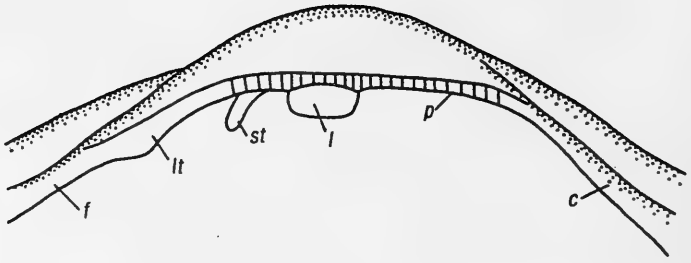


Figure 18: Scheme of the hinge system of bivalves.
c — crest; f — flange; l — ligament; lt — lateral tooth; p — provinculum; st — special tooth.

margin of one valve and corresponding alveoli in the hinge margin of the other. The shape, number, and arrangement of teeth differ in different species. Lateral to the provinculum lies the lateral hinge system. It consists of thick dorsolateral margins on one valve — flanges — and thin internal crests running parallel to these margins. The lateral teeth — flange projections edging the provinculum — comprise the lateral hinge system. In some species there are so-called special teeth that belong neither to the provinculum nor to the lateral teeth (Rees, 1950; Chanley and Andrews, 1971; Le Pennec, 1980).

The anterior and posterior sides of the teeth usually bear ridges and furrows that correspond to the ridges and furrows in the alveolar walls of the other valve (Figure 19). The center of curvature of these ridges and furrows lies roughly on the axis of rotation of the valves. It has been demonstrated in adult bivalves that such a system of ridges and furrows decreases the gap between partially open valves. Larvae of *Rangia cuneata* (Chanley, 1965), *Tiostrea (Ostrea) lutaria, T. chilensis* (Chanley and Dinamani, 1980), *Gemma gemma, Lyonsia hyalina* (Chanley and Andrews, 1971), and some other species with lecithotrophic development lack teeth on the prodissoconch.

Closure of the shell valves is achieved, first of all, by the working of the anterior adductor. Initially, it is situated behind the dorsal edge of the velum and is the most prominent of all the veliger muscles. The anterior adductor is formed and functions also in those larvae whose adults have only a posterior adductor developing later. In *Planktemya henseni*, the two adductors are similar in size (Allen and Scheltema, 1972). Besides the adductor, the velum retractors and three lateral muscles are attached to the valves; they extend from the valves in the region of attachment of the anterior adductor and muscles and terminate in the body wall (see Figure 8) (Cragg, 1985).

Rudiments of definitive organs : In addition to functional organs, the body of the veliger contains rudiments of definitive organs that develop later and begin to function after the larva has settled to the bottom; sometimes the rudiments of certain larval organs are also present but not developed in the

Figure 19: Ridges and furrows on lateral surfaces of teeth and alveoli of veliger valve of *Mizuhopecten yessoensis*.

veliger since they function only in the later larva — the pediveliger. The first group comprises rudiments of gills, renopericardic complex, some elements of the nervous system, rudiments of the foot, byssus gland, some sense organs, and the reproductive system. In view of the secondary simplification of the adult organism, in some mollusks the foot, byssus gland, and sense organs — eyes and statocysts — exist only in the later periods of larval life. Such, in particular, is the case in ostroids and pectinids.

The stages of the developed veliger with umbo and the last larval stage — the pediveliger — are often combined in the term veliconcha or veliconch, which was introduced by Werner (1939).

Pediveliger

In this stage the larva, having attained maximum size, bears a functional foot with which it can creep, while simultaneously retaining the ability to swim by means of its developed velum (Figures 20 and 21). The ultimate objective of the pediveliger is to select and colonize a substrate and then to change over to a definitive mode of feeding and locomotion. Hence the pediveliger characteristically has functional sense organs — eyes and statocysts, and a functional organ of locomotion and attachment, the foot. Concomitant with these larval organs, definitive organs are present in the body of the pediveliger,

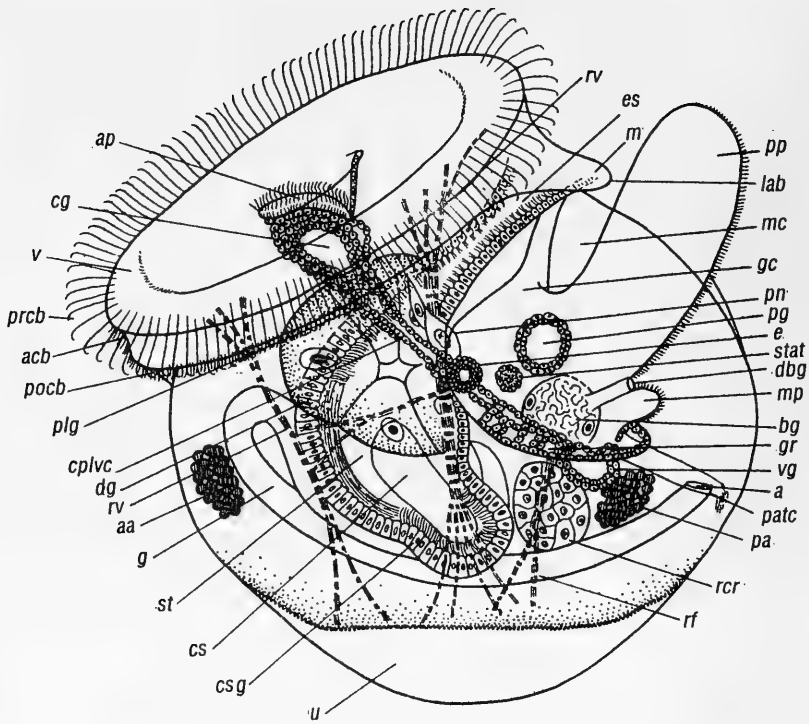


Figure 20: Pediveliger of *Ostrea edulis* L. (from Erdmann, 1935).

a — anus; aa — anterior adductor; acb — adoral ciliary band; ap — apical plate; bc — buccal cavity; bg — byssus gland; cg — cerebral ganglion; cplvc — cerebropleurovisceral connective; cs — crystalline style; csg — crystalline style gland; dbg — duct of byssus gland; dg — digestive gland; e — eye; es — esophagus; g — gut; gc — gill cavity; gr — gill rudiment; lab — "mouth lobe" or "labium"; m — mouth; mc — mantle cavity; mp — metapodium of foot; pa — posterior adductor; patc — postanal tuft of cilia; pg — pedal gaglion; plg — pleural ganglion; pn — protonephridium; pocb — postoral ciliary band; pp — propdium of foot; prcb — preoral ciliary band; rcr — rudiment of cerebrorenal organ complex; rf — retractor of foot; rv — retractor of velum; st — stomach; stat — statocyst; u — umbo; v — velum; vg — visceral ganglion.

which have yet to undergo the last stage of development during metamorphosis before they can become functional.

Feeding : The digestive system of the pediveliger differs very little from that of the veliger. The digestive gland enlarges and the small intestine elongates, forming a long loop in many species.

Respiration : A functional specialized respiratory system is absent in the pediveliger. To the structures described earlier for the veliger, which facilitate gas exchange, we may add the two to three gill filament processes which form

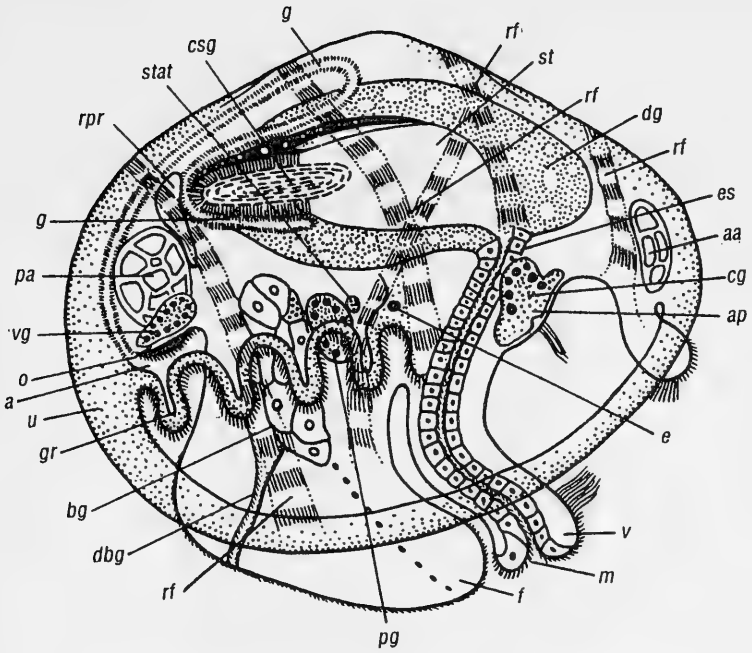


Figure 21: Pediveliger of *Mytilus edulis* L. (from Bayne, 1971).
f — foot; o — osphradium; rpr — renopericardial rudiment
Remaining legend same as in Figure 20.

on each gill rudiment (Bayne, 1971, 1976). During creeping, gas exchange is facilitated by the movement of cilia on the foot and of the foot itself. The circulatory and excretory systems do not change substantially during development from veliger to pediveliger.

Locomotion : In the pediveliger stage the velum, the initial organ of locomotion, attains maximum development, partly in connection with the increase in shell mass and in larval body size. In addition, the new locomotor organ—the foot—begins to function. Like most larval organs, the foot, too, is a multifunctional organ. Its primary function is to probe the substrate for settling and attachment of the larva by means of byssus threads or a cementing secretion. The foot develops as an ectodermal outgrowth on the ventral side of the body between the mouth and the anal pore (see Figures 10 and 13). The heel of the foot (metapodium) begins to develop early and is covered with short cilia. Ventral to it lies the toe (propodium), which later becomes larger than the metapodium. Between the propodium and metapodium lies a depression in which the duct of the byssus gland opens. A furrow, extending the entire length of the foot, divides it into two equal halves (Figure 22).

Figure 22: Foot of the pediveliger of *Ostrea edulis* L. ventral view (from Cranfield, 1973).

According to Creek (1960), in the pediveliger of *Cardium edule* the larval retractor of the foot is functional, and is replaced by a definitive structure once the larva has settled on the bottom. The posterior pair of retractors is attached to the shell in the region of the posterior adductor; these muscles then pass between the visceral ganglion and one of the pedal glands and are inserted in the ventral surface of the foot. The anterior pair of retractors originates on the dorsal side of each valve before the hinge line. These retractors pass along the sides of the digestive tract and bending around the pedal ganglion, are inserted in the dorsal surface of the foot along both sides of the furrow. The longitudinal muscles of the dorsal and lateral sides of the foot are attached along the dorsal side of each valve near the anterior adductor of the shell. The cruciate muscles participate in turning the foot, connecting its left and right sides to the opposite valve (Figure 23) (Cranfield, 1973).

The foot is covered with a ciliated epithelium. Each ciliated cell bears numerous microvilli. The cilia are irregularly arranged on the surface of the foot and are dense and very long at its tip and on its ventral and ventrolateral

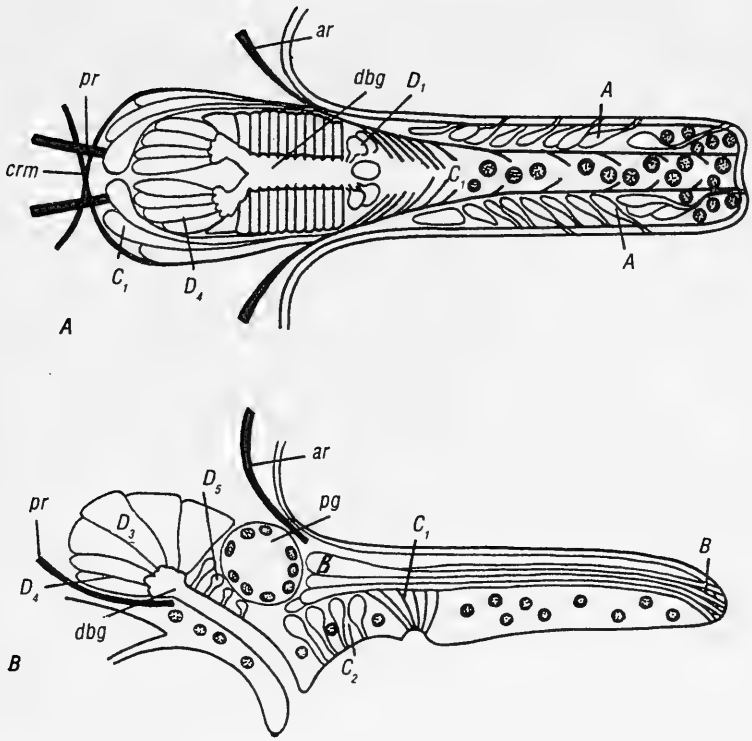


Figure 23: Pedal glands of the pediveliger of *Ostrea edulis* L. in frontal (A) and sagittal (B) sections (from Cranfield, 1973).

ar — anterior retractor; crm — cruciate muscle; dbg — duct of byssus gland; pg — pedal ganglion; pr — posterior retractor; A, B, C_1, C_2, D_1–D_4 — cells of nine glands of byssus complex.

surfaces (Lane and Nott, 1970). The subepidermal glands participating in the movement of the foot over the substrate and in the formation and attachment of byssus filament occupy the maximum volume in the foot of the pediveliger.

Swimming pediveligers generally exhibit a negative phototaxis and a positive geotaxis. Their highest density is observed in near-bottom water layers. While a larva is swimming, its foot may be extended, but on contacting the substrate functions in larval locomotion, namely, creeping. The sequence of locomotor acts during creeping are: (1) The slightly relaxed and extended foot moves over the substrate by means of cilia. Glands opening on the sole exude a secretion that contains weakly acidic mucopolysaccharides with a low viscosity. Smeared on the substrate, this secretion facilitates ciliary movement. (2) The anterior part of the foot is temporarily attached to the substrate by means of a proteinaceous secretion, which is released by another gland

opening at the tip of the foot. Such a gland has been reported for the pediveliger of *O. edulis* and *M. edulis*, but is absent in the pediveliger of the scallop *Placopecten magellanicus*. Hence during creeping the latter larva is not attached to the substrate (Gruffydd *et al.*, 1975). Contraction of the posterior part of the foot hauls the entire larva forward. (3) The foot relaxes and the locomotory cycle is repeated after a few seconds.

Creeping serves to attach the larva to the substrate. Once the foot is retracted, i.e., loses contact with the substrate, swimming is resumed (Lane and Nott, 1970).

Nervous System : In the pediveliger stage those elements of the nervous system are most developed which are associated with the functioning of the foot. The pedal ganglia, interconnected with commissures, constitute the terminal point of the anterior pedal nerves passing along the tip of the foot, which send sensory impulses from the ciliated sense organs. Besides the cerebral and pedal ganglia, visceral ganglia are also developed, which are situated near the posterior adductor. Rudiments of the pleural ganglia are located near the cerebral ganglion and later merge with the latter in all bivalves except the protobranchia (Figure 24) (Hickman and Gruffydd, 1971; Cranfield, 1973).

Sense organs : Ciliated sense organs of the pediveliger are represented by the apical plate and sensory cilia situated on the foot, primarily the long mobile cilia on its tip. Sensory cilia also occur in the furrow and byssus duct of the foot.

In many pediveligers there are statocysts and eyes in the mantle cavity. A highly developed nervous system and sense organs are characteristic of planktotrophic larvae, which live for a long time in the plankton. In the planktotrophic pediveliger of *O. edulis* there are two openings 7–9 μm in diameter along the sides of the base of the foot, which lead into the statocyst cavity. These openings are surrounded by two rings of cilia: short cilia 2–4 μm long and long cilia about 15 μm long (Waller, 1981; see Figure 13). A statolith forms in the cavity of the statocyst. The duct is later blocked and the statocyst becomes a closed vesicle (Figures 25 and 26). In *O. edulis*, the duct of the statocyst is retained even in the adult. Here, not far from the base of the foot, there are two eyes in the larvae of many species. Each eye is an almost round cup of pigmented epithelium filled with a jellylike substance (Hickman and Gruffydd, 1971). The opening of the cup is covered with a transparent crystalline lens. The size of the eye spot in *Mytilus edulis* and *Modiolus modiolus* is 5–10 um (Schweinitz and Lutz, 1976) and in *Tiostrea (Ostrea) lutaria*, 26–34 μm (Chanley and Dinamani, 1980). Nerves to the statocysts and eyes arise from the cerebral ganglion. In the pediveliger of *M. edulis*, as described by Bayne (1971), a band of ciliated cells passes from the roof of the

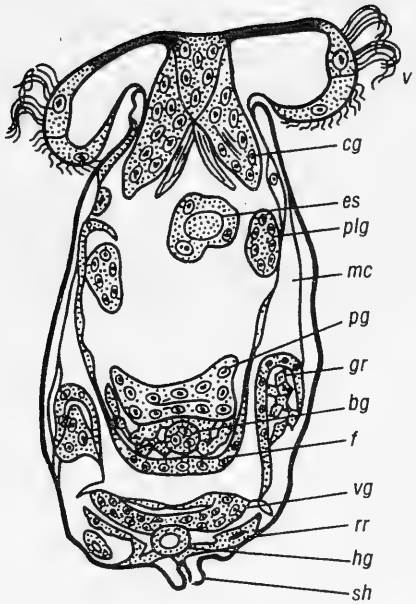


Figure 24: Frontal section through the pediveliger of *Dreissena polymorpha* Pall. at level of ganglia (from Meisenheimer, 1901).

bg — byssus gland; cg — cerebral ganglion; es — esophagus; f — foot; gr — gill rudiment; hg — hind gut; mc — mantle cavity; pg — pedal ganglion; plg — pleural ganglion; rr — renal rudiment; sh — shell; v — velum; vg — visceral ganglion.

mantle cavity to the visceral ganglia. He considers this band an osphradium — a chemosensory organ that assesses the quality of the water entering the mantle cavity.

Bayne (1964) has also reported that each larval stage has its own reaction threshold to external stimuli. The nature and intensity of the response are greatly influenced by temperature. The various responses of the larval stages of *M. edulis* to direct light, gravity, and pressure under laboratory conditions are presented in Table 1 (from Bayne, 1976).

Integument : As in the veliger, the main protective system in the pediveliger is the shell. At this stage the prodissoconch II markedly enlarges, the hinge system develops, the provinculum lengthens, and the number of teeth increase. In addition to the anterior adductor, a posterior adductor develops, which is located behind the visceral ganglion above the hind gut. In *O. edulis*, the posterior adductor is present even in the veliger (Fujita, 1933).

Attachment apparatus : In the pediveliger the byssus gland develops rapidly and begins to function; it forms as a depression in the actoderm along the

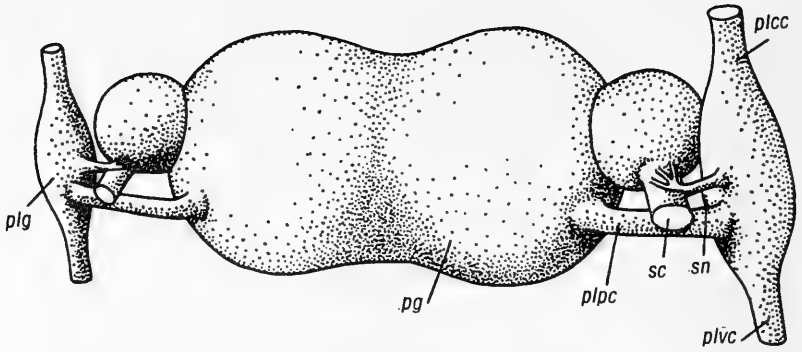


Figure 25: Nervous system of the pediveliger of *Pecten maximus* (1) in the statocyst region (from Cragg and Nott, 1977).

pg — pedal ganglion; plcc — pleurocerebral connective; plg — pleural ganglion; plpc — pleuropedal connective; plvc — pleurovisceral connective; sc — statocyst canal; sn — statocyst nerve.

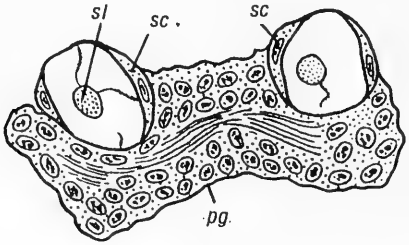


Figure 26: Pedal ganglion and statocysts of the pediveliger of *Dreissena polymorpha* Pall. in section (from Meisenheimer, 1901).

pg — pedal ganglion; sc — statocyst; sl — statolith.

Table 1: Relative intensity of response of different larval stages of *M. edulis* to external stimuli* (from Bayne, 1976)

	External stimuli		
Larval stage	Light	Gravity	Pressure
Trochophore	o	o	o
Veliger	−	o	o
Veliconcha**	+++	o	+++
Pediveliger (swimming)	—	+	o
Pediveliger (crawling)	—	—	o

* o = no response; (−) = negative response, (+) = positive.

** According to Bayne, the veliconcha stage corresponds to that of developed veliger with umbo.

midline of the foot in the region of the pedal ganglia. The byssus gland or, more precisely, the byssus complex, comprises a series of glands producing different secretions that facilitate the formation and attachment of byssus threads to the substrate. The byssus threads of the pediveliger of *O. edulis* comprise two strands, 3–7 μm in diameter, joined together and enveloped in a common cover (Figure 27). In addition to the glands of the byssus complex, the foot of the pediveliger may contain other glands (see Figures 23 and 28). In the pediveliger of *M. edulis* and *O. edulis*, nine different types of glands have been recorded in the foot; in *Pecten maximus*, there are five types of glands (Gruffydd *et al.*, 1975). Gruffydd and his colleagues divide the pedal glands of the pediveliger into three groups: (1) glands producing very thin primary and secondary byssus threads; (2) glands producing mucus on the tip and sole of the foot, which facilitates creeping; and (3) glands present but functioning only after metamorphosis; and producing a secretion for attachment of the shell or secondary byssus threads to the substrate (Table 2). The blanks in Table 2 are probably due not so much to the absence of some glands, as to inadequate study of the structure of the larvae. The number of cells in the glands of the foot of the pediveliger vary in *O. edulis* from 10 to 250 (Cranfield, 1973).

Cranfield (1973) has identified five phases in the behavior of the pediveliger of *O. edulis* during settling. These, in his opinion, represent the sequence of

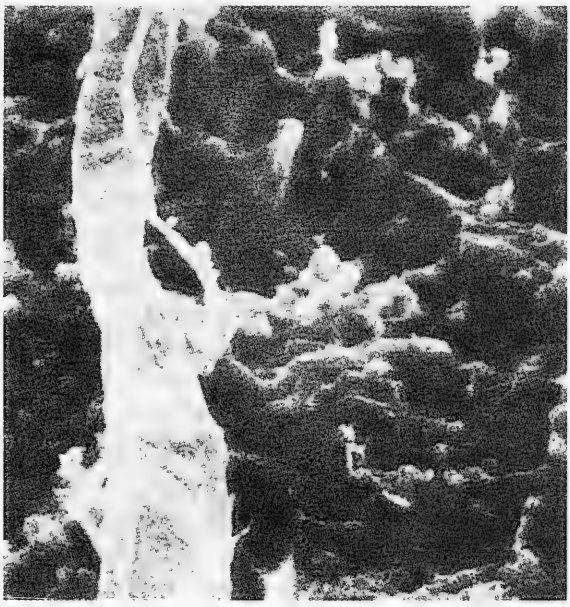


Figure 27: Byssus threads of the pediveliger of *Ostrea edulis* L. (from Cranfield, 1973).

hierarchic, fixed motor reactions leading to the final act of cementing. In the absence of stimuli specific for a particular response, the latter is not produced and the larva returns to an earlier phase of settling. In the opinion of Cranfield, settling of bivalves and polychaetes is very similar. During settling the pediveliger changes from a ciliary to a muscular mechanism of locomotion over the substrate; in this case the viscosity of the mucopolysaccharide secretion increases and the secretion of byssus threads begins. At the end of settling, a secretion is produced which cements the larva to the substrate. The first exploratory stages of behavior of the pediveliger during settling were described above. In the pediveliger of *O. edulis*, later, in the course of settling, the muscular movement of the foot becomes sharper and stronger and the speed of locomotion decreases. The body turns occur more often in locomotion. Initially, the larva creeps in a straight line, rarely turning. Subsequently, movement becomes zigzag. With an increase in frequency of turning, the angle of the path of movement decreases; the track of a pediveliger resembles a star and then a circle. The last phase of settling — cementing of the pediveliger of an oyster commences with a turn to the right (all previous turns have been to the left), the shell rests on the foot, and the larva rotates on the foot, which is attached to the substrate by its tip, and the left valve. Similar processes were observed by Coon and Borne (1985) during settlement of the pediveliger of *Crassostrea gigas*. The larva, ready to settle, after having swum with contracted legs, now begins to extend its legs forward during swimming. It then drops to the bottom and moves over the substrate, executing a series of sliding

Table 2: Pedal glands of pediveliger of various bivalves (from Gruffydd *et al.*, 1975)

Species	Mucous glands	Glands of furrows (tentatively producing and attaching secondary byssus threads)	Glands of primary byssus threads
Nucula delphinodonta	-	-	+
Mytilus edulis	+	+	+
Pecten maximus	+	+	+
Crassostrea virginica	-	+	+
Ostrea edulis	+	+	+
Musculium securis	-	-	+
Sphaerium notatum	-	-	+
Dreissena polymorpha	-	-	+
Lasaea rubra	+	+	+
Chione cancellata	-	-	+
Mercenaria mercenaria	-	-	+
Venerupis pullastra	-	-	+
Venus striatula	-	-	+
Xylotrya gouldi	+	-	+

movements. If the substrate is not congenial for settling, the larva abandons it and begins to swim again. If the substrate is suitable for settling, the larva cements itself to it and metamorphoses into a juvenile oyster.

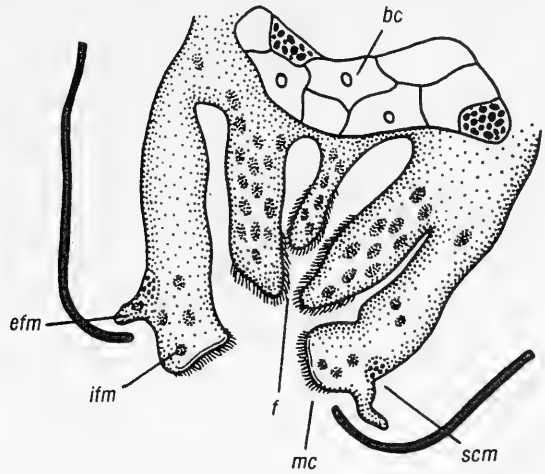


Figure 28: Foot and byssus complex of the pediveliger of *Mytilus edulis* L. in transverse section (from Bayne, 1971).

bc — byssus complex; efm — external fold of mantle; f — foot; ifm — internal fold of mantle; mc — mantle cavity; scm — secretory cells of mantle.

Rudiments of the definitive organs: The gill apparatus, renopericardiac complex, and circulatory and reproductive systems are not fully developed and are nonfunctional in the pediveliger.

METAMORPHOSIS

Metamorphosis, the most crucial period in the life cycle, is completed when the pediveliger, while creeping, finds a substrate suitable for settling and, discharging the byssus threads, attaches itself to the selected site. Larvae of different species exhibit a well-defined substrate specificity. In the absence of a desirable substrate the larva may postpone metamorphosis. According to Bayne (1976), the larvae of *M. edulis* are capable of delaying metamorphosis by 40 days at a temperature of 10°C and by two days at 20°C; larvae of *O. edulis* can delay metamorphosis by several days (Cranfield, 1973) and larvae of *Pecten megellanicus* by a month (Culliney, 1974). In some species, during an overall delay of metamorphosis, the velum is discarded and the larva loses its ability to swim; in other species the larva continues to swim by means of the velum. In *Brachiodontes glomerata*, in the absence of a substrate not only the velum may disappear, but a narrow band of the dissoconch may form (Campos and Ramorini, 1980).

In many bivalves metamorphosis with total or partial resorption of many larval organs is characteristic. The *digestive system*, except for the trapping apparatus, is subject to comparatively less change (Bayne, 1971). The oral opening is shifted and occupies an anterodorsal position near the hinge line. The anal opening likewise shifts and occupies a posteroventral position. The digestive gland acquires a definitive structure. Disappearance of the larval liver has been reported in protobranchs (Drew, 1899).

The *respiratory function* changes over from nonspecialized external tissues to a gill apparatus that, in most bivalves except protobranchs, performs simultaneously the function of catching food. After the foot has shifted forward during metamorphosis, the gill filaments from each side of the mantle cavity fuse and divide the mantle cavity into an incurrent and excurrent chamber. This ensures efficient filtration of the incurrent water by the gill filaments. The number of gill filaments increases after metamorphosis (Bayne, 1976). In most bivalves in the superorder Autobranchia, the preoral lobes assist in directing the food particles caught by the gill filaments to the mouth. In many mollusks the mantle edges fuse along the median line and muscular tubules form anteriorly and posteriorly — incurrent and excurrent siphons — which regulate the flow of water through the mantle cavity (Figure 29). Soon after settling, the transport of substances within the organism is accomplished as in the larva. The (blood) circulatory system develops later.

The larval *excretory system* disintegrates and is replaced by definitive kidneys originating from the pericardial cavity, which open through ducts into the mantle cavity.

The velum, or *locomotor apparatus*, of the veliger and the pediveliger disintegrates (Figure 30). It is invaded by phagocytes, which absorb the velar

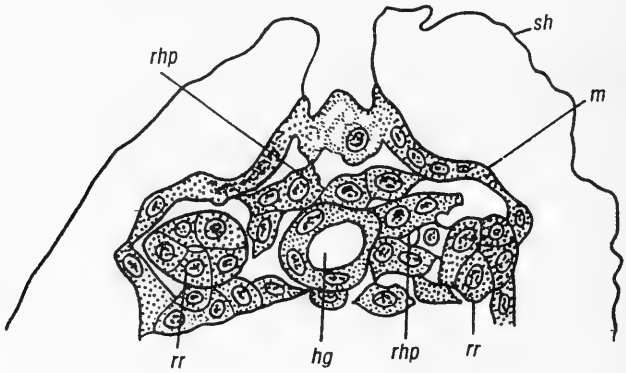


Figure 29: Renopericardial rudiment in *Dreissena polymorpha* Pall. (from Meisenheimer, 1901).

hg — hind gut; m — mantle; rhp — rudiment of heart and pericardium; rr — renal rudiment; sh — shell.

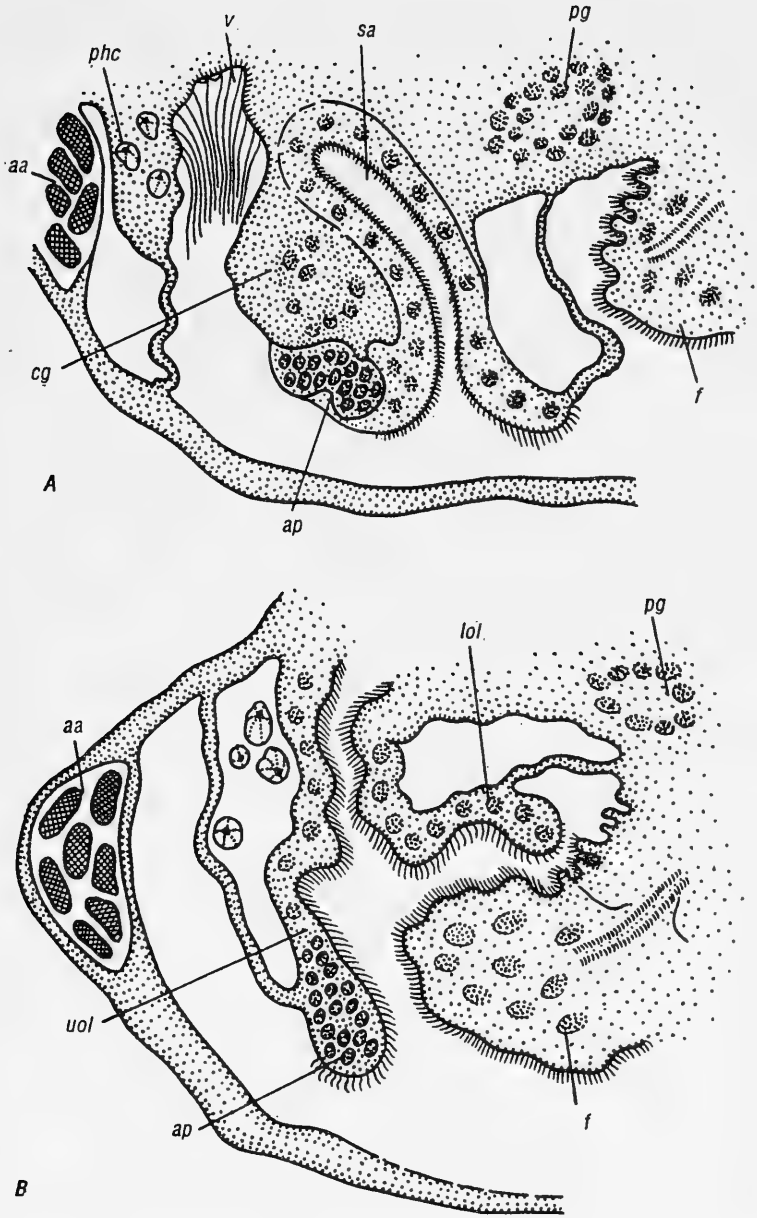


Figure 30: Metamorphosis of the pediveliger of *Mytilus edulis* L. (from Bayne, 1971).
A — degeneration of velum; B — formation of oral lobes; aa — anterior adductor; ap — apical plate; cg — cerebral ganglion; es — esophagus; f — foot; lol — lower oral lobe; pg — pedal ganglion; phc — phagocytized cells; uol — upper oral lobe; v — velum.

cells. The muscular system which served the velum is also destroyed (Bayne, 1971). In *Placopectan magellanicus*, large parts of the velum are discarded during metamorphosis; only the apical part is retained, which participates in the formation of the upper preoral lobe (Culliney, 1974). As a result of these processes, the larval mechanisms of swimming and catching food disappear. The locomotor functions are usually passed to the foot and the function of particle capture to the gills and preoral lobes; the lower lobe makes contact with the first gill filaments. The change in mechanisms of food capture may require several days, during which time the larva does not feed, and uses its reserve nutrients. The foot in burrowing mollusks develops further, shifting anteriorly in the mantle cavity. The larval muscles of the foot are replaced by definitive ones. In attached (sessile) species, however, the foot is usually totally or partly reduced, and its cells are phagocytized (Hickman and Gruffydd, 1971).

The *central nervous system* generally retains its structure. Ganglia occupy definitive positions. The visceral ganglion is further developed, the relative size of the cerebral ganglion decreases, and the pedal ganglia are reduced if the foot is reduced. The cerebrovisceral connective develops. In many, especially immobile species, the eyes and statocysts disappear. Ultimately, in all species the apical tuft of cilia disappears. In mobile forms definitive sense organs, lacking in larvae, are formed.

Changes in the structure of the *shell* represent the concluding stage of metamorphosis. The microstructure and mineralogy of the shell drastically change; layers of the new definitive shell — the dissoconch — are formed (Wilbur, 1964). The larval hinge is also replaced by a definitive one. Changes in the hinge system may precede metamorphosis, or follow it, depending on the family. The shell changes considerably in specialized forms such as wood- and rock-boring species (Kiseleva, 1970; Turner and Johnson, 1971; Boyle and Turner, 1976).

The definitive shell is in a partially open state due to the ligament that first appears in the prodissoconch or dissoconch (Lutz and Hidu, 1979). This ligament is an elastic cord connecting the valves of the shell. It begins to form in the ligament fossa of the shell. The position of this fossa and hence of the ligament proper, differs in different families. In the vast majority of bivalves it is situated ventral to the hinge line. It should be pointed out that the ligament may not always be present in larvae; if present, it does not always develop in the adult.

In the family Teredinidae, new protective structures appear during metamorphosis: a calcified cone, made of detritus, over the inlet to the passage made by the mollusk; a calcified bed in the passage; and plates or palettes near the siphon (Figure 31) (Turner, 1966).

In the two species of bivalves of the family Pholadidae — *Zirphaea crispate* (Warner, 1939) and *Martesia striata* (Boyle and Turner, 1976) — a ventral tooth and alveolus form; these are situated on the ventral edge of the shell facing the umbo (Figure 32). The ventral hinge is used only in the period of metamorphosis and settling, after which it totally disappears. After termination of metamorphosis, the clasping apparatus in mobile mollusks may become reduced (Broom, 1985).

In monomyarian mollusks the anterior adductor of the shell is destroyed during metamorphosis and its place occupied by the posterior adductor. Upon

Figure 31: Posterior end of *Bankia rochi* Mall. with siphons and palettes (from Turner, 1966). p — palettes; s — siphon.

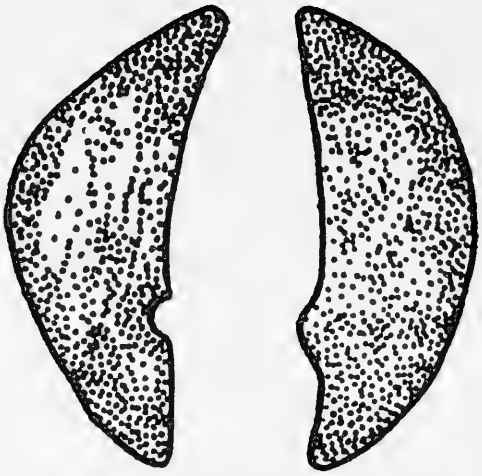


Figure 32: Valves of the pediveliger I of *Martesia striata* L. with tooth and alveolus on ventral side (from Boyle and Turner, 1976).

completion of metamorphosis, the attachment system in mobile mollusks may be reduced.

The development of the genital system lags behind the development of all other systems and occurs only after the termination of metamorphosis. The primary germ cells in the freshwater mollusks *Sphaerium* are already visible in the early stages of development of the embryo, in the mesodermal bands; in other species, these cells become visible only after metamorphosis in the region of the ventral part of the pericardium (Okada, 1936; Coe and Turner, 1938; Lucas, 1975).

On the whole, metamorphosis is a distinct sequence of processes transforming the larva into a juvenile. A disturbance of this sequence or blockage of any stage leads to deformity or mortality (Turner, 1976).

Lecithotrophic Larvae and Direct Development

In evolution, primary development with planktotrophic larvae is typical of bivalves (Jagersten, 1972), yet in many families a lecithotrophic development phase is observed, which is usually linked with larviparity of ovoviviparity (Thorson, 1936; Ockelmann, 1962). This phenomenon has been detailed for bivalves by Sellmer (1967) and Blacknell and Ansell (1974). Duration of the lecithotrophic phase can be determined from the size of the eggs and prodissoconch I. In most bivalves the duration of this phase terminates in the early differentiation of the digestive tract and formation of the straight-hinged veliger with emergence from its envelopes. However, in more than 25 families,

the lecithotrophic phase extends beyond the limits of the trochophore stage (Blacknell and Ansell, 1974). The development of lecithotrophic larvae and of brood care are common for small (usually less than 1 cm long) bivalves. If the lecithotrophic larva does not leave the egg capsule before metamorphosis, it loses the adaptation for swimming. Thus, in the larvae of *Lasaea rubra* (Oldfield, 1964), *Thyasira gouldi* (Blacknell and Ansell, 1974), and *Cardiamya pectinata* (Gustafson *et al.*, 1986) developing in the egg capsule, the velum loses cilia and becomes a vitalline receptacle.

Some mention should be made of the unique larvae of the primitive bivalves of superorder Protobranchia (Drew, 1897, 1899a, b; 1901). From the yolk-rich eggs of *Nucula delphinodonta* and *Yoldia limatula*, barrel-shaped lecithotrophic larvae develop, swim briefly in plankton. In contrast to most Bivalvia, the prototroch and pretrochal ectoderm are not modified into the velum in these larvae. Growing in size, they cover the entire larval body, forming a temporary larval mantle which consists of five transverse rings of large vacuolated cells. The long cilia of the cells of the middle rings form three ciliary bands. The anal group of small cells produces a tuft of sensory cilia. Under the integument of the larval mantle, the development of the definitive mollusk precedes (Figure 33). During metamorphosis the larval mantle is discarded.

Jagersten (1972) considers this bell-shaped larva a secondarily modified one that was lost by the trochophore of mollusks even before the veliger appeared in evolution. Other authors (for example, Fioroni, 1971; Salvini-Plawen, 1972, 1973; Starobogatov, 1979) consider the lecithotrophic larva of Protobranchia to be the starting point for bivalves. In our opinion, Jagersten's viewpoint, also supported by Ivanova-Kazas (1977), is more justifiable.

Development that includes lecithotrophic larvae is observed in all Protobranchia irrespective of place of habitation — the Arctic, Antarctic, tropics and littoral or benthic zones. Development may or may not include a brief pelagic stage.

In addition to Protobranchia, development without a planktotrophic larva is typical of the suborders Carditida and Lucinida and coincides with different forms of brood care. Some young are attached with the egg envelopes to the substrate (Astartidae), others are carried in the gills right up to the juvenile stage (genus *Cardita*), and still others, after brooding in ctenidia, are carried in a chamber that forms on the ventral side of the shell of the female (*Milneria kelseyi* and *Thecalia concamerata*) (Dall, 1903; Yonge, 1969). Development without a planktotrophic larva is also typical of the order Pholadomyida (superfamilies Myochamoidea, Clavigelloidea, Pandoroidea, Thracioidea). Thus, in Pandoroidea a swimming larva emerges from the envelope after completing metamorphosis within a few days (Pelseneer, 1911; Allen, 1961). A tendency

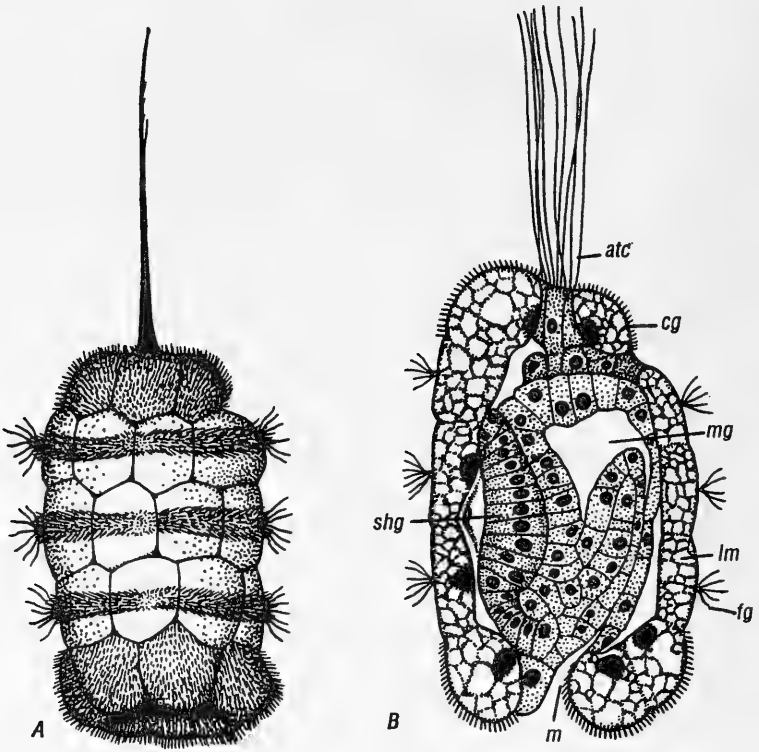


Figure 33: Lecithotrophic larva of *Yoldia limatula* Dall (from Drew, 1899).
A — external appearance; B — median section; atc — apical tuft of cilia; cg — cerebral ganglion; fg — foregut; lm — larval mantle; m — mouth; mg — midgut; shg — shell gland.

to lengthen the lecithotrophic phase is observed in the superfamily Ostreoidea. In *Crassostrea gigas* and *C. virginica*, fertilization takes place in the external medium (water) and the larva takes to active feeding in the straight hinge stage. In *Ostrea edulis*, fertilization occurs in the mantle cavity and brooding in the gills continues until the larval shell has reached a length of about 160 µm. In *O. chinensis* and *O. lutaria*, females bear larvae up to the pediveliger stage which, soon after their emergence in the sea, settle and metamorphose (Millar and Hollis, 1963); in the absence of a substrate for settling, metamorphosis may be delayed for several days (Chanley and Dinamani, 1980). In the family Teredinidae, fertilization occurs in water in *Bankia* and the lecithotrophic phase is confined to the trochophore stage. In *Lyrodus* and *Teredo*, the duration of the planktotrophic phase may be considerably shortened. This tendency appears, obviously, independent of geographic distribution of the species and

is associated with specific conditions of existence. In the superfamily Veneroidea, predominance of the lecithotrophic phase is related to colonization of polar waters (Ockelmann, 1958; Dell, 1972) in one line, and in another to reduction in body size (Hansen, 1953; Oldfield, 1964). In the superfamilies Tellinoidea and Mytiloidea, development with lecithotrophic larvae is observed in species colonizing arctic waters. Lecithotrophic larvae and direct development are also characteristic of the suborder Erycinina, in which brooding of young up to the juvenile stage is observed, as well as male dwarfism an uncommon phenomenon in bivalves. In the family Galeommatidae, male dwarfism is observed in *Ephippodonta oedipus* and *Chlamydoconcha orcutti*. Male dwarfism evolved from secondary brooding of juveniles under the protective mantle of the adult mollusk (Morton, 1976, 1981). According to Morton, male dwarfism is a temporary phase in the development of these mollusks, which later grow into animals of definitive size. In the family Montacutidae, dwarf males are found in commensal forms — *Montacuta floridiana, M. percompressa* (Jenner and McCrary, 1968), and *M. phascolionis* (Deroux, 1960). Recently, dwarf males were reported for two species of teredinides — *Zachsia zenkewitchi* and *Z. serenei* — inhabiting the roots of sea grass (Terner and Yakovlev, 1981, 1983; Yakovlev, 1988).Yakovlev and Malakhov (1985, 1988) have shown that dwarf males of *Z. zenkewitchi* combine features of neotany, regression and specialization.

Mollusks of the suborder Erycinina are the smallest bivalves (less than 1 cm), exhibiting a sharp fall in fecundity with extended periods of brooding. Thus *Arthritica bifurca,* living in silt singly or with the polychaeta *Pectinaria australis* (Wear, 1966), incubates numerous larvae only up to a length of 120 μm, while *Lasaea rubra* cares for its progeny up to the juvenile stage (Oldfield, 1955, 1964); in this species there is a maximum of 33 embryos, which reach a length of 500 μm. Booth (1979) observed one sexually mature *L. rubra hinemoa*, 1 mm in length, brooding two embryos, each 400 μm long.

Table 3 presents data from tables compiled by Sellmer (1967), Blacknell and Ansell (1974), Sastry (1979), as well as data from other researchers, on species of marine and brackish-water mollusks with some form of brood care. The list, of course, is not exhaustive. The classification of bivalves is that given by Skarlato and Starobogatov (1979), except for the genus *Chlamydoconcha*, which is included in the family Galeommatidae.

IDENTIFICATION OF PELAGIC LARVAE OF BIVALVES (Terminology and Taxonomic Characters)

In larvae, a distinction is made between the anterior and posterior, and upper and lower (dorsal and ventral) margins of the shell. The velum and adductor

Table 3: Brood care in marine and brackish-water bivalves

	Species	Mean or maximum length of mollusk, mm	Type of brood care	Source
			Superorder PROTOBRANCHIA	
			Superfamily NUCULOIDEA	
1.	*Nucula nucleus*	23.0	Shortening of pelagic period	Jørgensen, 1946
2.	*N. tenuis*	4.7	Pelagic period short or absent	Thorson, 1936
3.	*N. t. expansa*	17.4	Pelagic period short or absent	Ockelmann, 1958
4.	*N. proxima*	—	Shortening of pelagic period in connection with large quantity of yolk in egg	Blacknell and Ansell, 1974
5.	*N. delphinodonta*	5.0	Pelagic period absent; development in capsules attached to valves	Drew, 1901
			Superfamily NUCULANOIDEA	
6.	*Nuculana pernula*	32.0	Pelagic period very short	Ockelmann, 1958
7.	*N. minuta*	15.7	Same	Ockelmann, 1958
8.	*Megayoldia thracieformis*	35.5	Same	Ockelmann, 1958
9.	*Yoldia amygdalea*	44.7	Pelagic period short or absent	Ockelmann, 1958
10.	*Y. limatula*	—	Pelagic period short in connection with large quantity of yolk in egg	Drew, 1899b
11.	*Yoldiella lenticula*	8.3	Pelagic period short or absent	Ockelmann, 1958
12.	*Portlandia fraterna*	3.7	Same	Ockelmann, 1958
13.	*P. arctica*	28.5	Pelagic period short	Ockelmann, 1958

		Superorder AUTOBRANCHIA		
		Superfamily ARCOIDEA		
14.	*Arca vivipara*	—	Brooding	Pelseneer, 1906
15.	*A. petincutoides grandis*	16.9	Pelagic period short or absent	Ockelmann, 1958
16.	*A. glacialis*	25.6	Same	Ockelmann, 1958
17.	*A. freili*	16.9	Same	Ockelmann, 1958
18.	*Adacnarca nitens*	—	Brooding	Burne, 1920
		Superfamily LIMOPSOIDEA		
19.	*Limopsis* sp.	6.4–12.7	Broooding	Pelseneer, 1906
20.	*Cyrilla minuta*	—	Same	Howard, 1953
21.	*Hochstellaria* sp.	—	Same	Bernard, 1897
22.	*Philobrya setosa*	2.7	Same	Howard, 1953
23.	*P. costata*	—	Same	Bernard, 1897
24.	*P. aviculoides*	—	Same	Bernard, 1897
		Superfamily MYTILOIDEA		
25.	*Dacridium vitreum*	6.2	Pelagic period short or absent	Ockelmann, 1958
26.	*Musculus nigra*	47.0	Filiform clutch; eggs attached to byssus of mother organism	Ockelmann, 1958
27.	*M. lateralis*	25.0	Development in clutch	Miner, 1950
28.	*M. discors*	25.0	Filiform clutch; eggs attached to mother organism	Thorson, 1936; Ockelmann, 1958
29.	*M. laevigatus*	—	Filiform clutch; eggs attached to mother organism	Kaufmann, 1977
30.	*Musculista senhousia*	14–29	Development up to veliger stages in clutch	Kulikova, 1978; Matveeva, 1979

(Table 3 contd.)

	Species	Mean or maximum length of mollusk, mm	Type of brood care	Source
31.	*Vilasina pilluta*	15	Development in clutch; pelagic stage short or absent	Matveeva, 1979
32.	*Crenella glandula*	6.4	Development in clutch	Miner, 1950
33.	*C. decussata*	4–6	Pelagic period short or absent	Ockelmann, 1958
			Superfamily OSTREOIDEA	
34.	*Ostrea edulis*	80.0	Development up to veliger stage in pallial or gill cavities	Abbott, 1954
35.	*O. lurida*	75.0	same	Abbott, 1954
36.	*O. permollis*	75.0	same	Abbott, 1954
37.	*O. frons*	50.0	same	Abbott, 1954
38.	*O. equestris*	50.0	same	Abbott, 1954
39.	*O. angasi*	—	same	Abbott, 1954
40.	*O. lamellosa*	—	same	Matveeva, 1979
41.	*O. chinensis*	—	Development up to pediveliger stage in pallial or gill cavities	Chanley and Dinamani, 1980
42.	*O. lutaria*	—	same	Chanley and Dinamani, 1980
43.	*Alectryonella plicatula*	—	Brooding	Amemiya, 1929; Wada, 1953
44.	*Lopha cristagalli*	—	same	Wada, 1953

		Superfamily PERNOPECTINOIDEA		
45.	*Propeamussium imbriferum*	20.8	Brooding	Wada, 1953
46.	*P. groenlandicum*	29.5	same	Wada, 1953
		Superfamily ASTARTOIDEA		
47.	*Tridonta borealis*	24–55	Eggs in gelatinous envelopes, attached to substrate	Thorson, 1936
48.	*Nicania montagui*	26	Same	Thorson, 1936
49.	*Astarte elliptica*	40	Same	Thorson, 1936
50.	*A. crenata*	32	Eggs attached; pelagic period short or absent	Ockelmann, 1958
51-52.	*A. sulcata*	23	Same	Ockelmann, 1958
		Superfamily CARDITOIDEA		
53.	*Milneria kelseyi*	6.4	Development in outer chambers on ventral edge of shell, covered with periostracum	Abbott, 1954
54.	*Thecallia concamerata*	—	Development in outer chamber in shell fold	Bernard, 1898; Dall, 1903
55.	*Cardia ballyi*	7–12	Brooding in gills; pelagic period absent	Jones, 1963; Gilbert, 1963
56.	*C. barbarensis*	7–12	Brooding in gills; pelagic period absent	Jones, 1963; Gilbert, 1963
57.	*C. ventricosa*	7–12	Same	Jones, 1963; Gilbert, 1963
58.	*Venericardia purpurata*	—	Brooding	Brune, 1920
59.	*Cyclocardia crebicostata*	40	Brooding in inner Demibranchs	Scarlato, 1981
60.	*Crassicardia crassidens*	13–25	Same	Scarlato, 1981
		Superfamily CONDILOCARDIOIDEA		
61.	*Condilocardia* sp.	—	Brooding; pelagic period absent	Pelseneer, 1935
62.	*Modiolarca trapezina*	—	Brooding in gills	Pelseneer, 1935
63.	*Modiolarca magellanica*	11.0	Brooding in gills	Pelseneer, 1935

(Table 3 contd.)

	Species	Mean or maximum length of mollusk, mm	Type of brood care	Source
			Superfamily CYAMOIDEA	
64.	*Cyamium minutum*	3.0	Eggs in capsules, attached to substrate	Matveeva, 1953
65.	*Turtonia minuta*	3.0	Eggs in capsules, attached to substrate or byssus	Ockelmann, 1958; Oldfield, 1964
			Family Thyasiridae	
66.	*Thyasira gouldi*	9.0	Development in capsules; pelagic period absent	Ockelmann, 1958; Blacknell and Ansell, 1974
66a.	*T. flexuosa*	—	Pelagic period absent	Thorson, 1936
67.	*T. equalis*	8.8	Pelagic period short or absent	Ockelmann, 1958
68.	*Axinopsis orbiculata*	4.6	Pelagic period short or absent	Ockelmann, 1958
			Family Lucininae	
69.	*Lucina* sp.	6.6	Development in gills	Ockelmann, 1958
70.	*L. lactea*	12.0	Brooding; pelagic period present	Pelseneer, 1926
			Superfamily LEPTONOIDEA	
71.	*Loripes lucinalis*	30	Development in folds up to veliger stage	Zakhvatkina, 1972
72.	*Montacula feruginosa*	0.7–9.7	Brooding in gills up to late veliger stage	Pelseneer, 1935; Oldfield, 1964
73.	*M. clarkiae*	2.5	Brooding; pelagic period present	Pelseneer, 1935
74.	*Montacula percompressa*	—	Brooding in epibranchial cavity up to veliger stage	Chanley and Chanley, 1970

75.	*M. substriata*	4.0	Brooding in gills up to late veliger stage	Oldfield, 1964
76.	*M. phascolionis*	3.5–4.5	Brooding; pelagic period absent	Pérès, 1937; Deroux, 1960
77.	*Montacutona compacta*	—	Brooding	Morton, 1980
78.	*Isoconcha sibogai*	5.5	Brooding	Pelseneer, 1911
79.	*Synapticola* sp.	—	Brooding	Pelseneer, 1911
80.	*Jousseaumiella* sp.	—	Brooding	Pelseneer, 1911
81.	*Lepton parasiticum*	—	Brooding in mantle cavity; pelagic period absent	Pelseneer, 1935
82.	*Lasae rubra*	2.5	Brooding in gills; pelagic period absent	Pelseneer, 1935
83.	*L. rubra hinemoa*	—	Brooding in gills; pelagic period absent	Booth, 1979b.
84.	*Bornia longipes*	8.5	Brooding	Pelseneer, 1906
85.	*B. corbiculoides*	—	Brooding	Bernard, 1898
86.	*Mysella bidentata*	—	Brooding	Howard, 1953
87.	*M. japonica*	—	Brooding	Miyazaki, 1935
		Superfamily KELLIOIDEA		
88.	*Kellia suborbicularis*	3.7	Brooding in gills up to veliger stage	Howard, 1953
89.	*K. japonica*	—	Brooding in mantle cavity up to straight hinge veliger stage	Personal data
		Superfamily GALEOMMATOIDEA		
90.	*Galeomma turtoni*	5.0	Brooding in mantle cavity up to straight hinge veliger stage	Lebour, 1938
91.	*G. takii*	—	Brooding in mantle cavity; pelagic period absent; secondary brooding in mantle	Morton, 1973
92.	*Ephippodonta oedipus*	—	Brooding	Morton, 1976
93.	*Chlamydoconcha orcutti*	—	Brooding	Morton, 1981
94.	*Entovalva mirabilis*	—	Brooding in pallial cavity; pelagic period present	Voeltzkow, 1891
95.	*Sciobervetia* sp.	—	Brooding	Pelseneer, 1911

(Table 3 contd.)

	Species	Mean or maximum length of mollusk, mm	Type of brood care	Source
			Superfamily CARDIOIDEA	
96.	*Cerastoderma elegantulum*	13.4	Development in chambers formed by folds of ventral areas of mantle	Matveeva, 1953 Ockelmann, 1958
97.	*C. clodiense*	31	Development in capsules, attached to substrate, up to veliger stage	Zakhvatkina, 1972
98.	*Parvicardium exiguum*	—	Development in membrane, attached to substrate, up to veliger stage	Jørgensen, 1946
99.	*Pseudokellia cardiformis*	—	Brooding in gills	Pelseneer, 1906
			Superfamily VENEROIDEA	
100.	*Psephidia lordi*	6.4	Brooding	Abbott, 1954
101.	*P. ovalis*	4.0	Brooding	Howard, 1953
102.	*P. brunnea*	4.5	Brooding	Howard, 1953
103.	*Parastarte triquetra*	3.2	Brooding	Dall, 1903
104.	*Transenella tantilla*	6.0	Brooding in gills; pelagic period absent	Hansen, 1953
105.	*Gemma gemma*	5.0	Brooding in gills; pelagic period absent	Sellmer, 1967
			Superfamily TELLINOIDEA	
106.	*Macoma moesta*	30.1	Pelagic period short or absent	Ockelmann, 1958
107.	*M. lovenii*	16.7	Pelagic period short or absent	Ockelmann, 1958
108.	*M. torelli*	13.6	Pelagic period short or absent	Ockelmann, 1958
			Superfamily SCORBICULARIOIDEA	
109.	*Abra ovata*	25	Development in clutch up to veliger stage	Zakhvatkina, 1972

			Family Teredinidae	
110.	*Teredo navalis*	51.0	Brooding in gills up to straight hinge veliger stage	Hill and Kofoid, 1927; Turner and Johnson, 1971
111.	*T. diegensis*	50.0	Brooding	Hill and Kofoid, 1927
112.	*T. bartschi*	—	Brooding in gills up to pediveliger stage	Turner and Johnson, 1971
113.	*T. clappi*	—	Same	Turner and Johnson, 1971
114.	*T. furcifera*	—	Same	Turner and Johnson, 1971
115.	*T. poculifera*	—	Same	Turner, 1966
116.	*T. somersi*	—	Brooding in gills	Turner, 1966
117.	*Lyrodus massa*	—	Brooding in gills up to straight hinge veliger stage	Turner and Johnson, 1971
118.	*Lyrodus pedicellatus*	—	Brooding in gills up to pediveliger stage	Turner and Johnson, 1971
119.	*L. afinis*	—	Brooding in gills	Turner, 1966
120.	*L. mediolobata*	—	Brooding in gills	Turner, 1966
121.	*Zachsia zenkewitchi*	—	Brooding in gills up to veliger stage	Turner and Yakovlev, 1981
			Family Pholadidae	
122.	*Xylophaga africana*	—	Pelagic period absent; juvenile mollusks attached by byssus to shell of maternal organism	Knudsen, 1961
123.	*X. bruuni*	—	Same	Knudsen, 1961
124.	*X. lobata*	—	Same	Knudsen, 1961
125.	*X. panamensis*	—	Same	Knudsen, 1961
126.	*X. tubulata*	—	Pelagic period absent; juvenile mollusks attached to edge of mantle of maternal organism	Knudsen, 1961

(Table 3 contd.)

	Species	Mean or maximum length of mollusk, mm	Type of brood care	Source
127.	*Xylophaga concava*	—	Pelagic period absent; juvenile mollusks attached to edge of mantle of maternal organism	Knudsen, 1961
128.	*X. wolffi*	—	Same	Knudsen, 1961
129.	*Barnea candida*	65	Development in suprabranchial cavity up to veliger stage	Zakhvatkina, 1972
			Superfamily MYOCHAMOIDEA	
130.	*Lyonsia arenosa*	24.6	Pelagic period short or absent	Ockelmann, 1958
131.	*Anatina elliptica*	—	Brooding	Burne, 1920
			Superfamily CLAVIGELLOIDEA	
132.	*Aspergillum javanicum*	—	Brooding	Lacaze-Duthiers, 1870
			Superfamily PANDOROIDEA	
133.	*Pandora rostrata*	—	Brooding	Pelseneer, 1911
134.	*P. elongata*	—	Brooding	Pelseneer, 1911
135.	*P. glacialis*	27.3	Pelagic period short or absent	Ockelmann, 1958
			Superfamily THRACIOIDEA	
136.	*Thracia distorta*	25.8	Brooding	Pelseneer, 1935
137.	*T. septentrienalis*	—	Pelagic period short or absent	Ockelmann, 1958
138.	*T. myopsis*	33.0	Same	Ockelmann, 1958
139.	*T. devexa*	40.0	Same	Ockelmann, 1958

		Superorder SEPTIBRANCHIA		
		Superfamily VERTICORDIOIDEA		
140.	*Lyonsiella abyssicola*	5.3	Pelagic period short or absent	Ockelmann, 1958
			Family Cetoconchidae	
141.	*Cetoconcha* sp.	—	Brooding	Pelseneer, 1911
			Family Poromyidae	
142.	*Poromya granulata*	12.0	Pelagic period short or absent	Ockelmann, 1958
			Family Cuspidariidae	
143.	*Cuspidaria obesa*	11.0	Pelagic period short or absent	Ockelmann, 1958
144.	*C. subtorta*	8.4	Same	Ockelmann, 1958
145.	*C. glacialis*	28.4	Same	Ockelmann, 1958

in the veliger and the velum and foot in the veliconcha, are situated in the anterior margin. The opposite end, where siphons later develop, is called the posterior. Morphologically, the valves join on the dorsal margin. Since in larvae the hinge develops along the dorsal margin, this margin is also termed the hinge margin. The margin opposite to the hinge is called the ventral margin. The anterior part of the dorsal margin (up to the umbo) is called the anterior shoulder, and the posterior part (from the umbo), the posterior shoulder (Figure 34).

Sculpturing, concentric (lines of growth) and radial lines appear on the outer surface of the valves. In individual species the pallial line, the imprint of the mantle muscle, is quite noticeable on the inner surface (Figure 34).

The hinge in larvae consists of a provinculum and a lateral system (see Figure 18). The provinculum is a thickening of the hinge margin and bears cardinal teeth. The lateral hinge system is represented by flanges and crests (Rees, 1950; Zakhvatkina, 1959). In a closed shell the thicker dorsal margins of the flanges of one valve are overlapped by the thinner dorsal margins and inner crests of the other valve. Sometimes lateral teeth develop on the flanges where their ends touch the provinculum. In some species there are special teeth, which belong neither to the provinculum nor to the lateral hinge system.

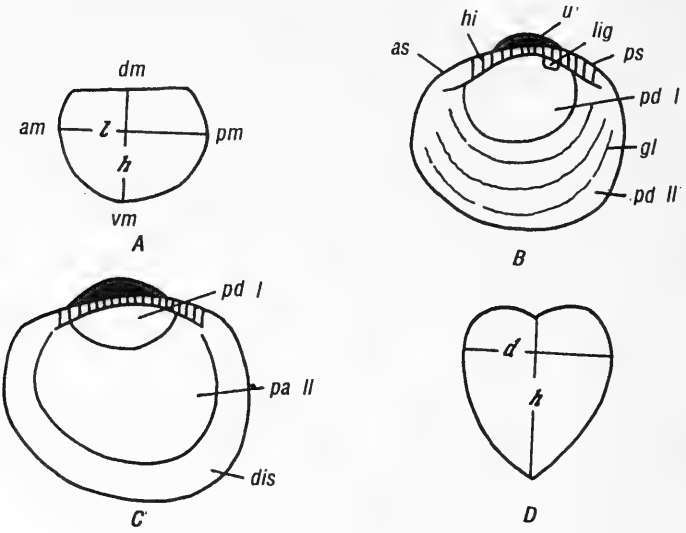


Figure 34: Schematic structure of the larval shell in different stages.
A — veliger; B — veliconcha; C — spat; D — veliconcha.
am — anterior margin; as — anterior shoulder; d — shell thickness; dis — dissoconch; dm — dorsal margin; gl — growth line; h — shell height; hi — hinge; l — shell length; lig — ligament; pd I — prodissoconch I; pd II — prodissoconch II; pm — posterior margin; ps — posterior shoulder; u — umbo; vm — ventral margin.

The valves of larvae are connected by a ligament. This ligament may be external or internal to the hinge line (see Figure 18). The ligament is termed anterior, median, or posterior according to its position relative to the midline of the hinge. In identification of larvae the following parameters and characters are taken into consideration.

1. *Size parameters of larva* : Length, height and thickness of shell (Figure 34). Length of shell is the maximum distance between the anterior and posterior margins parallel to the hinge line. Height of shell is the distance from the apex of the umbo to the ventral margin perpendicular to the hinge line. The thickness, which characterizes the degree of convexity of valves, is the distance between the most convex areas of the valves. The length of the anterior and posterior ends of the shell may be used as an auxiliary parameter; it is the distance from the anterior or posterior margins of the shell to the line of height. Many researchers (Rees, 1950; Zakhvatkina, 1959; Loosanoff *et al.*, 1966; Gal'perina, 1969; Chanley, 1968; Schweinitz and Lutz, 1976; and others) use relative size parameters (ratio of shell height to length and height to thickness) as identification characters.

2. *Shape of larva* : The shape of a larva is determined by the following characteristics : (a) length and mutual disposition of shoulders (these may be equal or unequal in length and slope to the umbo at a definite angle or parallel to each other); (b) length and shape of anterior, posterior, and ventral margins of the shell (these may be straight or curved, sharp or blunt, and also slope to one or the other end); and (c) shape and size of the umbones (these may be knob-shaped, slanted, round, flat, or obtuse) (Figure 35).

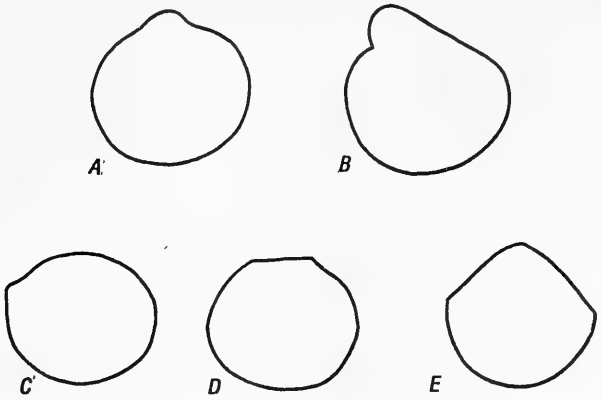


Figure 35: Shape of umbones of larvae.
A — knob-shaped; B — slanted; C — irregularly rounded; D — obtuse; E — angular.

In accordance with variations in these morphological indices, the shell may be round, ovate, trigonal-ellipsoid, and so forth. It may also be equi- or inequilateral. In equilateral shells the anterior margin of the valve is symmetric or nearly symmetric to the posterior margin; in inequilateral shells it is asymmetric. In the larvae of some species the left and right valves of the shell may be different in shape and size. Shells with equal-sized valves are called equivalve and those with unequal valves, inequivalve.

3. *Structure of hinge*: Length of provinculum, number of teeth on each valve, their shape and size, and also the number and shape of special teeth, and the structure of the lateral hinge system — these are of taxonomic importance.

4. *Presence, disposition, and structure of ligament*: In position, the ligament may be outer or inner. The inner ligament may be anterior, median or posterior relative to the hinge line. In transverse section it may be rounded, rectangular, square, or oval.

5. *Sculpture of larval shell.*

6. *Thickness of valves and their transparency.*

7. *Presence of eyes*: Visible as dark pigment spots, distinct on both sides of the shell, in live as well as mounted larvae.

8. *Color of larva and presence of characteristic pigmentation* of internal organs preserved in mounted material.

In identification of live larvae such features may be taken into consideration: size and shape of velum; presence or absence of apical ciliary tuft and length of its cilia; shape of intestinal spiral; position and structure of gill filaments; shape of depression leading to duct of byssus gland; position and number of retractors of the foot and velum, and so on (Lebour, 1938; Allen, 1961; D'Asaro, 1967; Chanley and Andrews, 1971; Chanley and Castagna, 1971; Dinamani, 1973; Culliney, 1974; Turner and Boyle, 1974; Culliney *et al.*, 1975). However, one must exercise caution in using these parameters because the internal structure in developing larvae even at the same stage is highly variable, making interspecific comparison difficult. The fairly useful index for identification of larvae of different species is their behavior, since each "tracks" differently while swimming, as does the pediveliger while creeping (Turner, 1975).

In view of the fact that in general practice the identification of larvae is based on mounted specimens, and that larval tissue becomes deformed during mounting, the principal method of identification relies on features characterizing the larval shell. However, the most apparent taxonomic character of shell structure — structure of the hinge system of the larva — is difficult to ascertain during examination of large plankton samples. Considerable time is re-

quired to examine the structure of the valve hinge in each larva. It is necessary to separate the valves and mount them for microscopic examination at high magnification. The method proposed by many researchers (Turner and Boyle, 1974; Schweinitz and Lutz, 1976; Lutz and Hidu, 1979; Le Pennec, 1980), based on a detailed examination and comparison of shell structures and hinge systems using a scanning electron microscope, ensures accuracy of identification but is not practicable for working with a large number of larvae. Identification predominantly based on size parameters of larvae also does not guarantee total accuracy since the larva of each species, even at the same stage, may change shape during growth; this hardly ensures constancy of relative size parameters. Hence, in preparing a key to the identification of larvae to family, it is expedient to use shape of shell as well as some more apparent individual characters, such as presence of dark pigmentation in members of the family Myidae or ocular spots in Mytilidae as the main taxonomic characters; these are retained in fixed specimens and are readily visible under a binocular microscope. Size parameters of larvae and structure of hinge are better used as second-order characters.

Key to Families for Larvae of Veliconcha Stage

The structure of the veliconcha shell according to families is presented in Figure 36 (larvae arranged with anterior and left and posterior and right). Orientation of larvae in photos random.

1 (4). Shell inequivalve.
2 (3). Valves differ considerably in shape and size. Left valve large, convex, with high umbo raised above right valve. Right valve small, flat, with low umbo. Anterior and slopes sharply. Pigmented eyes absent. . . . . **Ostreidae**, Figure 37.
3 (2). Valves differ slightly in shape and size. Left valve slightly more convex than right. Anterior and highly raised. Pigmented eyes present . . . . . **Pectinidae,** Figures 38, 55, 56.
4 (1). Shell equivalve.
5 (10). Shell round or nearly round.
6 (7). Shell flat, slightly colored, large. Valves thin, brittle. Umbones indistinct or very small. Striation barely perceptible. . . . . **Kelliidae,** Figure 39.
7 (6). Shell convex, intensely colored, moderate in size. Valves thick strong Umbones high, round. Striation well defined.
8 (9). Height of shell slightly more than or equal to length. Hinge system with three large rectangular teeth on right valve and two on left. . . . . .**Teredinidae,** Figures 40, 63, 64.

9 (8). Height of shell slightly less than, or equal to length. Hinge system with two equal teeth on left valve and two on right, one of which is longer and central in position . . . . . **Pholadidae**, Figure 41.

10 (5). Shell different in shape, not round.

11 (18). All margins of shell round and merge smoothly into one another.

12 (13). Shell transversely oval. Anterior margin ventrally produced. Anterior shoulder much longer than posterior. Anterior part of hinge line with special large tooth. Ocular spots absent . .**Tellinidae,** Figure 42.

13 (12). Shell longitudinally oval, ovate. Anterior margin not produced ventrally. Shoulders differ only slightly in length. Special teeth absent. Ocular spots present.

14 (15). Anterior margin blunt. Ventral margin broad, slightly rounded, parallel to hinge line. Relief of concentric lines quite distinct. . . . . **Lithophagidae,** Figure 43.

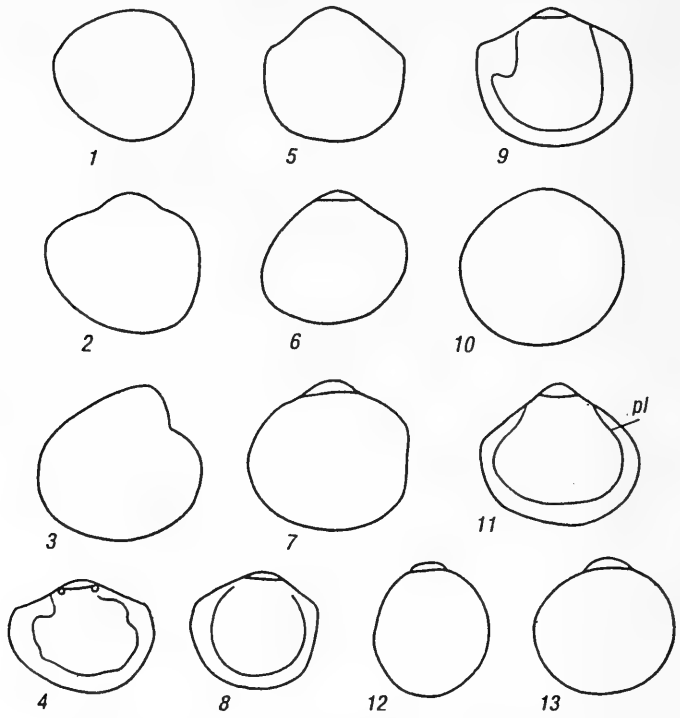


Figure 36: Structure of veliconcha shells in different families.

1 — Pectinidae; 2 — Mytilidae; 3 — Ostreidae, Cordiidae; 4 — Solenidae; 5 — Veneridae; 6 — Tellinidae; 7 — Mactridae; 8 — Myidae; 9 — Clinocardiidae; 10 — Kelliidae; 11 — Hiatellidae; 12 — Teredinidae; 13 — Pholadidae; pl — pallial line.

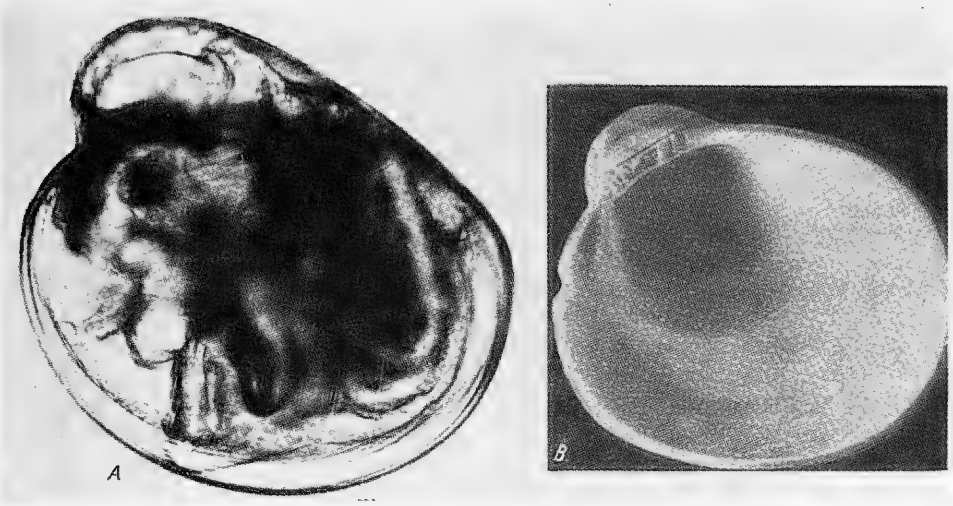


Figure 37 : Veliconcha of *Crassostrea gigas*.
A — external view; B — left valve.

15 (14). Anterior margin acute. Ventral margin appreciably rounded not parallel to hinge line. Concentric line of lesser relief indistinct.

16 (17). Provinculum consisting of a continuous row of denticles. . . . . **Mytilidae**, Figures 44, 52, 53, 54.

17 (16). Denticles absent in central part of provinculum. . . . . **Arcidae.**

18 (11). Margins of shell not rounded.

19 (22). Posterior margin of shell straight; anterior margin acute and stretched.

20 (21). Posterior margin appreciably slopes towards ventral margin. Umbones low and flat. Dark pigmentation present along mantle margin and shoulder. . . . . **Myidae**, Figures 45, 62.

21 (20). Posterior margin slopes slightly and almost perpendicular to ventral margin. Umbones are high conical. Pigmentation absent along the shoulders and mantle margin. . . . . .**Mactridae**, Figures 46, 60, 61.

22 (19). Posterior margin of shell rounded; anterior margin not tapering or almost net, and not stretched more than posterior margin.

23 (26). Shell triangular-oval with triangular apex in umbonal region. Shoulders drop steeply toward ventral side.

24 (25). Ventral and lateral sides form regular semicircle. Shoulders of almost equal or equal length, symmetrical. Pallial line absent. Height of shell equal to its length or slightly less . . . **Veneridae**, Figure 47.

25 (24). Ventral and lateral sides semioval. Anterior shoulder longer than posterior and slightly bent. Pallial line present. Height of shell less than its length . . . . . **Hiatellidae**, Figures 46, 58.

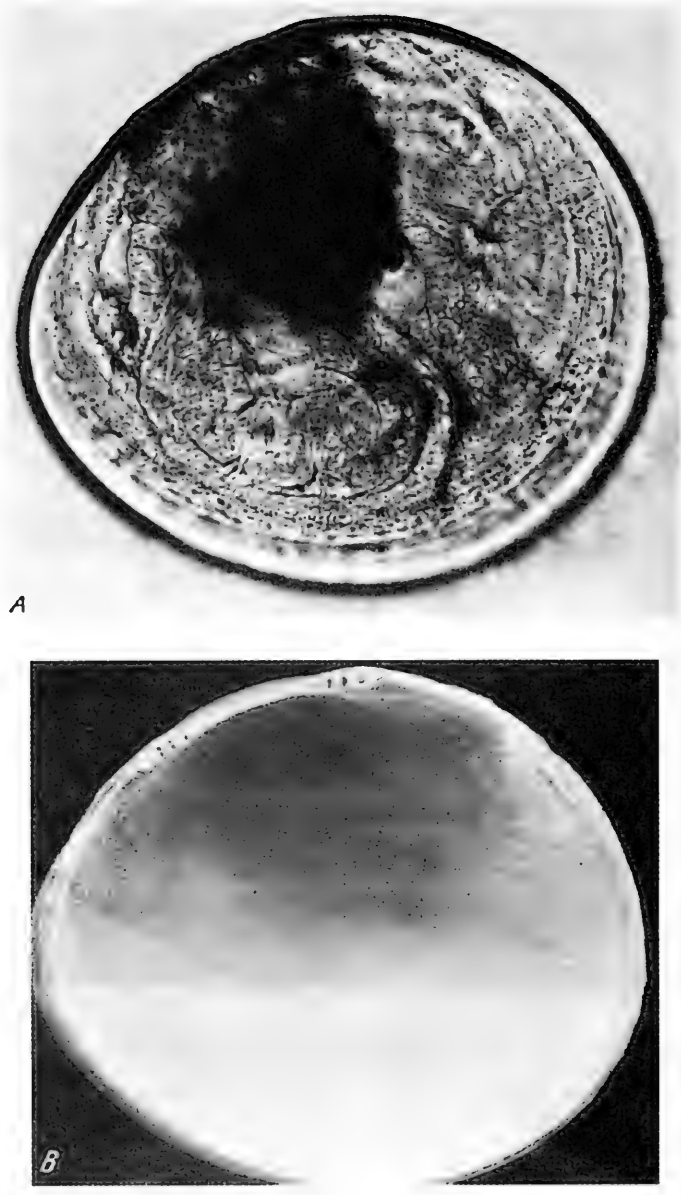


Figure 38: Veliconcha of *Patinopecten yessoensis*.
A — external view; B — right valve.

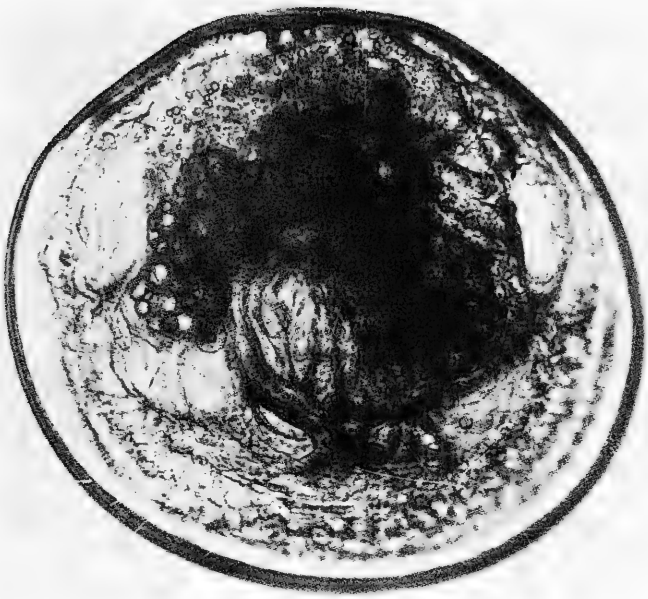


Figure 39: Veliconcha of *Kellia japonica*.

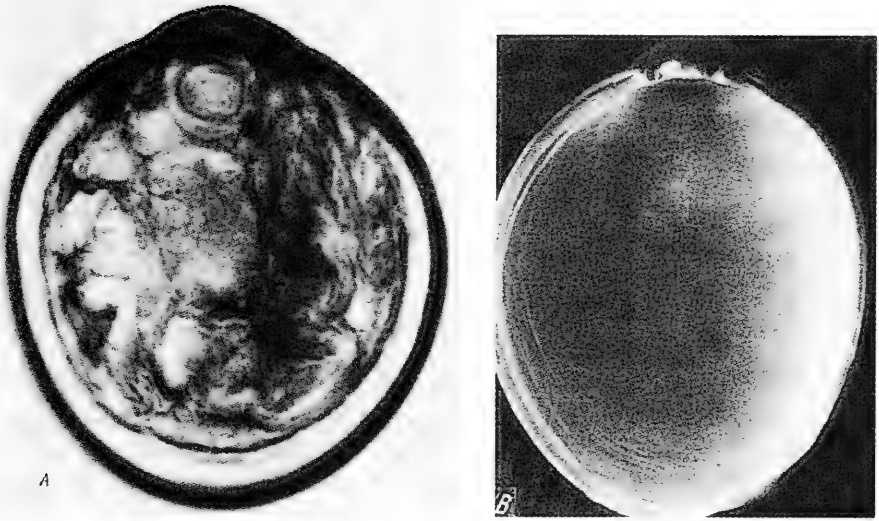


Figure 40: Veliconcha of *Teredo navalis*.
A — external view; B — right valve.

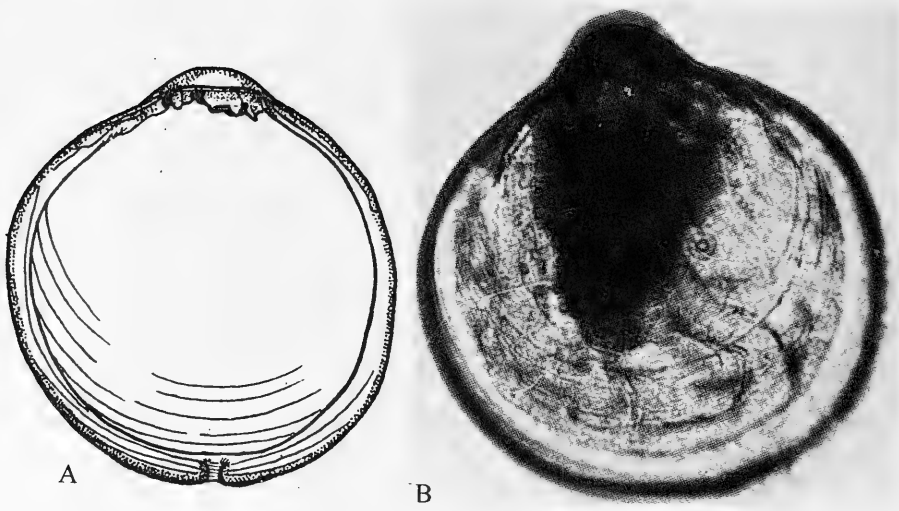


Figure 41: Right (A) and left (B) valve of the veliconcha of *Zirfnaea crispata*; veliconcha of *Barnea japonica* (C).

26 (23). Shell rectangular-oval. Shoulders almost parallel to ventral margin of shell.

27 (30). Anterior margin slightly, tapering. Ligament external. One tooth present at each end of locking line on right valve and a corresponding match on left valve.

28 (29). Shoulders rounded weakly sloping. . . . . **Solenidae**, Figure 49.

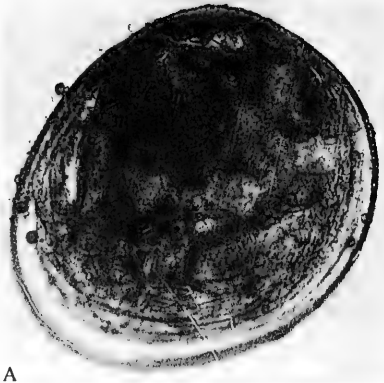
29 (28). Shoulders straight, appreciably sloping . . . . . **Cultellidae**, Figure 50.

30 (27). Anterior margin tapering no more than posterior margin. Ligament internal. Lock consists of row of denticles on right valve and notches on left. . . . . **Cardiidae**, Figure 51.

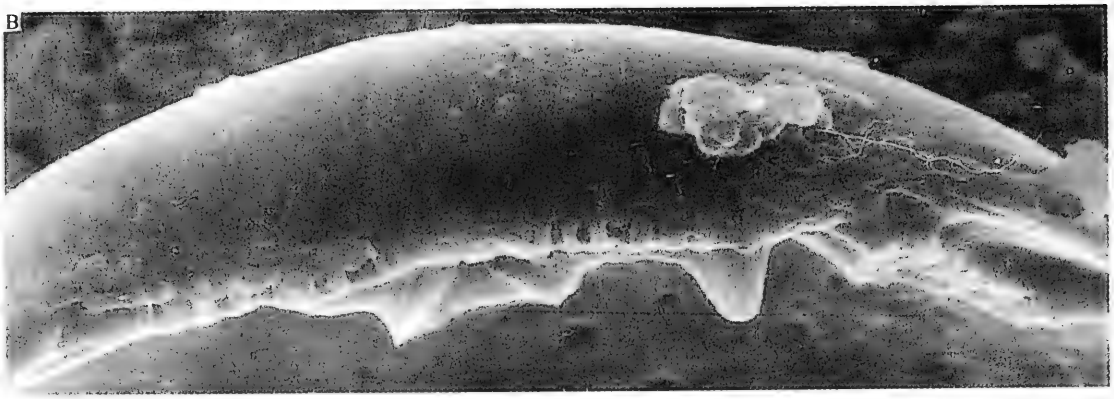
CHARACTERS OF LARVAE ACCORDING TO FAMILIES

Mytilidae

Both ends of the shell are rounded, but the anterior end is narrower than the posterior; the shape of the shell is therefore triangular-oval. The umbo is highly developed. The larvae are fairly large. The hinge line is longer relative to the total size of the shell and, unlike most members of other families, grows in length parallel to the growth of the shell. The hinge has a series of taxodont teeth along the entire hinge line; tooth size increases toward the ends of the row. The ligament is internal and posterior, rarely median. Pigmented spots (eyes) are visible in the veliconcha stage.



A



B

Figure 42: Veliconcha of *Macoma balthica*.
A — general view; B — lock.

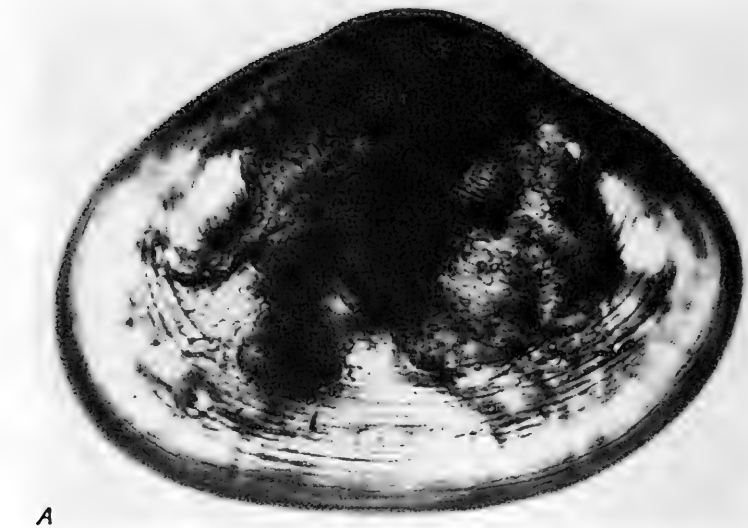


Figure 43: Veliconcha of *Adula falcatoides*.
A — external view; B — hinge of right valve.

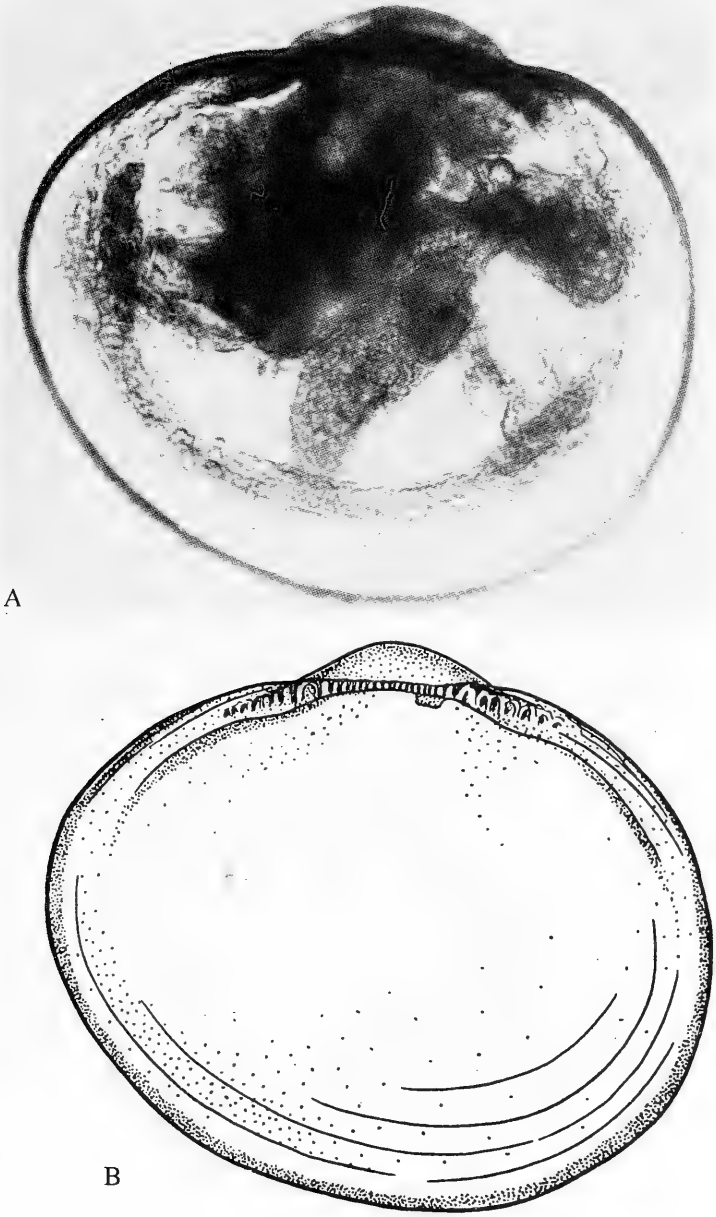


Figure 44: Veliconcha of *Mytilus trossulus*.
A — general view; B — right valve.

Figure 45: Veliconcha of (A) *Mya japonica* and (B) *Mya truncata*.

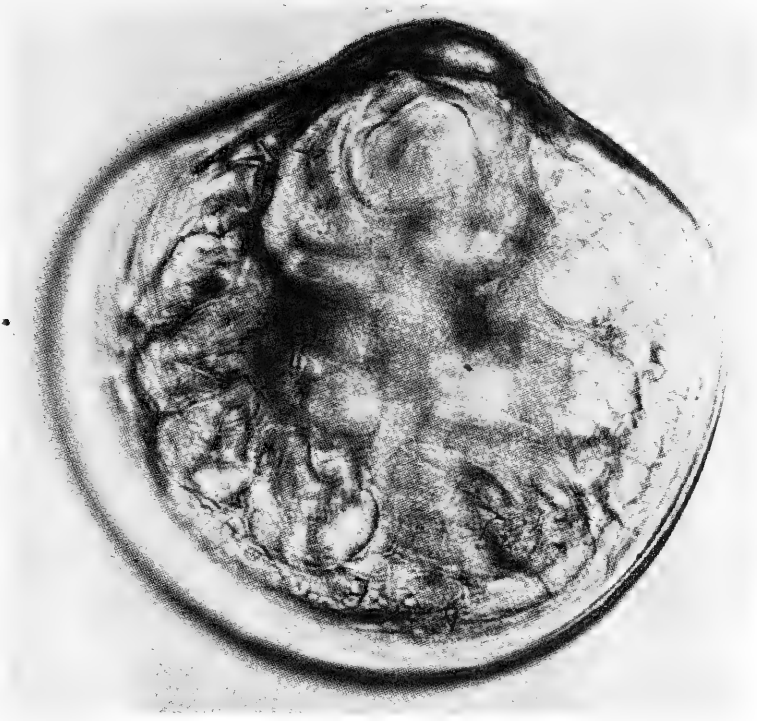
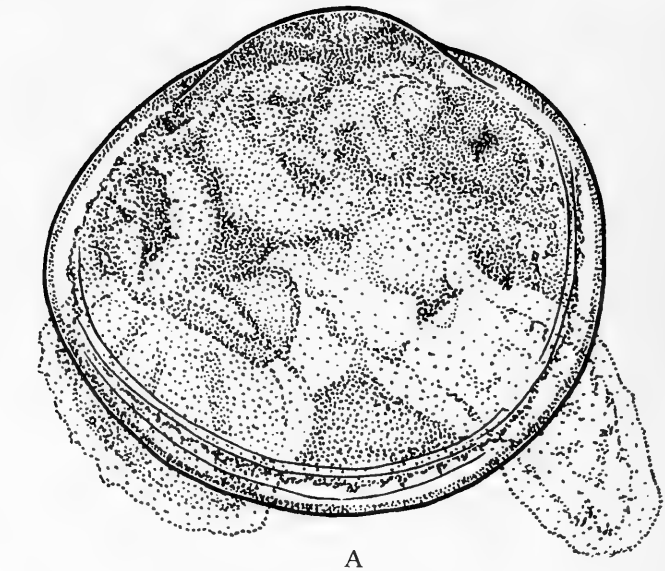
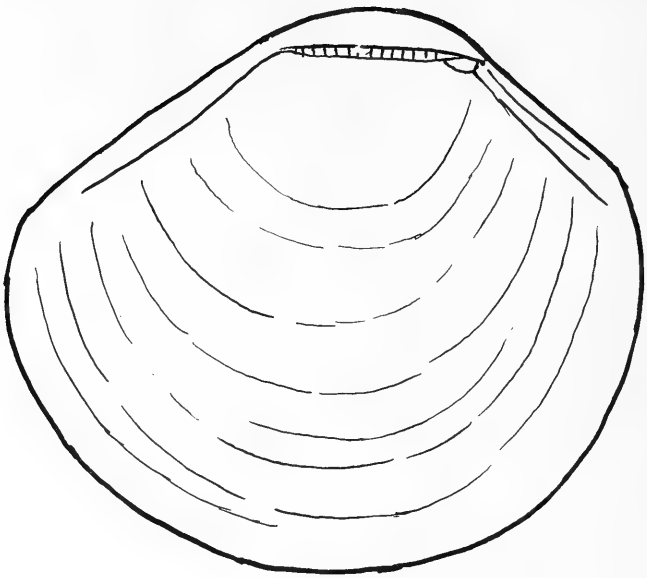


Figure 46: Veliconcha of *Mactra chinensis*.



A



B

Figure 47: (A) Veliconcha of the family Veneridae; (B) right valve of the veliconcha of *Ruditapes philippinarum.*

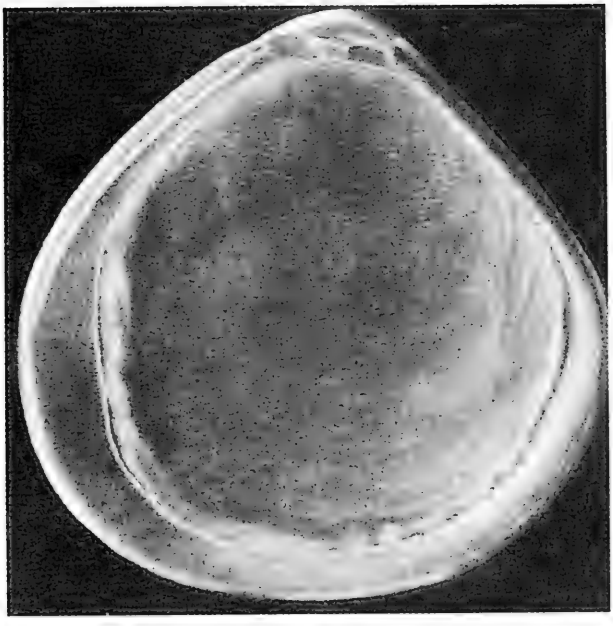


Figure 48: Left valve of the veliconcha of *Histella arctica.*

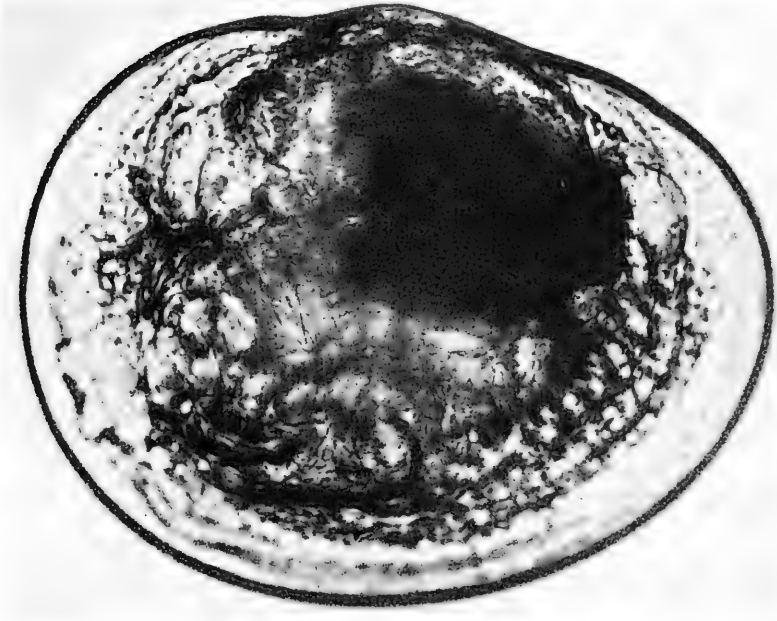


Figure 49: Veliconcha of *Solen krusensterni.*

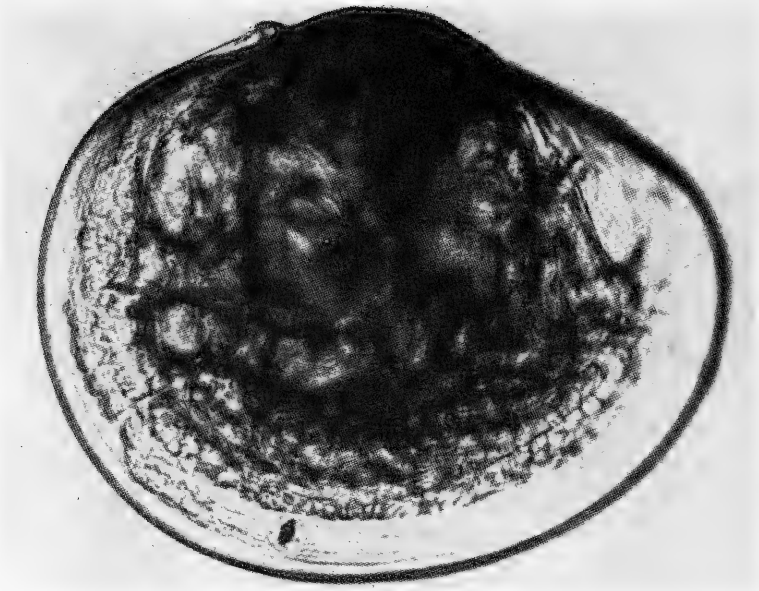


Figure 50: Veliconcha of *Siliqua alta.*

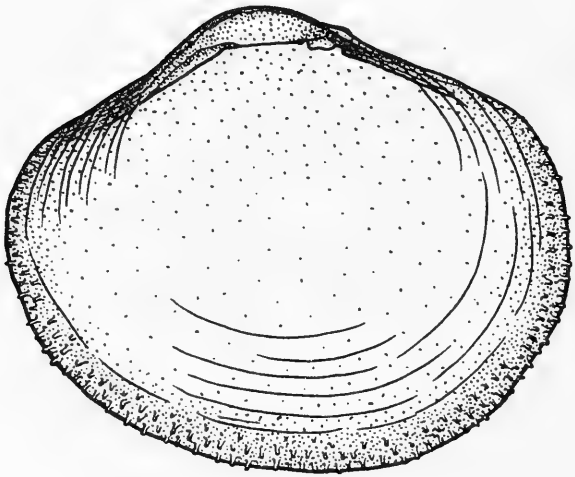


Figure 51: Right valve of the veliconcha of *Keenocardium californiense.*

Mytilus trossulus Gould (see below), *Mytilus coruscus* Gould (larvae not described), *Crenomytilus grayanus* (Dunker) (see below), *Modiolus difficilis* (Kuroda and Habe) (see below), and *Muculista senhousia* (Benson) (see below) inhabit Peter the Great Bay.

Arcidae

In shape, presence of eye spots, and structure of the lock, the larvae of the family Arcidae are very similar to the larvae of the family Mytilidae, more particularly to the Pacific mussel, *Mytilus trossulus,* and Gray's mussel, *Crenomytilus grayanus*. They differ mainly in that the larvae of the family Arcidae have a broader anterior margin and do not bear denticles in the center of the hinge line. The larvae of mussels are also more elongated and their umbones are less massive.

Boucard's arca, *Arca boucardi* Jousseaume, lives in Peter the Great Bay; larvae described below.

Lithophagidae

The shell is equivalve, longitudinally oval, and its ventral margin parallel to the hinge line. The length of the shell is much more than its height. The umbones are large, broad, and round. The hinge system is similar to that in the family Mytilidae, but teeth in the central part of the provinculum are lacking. The ligament is posterior. The shell is strong, with distinctively raised growth striae. Large dark ocular spots are present.

Adula falcatoides Habe inhabits Peter the Great Bay (see below).

Ostreidae

The veliconcha is large. The shell is inequivalve. The left valve is much larger than the right, more convex, and has a high umbo. The right valve is flat and has a low umbo. The anterior margin is more drawn out compared to the posterior.The hinge comprises two anterior and one to three posterior rectangular teeth. The space between the anterior and posterior teeth is smooth. The lateral hinge system is absent. The ligament is posterior. Eyes are present and visible at a shell length of 250–290 μm. In the mature veliconcha, dark pigmentation is perceptible in the subumbonal region.

Crassostrea gigas (Thunberg) inhabits Peter the Great Bay (see below).

Pectinidae

The shell is inequivalve. The left valve is slightly more convex than the right. The shell is triangular and its apex coincides with the anterior end, which is more acute and longer than the posterior, and produced frontally and dorsally. The ventral margin slopes sharply toward the anterior end. The dorsal margins are unequal, with the anterior margin usually longer than the posterior. The umbones are small, round, and slightly raised. The valves are brittle, thin, and colorless. The sculpture of the prodissoconch is fine and poorly visible. In the developing dissoconch in the pediveliger stage, the sculpture is alate, with radial ridges (veins). The taxodont hinge (provinculum) is very similar to that in Mytilidae and comprises several rectangular teeth on each margin of the tooth row. The number of teeth may increase as the larva grows. The central part of the provinculum is so thin that no teeth whatsoever are present (in most species) or the teeth are almost indistinguishable. The lateral hinge system is lacking. The ligament is median or posterior. Ocular spots appear in the veliconcha before metamorphosis.

Chlamys farreri nipponensis Kuroda (see below), *Swiftopecten swifti* (Bernardi) (see below), and *Mizuhopecten yessoensis* Jay (see below) inhabit Peter the Great Bay.

Hiatellidae

The veliconcha shell is equivalve and rounded-triangular. The anterior end is pointed and directed forward sharply. The umbones are round and distinct. The posterior margin is obtuse and straight while the ventral margin is roundish. There is a large tooth on the right valve, located in the anterior part. The left valve likewise has just one provincular tooth. One flange is located on the right valve and the other on the left valve. The ligament is large and posterior. Eyes are absent.

Hiatella arctica (Linné) inhabits Peter the Great Bay (see below).

Kelliidae

The shell is equivalve, large, flat, and roundish or slightly squared. The anterior end is more obtuse than the posterior. The umbones are small. The provincular teeth are absent. A rudimentary lateral tooth appears by the end of planktonic phase. The ligament is median or anterior. The posterior muscle — adductor — and growth striae become visible very late. The larva is lightly colored. The liver and velum are light, yellowish-green.

Kellia japonica Pilsbry is found in Peter the Great Bay and its larva is described below.

Cardiidae

The veliconcha shell is longitudinally oval and equivalve. The anterior end is narrow and slightly elongate; the posterior end obtuse and broad. The ventral margin is round. The anterior shoulder is equal to, or slightly longer than the posterior. The umbones may be high and round or low and broad. The shell is slightly inflated. The hinge comprises a row of small sharp teeth on the right valve and corresponding sockets on the left valve. Flanges are situated on the left valve and crests on the right. Both anterior and posterior lateral teeth are present. The ligament is posterior. Eyes are absent. The pallial line is distinct.

Keenocardium californiense (Deshayes) is found in Peter the Great Bay and the larva is described below.

Tellinidae

The shell is equivalve. The veliconcha shell is transversely oval. The shell is inequilateral. Although both ends are roundish, the anterior end is ventrally produced and often longer than the posterior. The shoulders are long and slope steeply. The umbo is initially round but later becomes knob-shaped. The provinculum consists of a row of small rectangular teeth. As the larva grows, special teeth develop in the anterior part of the provinculum. The lateral hinge system is present and consists of alternate crests and flanges — anterior crest and posterior flange on the right valve and anterior flange and posterior crest on the left valve. The ligament is median. Eyes are absent.

Macoma balthica (Linné) (see below), *Peronidia venulosa* (Schrenck) (larva not described). *Macoma incongrua* (Martens) (larva not described) and *Macoma orientalis* Scarlato (larva not described) inhabit Peter the Great Bay.

Veneridae

The shell is equivalve. The veliconcha shell is irregularly rounded and almost equilateral. The anterior margin is slightly more pointed and longer while the posterior margin is broader and shorter. The shoulders are long, straight, and sloped. The umbones are high, broad and roundish. The hinge system is of two types. In members of the genus *Venerupis*, starting from the end of the first week of life, several small indentations (teeth) develop on the prodissoconch; these do not develop in larvae of the genus *Venus*. In some species of the genus *Venus*, weak lateral processes appear, while in others it is difficult to see any hinge structures. The lateral hinge system consists of flanges and crests — flanges on the left valve and crests on the right. In some cases the hinge shows the presence of special teeth. The ligament is posterior. Eyes are absent.

These species are found in Peter the Great Bay: *Callista brevisiphonata*

(Carpenter), *Saxidomus purpuratus* (Sowerby), *Dosinia japonica* (Reeve), *Mercenaria stimpsoni* (Gould), *Protothaca jedoensis* (Lischke), *Protothaca euglypta* (Sowerby), and *Callithaca adamsi* (Reeve); their larvae have not been described.

The larva of *Ruditapes philippinarum* (Adams and Reeve) has been described (see below).

Cultellidae

The morphology of the larvae of this family is identical to that of the family Solenidae. The principal difference is that in the veliconcha of the family Cultellidae, the shoulders are straight, sloped, or slightly concave.

Siliqua alta (Broderip and Sowerby) (see below) inhabits Peter the Great Bay.

Solenidae

The shell of the veliconcha is equivalve, oval, and anteroposteriorly elongate. The anterior end of the shell is equal in length or slightly longer than the posterior. The umbo is broadly roundish. The hinge system consists of two large teeth (one on each end of the hinge line) on the right valve and corresponding sockets on the left valve. Between the sockets of the left valve, a thin row of very small sharp or blunt teeth occurs which, during closure of the shell, enter the alveoli on the right valve. The ligament is external. A pallial line is present on the inner surface of the valves. Eyes are absent.

Solan krusensterni Schrenck (see below) inhabits Peter the Great Bay.

Mactridae

In the veliconcha stage the larva is ovate or rounded-oval. The shell is equivalve. The anterior end is longer and more pointed than the posterior. As the posterior end is ventrally more produced than the anterior, it is considerably broader than the anterior. The shoulders are slightly rounded and slope slightly; the anterior shoulder is longer than the posterior. The umbo is broad and roundish, sometimes becoming triangular later. The hinge system has one rectangular tooth on the right valve and two teeth of different size on the left valve. In the anterior part of the hinge line a large lobate tooth occurs. There are also lateral teeth in the form of tubercles on both sides of the hinge on each valve. In some species of Mactridae, the hinge is similar on both sides, comprising a row of small rectangular denticles and one posteriormost distinct tooth. The lateral system comprises flanges and crests. The ligament is posterior. Eyes are absent.

Mactra chinensis Philippi (see below), *Spirula sachaliensis* (Schrenck) (see below), and *Spisula voyi* (Gabb) (larva not described) inhibit Peter the Great Bay.

Myidae

The veliconcha shell is equivalve. The posterior end is broader than the anterior. The dorsal margin is straight and slopes markedly, while the ventral margin is round. The umbones are flat and low. There is one provincular tooth on each valve. One flange occurs on the right valve (posterior) and another on the left (anterior). The ligament is posterior. Eyes are absent. Soft body with dark pigmentation.

Mya japonica Jay (see below) and *Mya truncata* (Linné) (see below) inhabit Peter the Great Bay.

Pholadidae

The veliconcha is large. The shell is equivalve, convex, and inequilateral. The anterior end is slightly longer than the posterior. The margins are smooth and broadly roundish. The dorsal margins are short, round, and slope abruptly. In the early veliconcha the umbones appear roundish but later become knob-shaped and considerably raised. The hinge has two teeth of the same size on the left valve and two on the right, one of which is longer and central in position while the second, smaller tooth is situated in the anterior part of the hinge line. The small teeth on the left valve are separated by a wide socket for the central tooth of the right valve. Flanges occur on the left valve and crests on the right. The ligament is posterior. The margins of the valves are edged with a dark band. A pallial line is present. Eyes are absent. The umbo is purplish-red. The anterior adductor is slightly larger than the posterior.

Barnea japonica (Yokoyama) (see below) and *Zirfaea crispata* (Linné) (see below) inhabit Peter the Great Bay.

Teredinidae

The shell of the veliconcha is round and highly convex. As it grows, the shell becomes somewhat oval and dorsoventrally produced. The anterior and posterior ends are broadly rounded and symmetric. The height of the shell is slightly greater than its length. The dorsal margins are short, round, and slope sharply. The umbo is round, becoming knob-shaped in late veliconcha. The hinge has large rectangular teeth — three on the right valve and two on the left. Flanges occur on the left valve and crests on the right. The ligament is posterior. The surface of the shell has concentric striation. The larva is dark colored (from

yellow to brown), especially in the umbonal region. Eyes are absent. A marginal band passes along the edge of the shell. The posterior adductor is larger than the anterior. The latter undergoes considerable reduction during larval development while the posterior adductor grows continuously.

Teredo navalis Linné (see below), *Bankia setacea* (Tryon) (see below), and *Zachsia zenkewitchi* Bulatoff and Rjabtschikoff (larva described by Terner and Yakovlev, 1981) inhabit Peter the Great Bay.

PACIFIC MUSSEL, *MYTILUS TROSSULUS* GOULD

(Mytilidae)*

Veliconcha

The shell is triangular-oval, its anterior end tapering and raised. The anterior shoulder is longer than the posterior, but just slightly. The umbone is conoid but not broad (see Fig. 44). Umbones appear at a small shell length of 125–135 μm. The larva is weakly colored. Striation is concentric and barely noticeable. Eyes appear in larvae with a shell length of 230–240 μm. The diameter of the eyes is 5–7 μm. The hinge line is weakly bent and its length more than the umbonal width, constituting 75–85 μm in the early veliconcha and 140–150 μm in the late veliconcha. The early veliconcha is 130–140 μm in size, with three-four large teeth in the anterior part, two-three teeth in the posterior part, and 11–13 denticles in the middle. The number of teeth increases as the larva grows, reaching 8–10 on each side of the hinge line in the late veliconcha. There are 15–20 denticles in the center (Figure 52). The ligament is large, oval, and posterior. Metamorphosis occurs at a shell length of 250–350 μm.

Ecology

Spawning of the Pacific mussel extends from May to September in Peter the Great Bay, Sea of Japan. Larvae appear in the plankton from June to mid-September at a water temperature of 13–23°C. The maximum number of larvae is found from the second half of June to mid-July (Kasyanov *et al.*, 1976, 1980; Shepel', 1979). In Avachin Inlet (southern Kamchatka) late larvae are found from mid-August to September at a water temperature of 8–15°C (Buyanovskii, 1987). In the waters of southern Sakhalin larvae of the Pacific mussel are found in the plankton (from early August to mid-October; with maximum occurring mid-August) at a water temperature of 8 20°C, settling en

* Using the method of protein electrophoresis, it was demonstrated that this species lives in the Far-Eastern seas of Russia, and not the closely related species, *Mytilis edulis* Linné (MacDonald *et al.*, 1990).

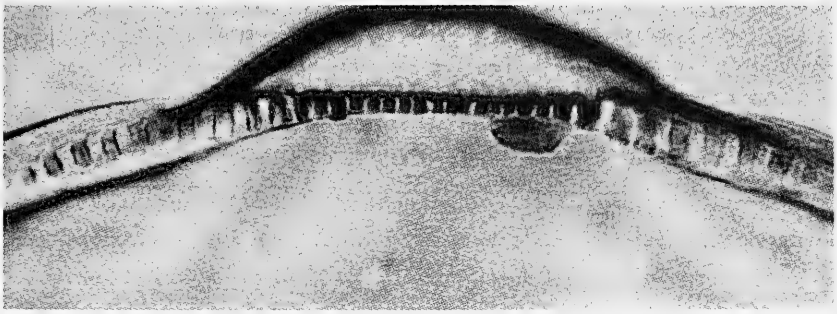


Figure 52: Hinge of right valve of the veliconcha of *Mytilus trossulus*.

masse at the end of August (Kulikova, 1975). Thus, during the reproduction of *M. trossulus* in the study area, the water temperature varies from 8 to 23°C.

CRENOMYTILUS GRAYANUS (DÜNKER)

(Mytilidae)

Veliconcha

The shell is equivalve and longitudinally oval. The anterior end is longer than the posterior and only slightly drawn dorsally. The umbones are broad, massive, and round (Figure 53 A, B). The larva is yellowish-brown; the umbo is more intensely colored. Striation of the shell is concentric, barely perceptible. The length of the provinculum is greater than the length of the umbones. The number of provincular teeth increases as the larva grows. In a developed larvae the provinculum has up to 20–25 central denticles and 10 large lateral teeth. The ligament is oval and located at the end of the row of denticles. The larva attains the veliconcha stage at a shell length of 120–130 μm and a hinge line length of 90 μm. As the larva grows, the length of the provinculum increases to 150 μm. Eyes appear in the larva at a shell length of 220 μm. The diameter of the eyes is 15 μm. The foot is fully formed and becomes functional in the larva at a shell length of 250 μm.

Larvae of *C. grayanus* differ from those of the Pacific mussel *Mytilus trossulus* and *Modiolus difficilis* primarily in shape of the shell. Compared to *M. trossulus*, the shell is shallower dorsoventrally and the provinculum bears a larger number of denticles. *C. grayanus* differs from the larvae of *Modiolus difficilis* mainly in having a wider and rounder anterior margin, a more fragile shell, less distinct concentric striation, and a lighter color.

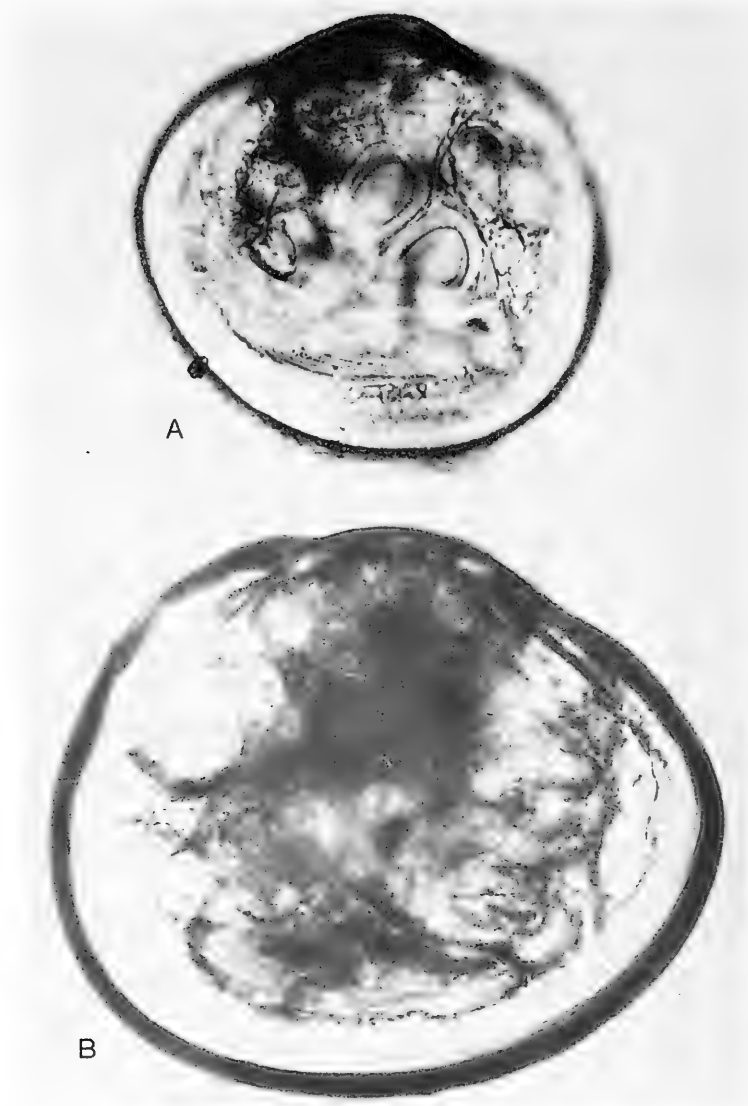


Figure 53: General view (A) and hinge of right valve (B) of the veliconcha of *Crenomytilus grayanus*; general view (C) of the veliconcha of *Modiolus difficilis*.

Ecology

C. grayanus breeds throughout the summer along the southern coast of Sakhalin, with larvae occurring in the plankton from July to early October. Breeding peaks earlier or later, depending on temperature conditions. More

often, it occurs from July to early August, when the water temperature is 16 –17°C. In Peter the Great Bay this species spawns twice, end of May to June and mid-August to September inclusively (Dzyuba, 1972; Kasyanov *et al.*, 1980). Larvae are found in the plankton of Vostok Bay (Peter the Great Bay) throughout summer; there are two population peaks in July and in September, and larvae develop in a temperature range of 13–22°C. Duration of the pelagic stage of development of *C. grayanus* along the southern coast of Sakhalin (Sea of Okhotsk) and in Peter the Great Bay is 5–6 weeks.

Drozdov and Kulikova (1979) have described the embryonal and postembryonal development of *C. grayanus*.

LONG-BRISTLED MODIOLUS, *MODIOLUS DIFFICILIS* (KURODA AND HABE)

(Mytilidae)

Veliconcha

The shell is oblong-ovate (see Figure 53,C). The anterior end is not raised and is slightly longer than the posterior end. The umbones are large and broad. The shell is compact. The prodissoconch II has noticeable concentric striation. The valves are massive. The larva is dense yellowish-brown. The hinge consists of eight–nine lateral teeth and 15–18 small central teeth. The length of the hinge is greater than the width of the umbones. The ligament is rectangular. Large, dark-colored eye spots appear at a shell length of 270 μm or more. The larva settles at a shell length of 280–300 μm.

Ecology

Modiolus larvae are found in August-September in the plankton of Vostok Bay (Peter the Great Bay).

Larvae of this species are not described in the literature.

MUSCULISTA SENHOUSIA (BENSON)

(Mytilidae)

Veliger and Veliconcha

M. senhousia forms a clutch in the shape of twisted cords which are composed of large adhesive eggs. Larvae hatch with a straight hinge margin. Their later development is pelagic (Matveeva, 1975). Morton (1974) stated that in the South China Sea, this species releases gametes in the water. The first and most minute larvae observed by us in the plankton had a shell length of

100 μm and height of 90 μm. The veliger valves have a straight hinge margin, bearing several minute, equal-sized teeth (Figure 54). The larva attains the veliconcha stage at a shell length of 120–130 μm. The shell is equivalve, ovate, and highly convex. The anterior margin is pointed and only slightly raised. The umbones are high and well developed. The ratio of length to height and thickness of the valves is 1.6:1.3:1.0. The larva is dark brown and due to the great convexity of the valves is less transparent. Striation on the shell is concentric and distinct. The eyes are small and almost imperceptible against the dark background of the shell (Figure 54). The hinge line is arcuate due to the development of large teeth, five–six, at each margin of the provinculum. There are 10–12 central rectangular denticles in the hinge row. The length of the hinge line does not exceed the width of the umbones, but is equal to it, reaching 100–110 μm in developed larvae. The ligament is posterior but, unlike the ligament in other members of the family Mytilidae, shifted much closer to the middle of the hinge line. The shell in the veliconcha stage ranges from 120–280 μm in length.

Ecology

The pelagic stage in *M. senhousia* continues for two–three weeks. Along the southern coast of Sakhalin (Aniva Bay, Sea of Okhotsk) and in Vostok Bay, larvae are found in the plankton for a fairly long time — from the end of July to September inclusive, with a maximum water temperature of 18–23°C.

Some data on the developmental biology of *Musculista* are available in works of Morton (1974) and Matveeva (1975). Kulikova (1978, 1979) has described the morphology of the pelagic larvae and their population dynamics in the plankton of Busse Lagoon (southern Sakhalin).

CRESCENT-SHAPED ADULA, *ADULA FALCATOIDES* HABE

(Lithophagidae)

Veliconcha

The shell of the veliconcha is longitudinally oval and its length considerably greater than its height. The ventral margin is almost parallel to the posterior, the anterior margin only slightly produced dorsally, and the posterior margin slightly produced ventrally. The shell is massive and strong. Concentric striation is distinct, uniformly arranged, and even visible in live larvae. The umbones are distinct — broad, round, and moderately high. The hinge system is similar to that in the family Mytilidae but the smaller teeth in the central part of the provinculum are either not visible or very weakly developed. The

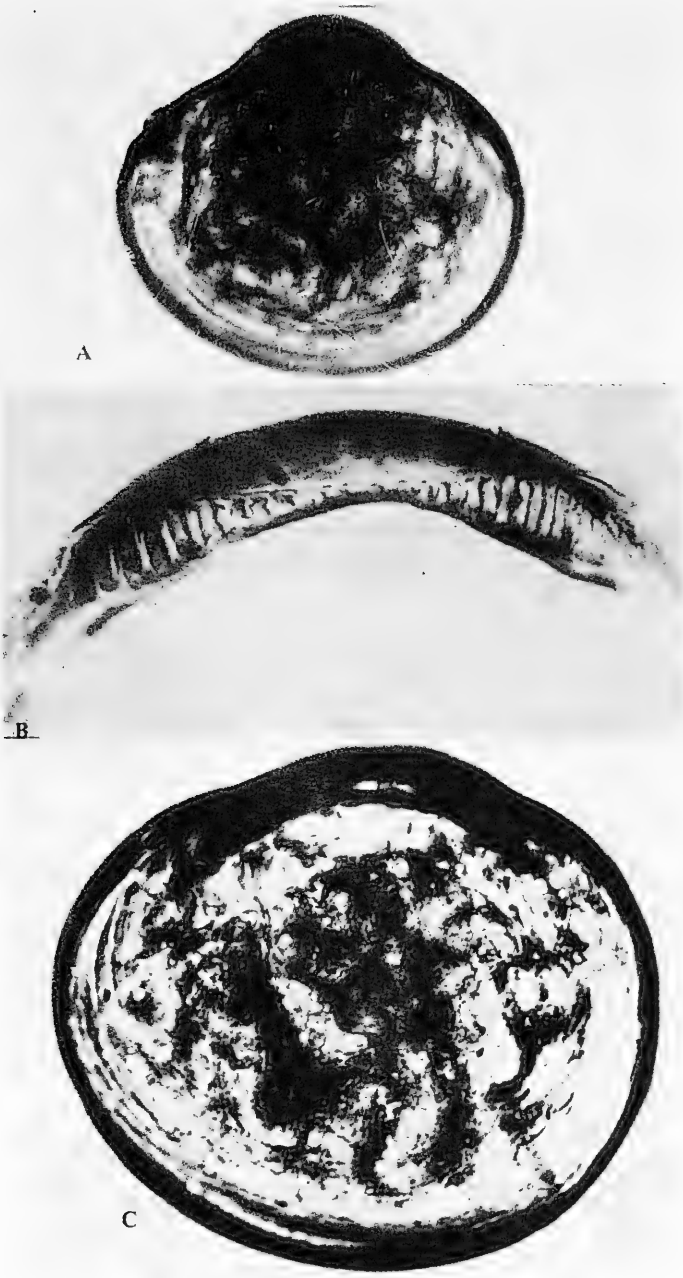


Figure 54: General view (A) and hinge of right valve (B) of the veliconcha of *Musculista senhousia*; general view (C) of the veliconcha of *Arca boucardi*.

hinge line of these *Adula* bears 12–13 large lateral teeth (see Figure 43). The larva is opaque, brownish. The large dark red eyes are very distinct. The shell of the veliconcha is 320–350 μm long. The larva of *A. falcatoides* is very similar in structure to the larva of *A. simpsoni* described by Rees (1950) from the North Sea.

Ecology

Larvae of *A. falcatoides* are observed in the second half of summer in Vostok Bay, mainly in August, at a water temperature of 18–20°C.

No data on the morphology and ecology of this species were found in the literature.

BOUCARD'S ARCA, *ARCA BOUCARDI* JOUSSEAUME

(Arcidae)

Veliconcha

The shell is equivalve and round, with its anterior margin narrower than the posterior (see Figure 54, C). The umbones form at a shell length of more than 150 μm; they are broad, not exceeding the hinge line in length, but equal to it. In a developed veliconcha, there are six large lateral teeth along each margin of the hinge line and ten central teeth, which are half the height of the lateral; thus there are eight teeth on each side. The provinculum is devoid of teeth. Large bright eye spots appear in larvae 210 μm long. Larvae settle with an average shell length of 224 μm.

Ecology

Arca larvae are found in the plankton of Vostok Bay (Peter the Great Bay) in July-August.

The morphology of Boucard's arca has been reported by Kulikova and colleagues (1987).

GIANT OYSTER, *CRASSOSTREA GIGAS* THÜNBERG

(Ostreidae)

Veliconcha

The shell is inequivalve. The left valve differs from the right in shape and size, being larger, more convex, and having a very well-developed umbo that is much higher than on the right valve. The right valve is smaller than the left, flattened, and with a low, round umbo. The height of the shell is somewhat greater than its length. The anterior margin is longer than the posterior. The

hinge comprises three anterior and two posterior rectangular teeth (see Figure 37). The height of each anterior tooth is twice that of the posterior teeth. The space between the anterior and posterior teeth is smooth. The ligament is posterior. Eyes are present; they develop and become distinct at a shell length of 250–270 μm. Concentric and radial striations are equally well-developed on both valves. In the umbonal region, the larva has a large black spot that corresponds to the digestive gland. The larva attains the veliconcha stage at a shell length of 100–120 μm and a hinge line length of 50 μm. As the veliconcha grows, the length of the hinge line increases to 65 μm.

The larva of *C. gigas*, like the larvae of *C. virginica* and of *C. angulata*, but unlike those of *C. glomerata* and *C. cucullata*, has an asymmetrical shell. The umbo is shifted back, the anterior margin more drawn out ventrally and larger, the three anterior teeth are two to three times longer than the posterior, and the entire provinculum is short.

Ecology

Along the southern Sakhalin coast (Aniva Bay, Sea of Okhotsk), spawning and development of oyster larvae in the plankton occurs in the warmest period of the year, i.e., July–September, at a water temperature of 16–22°C. In Vostok Bay, gamete release is observed from the second half of June to the first half of August (Kasyanov *et al.*, 1976, 1980). In Posjet Bay, larvae are found from June to September (Rakov, 1975), becoming maximum in July–August. In Vostok Bay, larvae are mainly found in the plankton in August. The duration of the pelagic phase of *C. gigas* in Peter the Great Bay is, on average, 26–28 days. A similar duration of this stage in the giant oyster has been reported by Thorson (1946) and His and Kriaris (1972) in the North Sea and in experimental culture.

Many works (Hori, 1926; Funita, 1933; Cahn, 1950; Loosanoff and Davis, 1963; Loosanoff *et al.*, 1966; Rakov, 1974) have described the structure of the larval shell of *C. gigas*, size characteristics, and methods of obtaining and culturing larvae. Le Pennec (1980) examined the ontogenetic development of the hinge of oysters. Data on the ecology of larval development are available in the works of Korringa (1957), Thorson (1946), His and Kriaris (1972), and Kulikova (1975, 1979).

CHLAMYS FARRERI NIPONENSIS KURODA

(Pectinidae)

Veliconcha

The maximum size of the larval shell is 220–230 μm with a provinculum 100–110 μm long. The shape of the shell of the Japanese scallop is typical of

the family, triangular-ovate. The valves are convex. The anterodorsal margin slopes downward and hence the anterior end of the larva is raised and somewhat pointed. The umbones are small and round. The shell is inequivalve, with the right valve slightly more massive than the left and its umbo somewhat

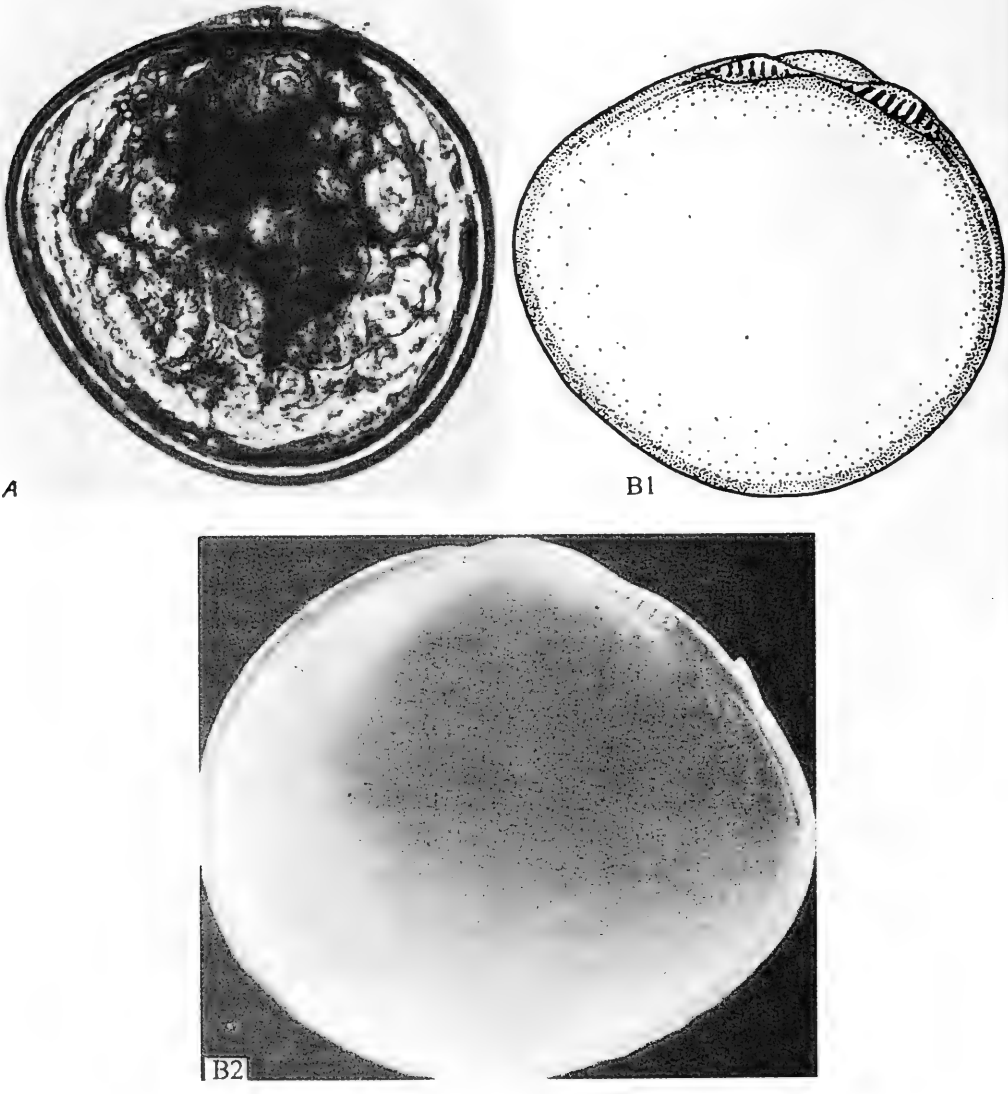


Figure 55: Veliconcha of *Chalmys farreri nipponensis*.
A — external view; B — right (1) and left (2) valves; C — hinge of right (1) and left (2) valves.

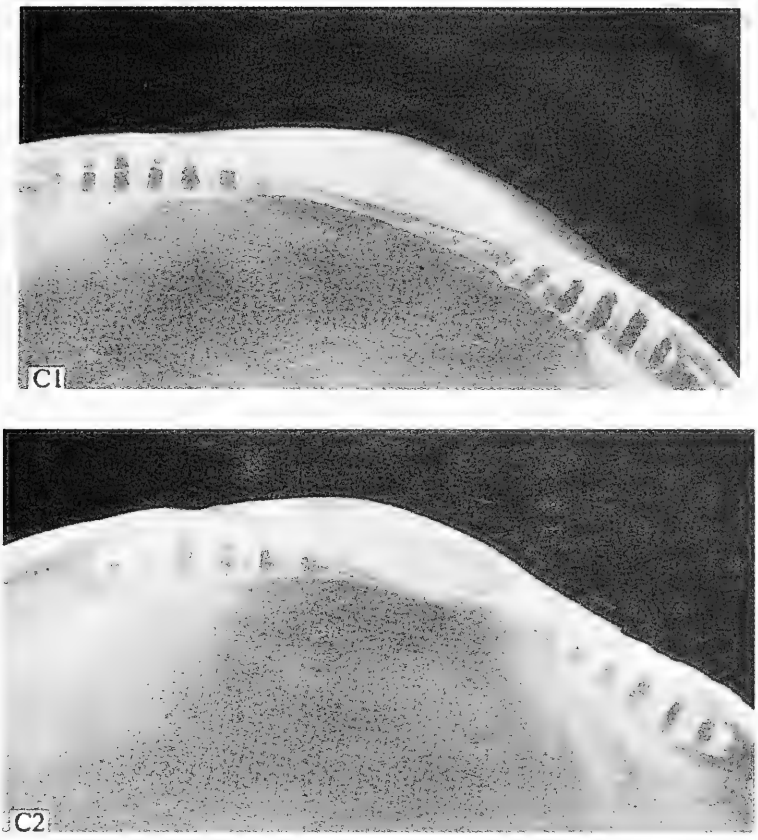


Figure 55 (contd.)

larger. Both valves are compact. Sculpture on the shell is indistinct. The provincular margin of *C. f. niponensis* bears five rectangular denticles. The central part of the provinculum lacks teeth; the length here is almost equal to the marginal areas bearing teeth (Figure 55). The margin of the shell is edged with a moderately wide, distinct band.

Ecology

In Peter the Great Bay, larvae of this scallop are found from the end of June to early August at a water temperature of 15–20°C. Larvae settled in mid-July.

Kulikov, Medvedeva and Guida (1981) describe the structure of the shell and of live larvae of this scallop. They present the characters that differentiate the larvae of this species from those of *Mizuhopecten yessoensis* and *Swiftopecten swifti*.

SWIFTOPECTEN SWIFTI (BERNARD)

(Pectinidae)

Veliconcha

The maximum length of the larval shell is 240–250 μm and the length of the hinge line 120–130 μm. The shell is triangular and the valves are convex. The anterodorsal margin slopes sharply downward. The umbones are high and acute. The larval shell is stout and richly colored. Radial striation is indistinct, while concentric striation is distinct. A broad marginal band is visible along the entire edge of the shell. The hinge line in a developed larva has up to seven large marginal teeth. The ligament is median and slightly shifted toward the anterior margin (Figure 56).

Ecology

Larvae of this scallop are found en masse in the plankton of Busse Lagoon (southern Sakhalin) and Peter the Great Bay during August–September at a surface water temperature of 15–20°C. Typically, these larvae are dominant near-bottom at depths of 10–20 m.

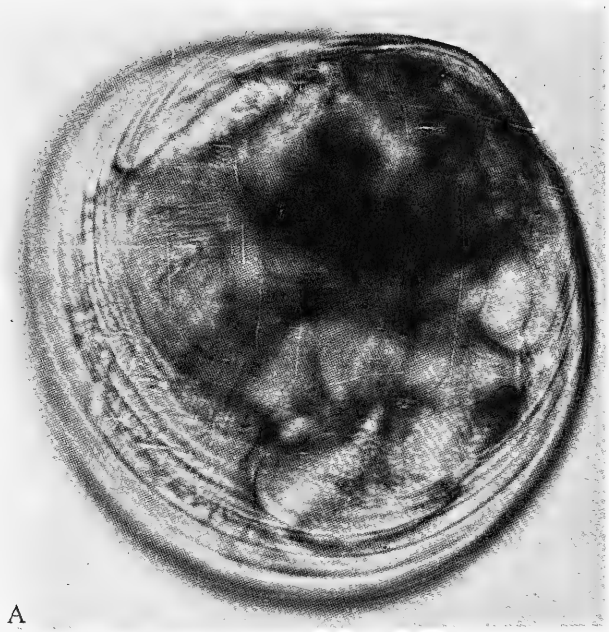
The morphology of larvae of *Swiftopecten swifti* has been described by Kulikov, Medvedeva and Guida (1981). No data on the ecological development of this species were found in the literature.

MIZUHOPECTEN YESSOENSIS (JAY)

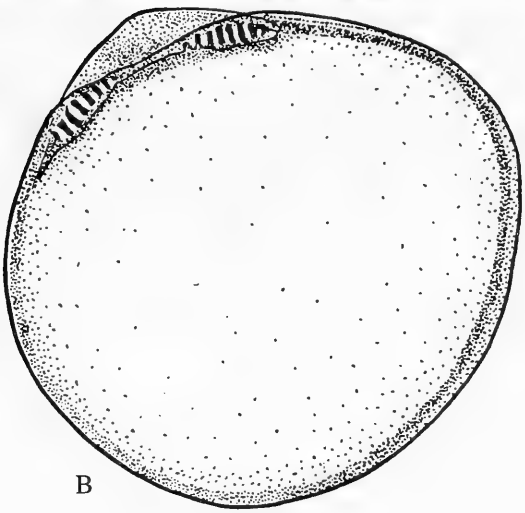
(Pectinidae)

Veliconcha

The larval shell is 260–270 μm long and the provinculum 100–110 μm long. The veliconcha shell of the Primorsk scallop is triangular-ovate. The anterior margin is short, round, and sharply drawn dorsally. The anterodorsal margin is longer than the posterior and almost straight due to the highly raised anterior end. The posterodorsal margin slopes sharply downward and gradually merges with the posterior margin of the shell. The umbo is small, round, and slightly raised over the hinge line. The larva is almost colorless and transparent. The shell is brittle, with distinct concentric and radial striations. The hinge is of the taxodont type, bearing rectangular teeth along the margins of the provinculum. A well-developed larva has five teeth on each side of the hinge row (see Figures 38 and 57).

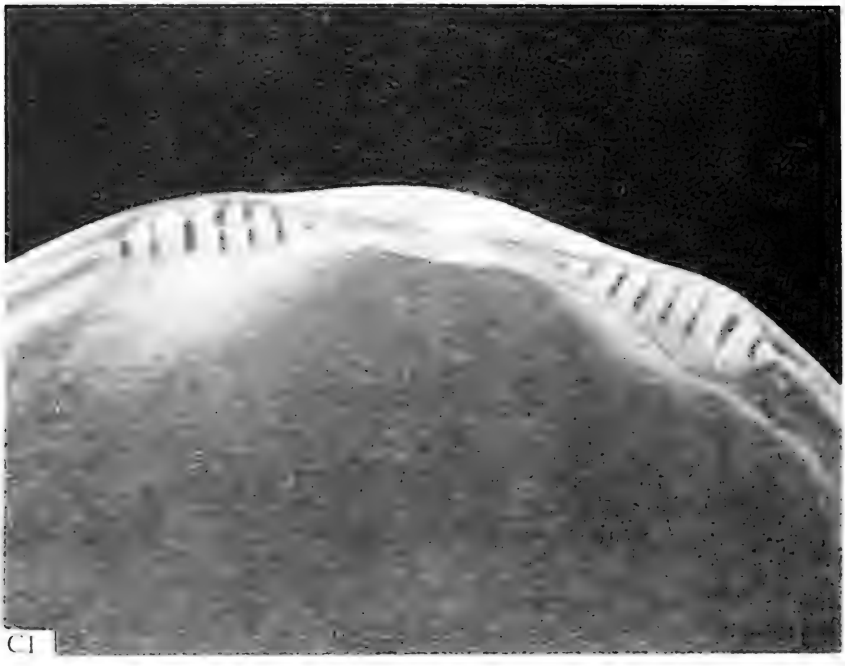


A



B

Figure 56: Veliconcha of *Swiftopecten swifti*.
A — external view; B — left valve; C — hinge of right (1) and left (2) valves.



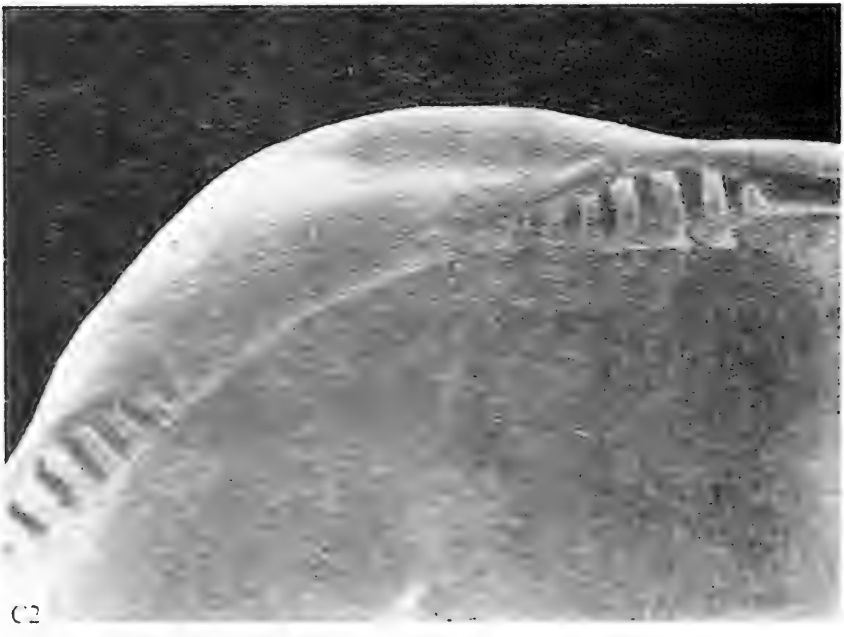


Figure 56 (contd.)

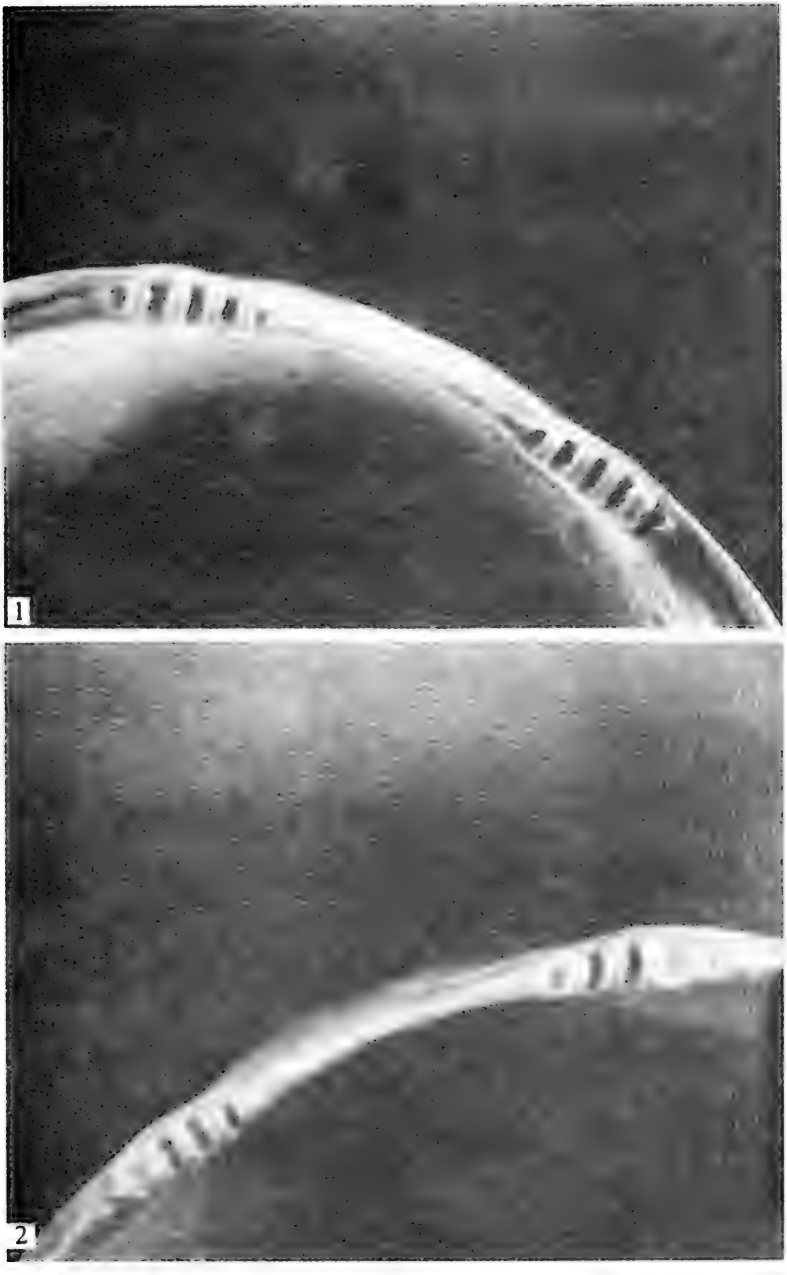


Figure 57: Hinge of right (1) and left (2) valves of the veliconcha of *Mizuhopecten yessoensis*

Ecology

In Busse Lagoon (southern Sakhalin), spawning of *M. yessoensis* and development of larvae in the plankton are observed from early July to early August. In Peter the Great Bay, larvae are found in the plankton for two months, from June to July, at a water temperature of 8–18°C. Their number is maximal from mid-June to mid-July. Duration of the pelagic stage of development of the scallop varies from 20–40 days.

The morphology of *M. yessoensis* larvae has been described by Yamamoto (1964), Maru (1972), and Kulikova, Medvedeva and Guida (1981). Data on the ecology of larval development of this species along the coast of Japan and in Mutsu Bay are available in Yamamoto's work (1951). The ecology of the larvae of this scallop along the southern Sakhalin coast was described by Kulikova and Tabunkov (1974) and for Peter the Great Bay by Belogrudov (1973, 1974).

HIATELLA ARCTICA LINNÉ

(Hiatellidae)

Veliconcha

The shell of the veliconcha is triangular. The anterior, posterior, and ventral margins are roundish, with the anterior margin more stretched than the posterior. The shoulders are straight, long, and slope steeply toward the ventral surface. The umbones are high and round. One tooth each is present on the right and left valves. The ligament is posterior (see Figures 48 and 58). The maximum shell length of the pelagic larva is 380–400 μm.

Ecology

In Busse Lagoon (southern Sakhalin), pelagic larvae of this species are found from early September to early October at a water temperature of 15–18°C. In Vostok Bay, larvae of *H. arctica* occur in the plankton in September. In the southern Adriatic (Poggiani, 1968), *H. arctica* reproduces from January to June–July at temperatures ranging from 6.0–23.5°C. Reproduction is maximum in March — first half of May at temperatures of 11–16 °C. In the northern Adriatic (Brenco, 1971), larvae of *H. arctica* are found in the plankton year-round, but are maximum in May–June. In Plymouth (La Mancha Strait), *H. arctica* larvae have been found in the plankton from early summer to December (Lebour, 1938). In Danish waters, according to Jørgensen (1946), pelagic larvae of this species are abundant from July to September–November. Along the eastern coast of Greenland (Ockelmann, 1958), this species reproduces from May to June.

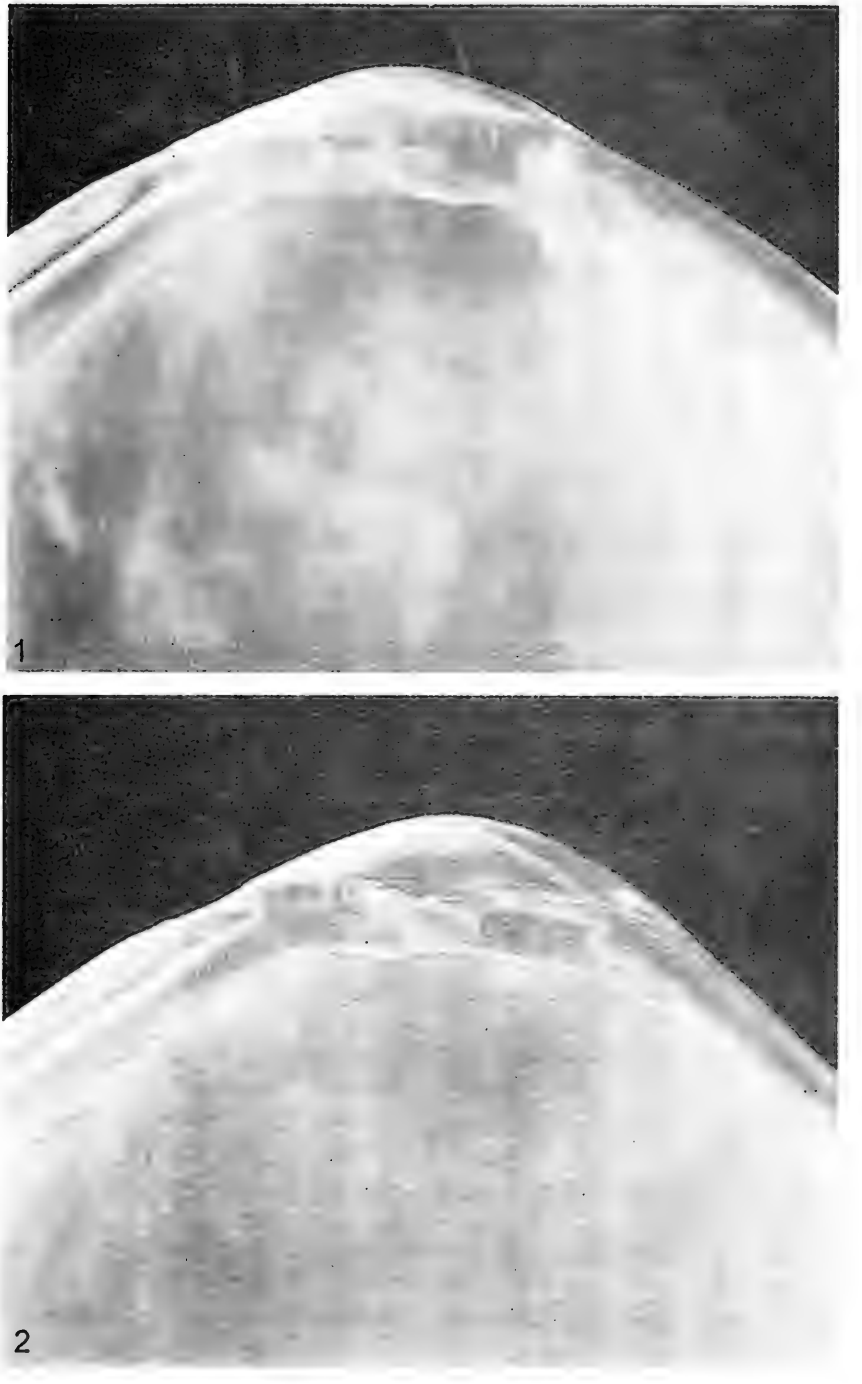


Figure 58: Hinge of right (1) and left (2) valves of the veliconcha of *Hiatella arctica*.

Data on the morphology of *H. arctica* larvae in the veliconcha stage are available in works by Odhner (1914), Lebour (1938), Jørgensen (1946), and Rees (1950). Reports on the ecology of reproduction of this species are quite numerous (see above).

KELLIA JAPONICA PILSBRY

(Kelliidae)

Veliger and Veliconcha

The larvae of *Kellia* are lecithotrophic and the pelagic period is brief. Veligers with a straight hinge at a shell length of over 150 μm, emerge from the mantle cavity of females into the plankton. The veliconcha shell is equivalve, round, and flat. The anterior margin is ventrally drawn. Umbones are lacking. The dorsal margin remains almost flat. The larval valves are brittle, transparent, and display weak concentric striation. The larva is yellowish-green. Provincular teeth are absent. The ligament is centered in the dorsal margin (see Figures 39 and 59). The shell of a swimming larva is 360–380 μm long.

Ecology

Along the southern Sakhalin coast (Aniva Bay, sea of Okhotsk) and in Vostok Bay, larvae of *Kellia* have been found in the plankton in the second half of summer at water temperatures of about 16–23°C.

No data on the morphology and ecology of larvae of this species were found in the literature.

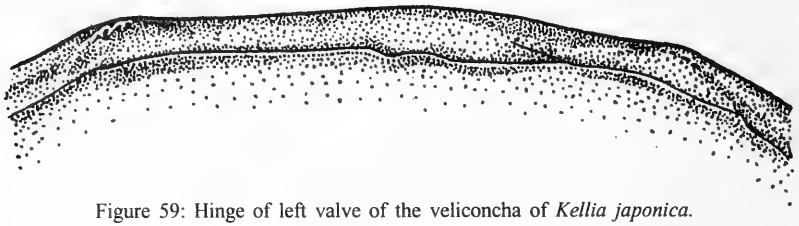


Figure 59: Hinge of left valve of the veliconcha of *Kellia japonica.*

KEENOCARDIUM CALIFORNIENSE (DESHAYES)

(Cardiidae)

Veliconcha

The description of this species corresponds to that of the entire family. The shell of the swimming larva reaches 280–300 μm in length, on average (see Figure 51).

Ecology

K. californiense larvae are found in the plankton of Peter the Great Bay in August–September.

No data on the development of this species were found in the literature.

BALTIC MACOMA, *MACOMA BALTHICA* (LINNÉ)

(Tellinidae)

Veliconcha

The length of the veliconcha shell is initially slightly more than its height. The anterior shoulder is much longer than the posterior. The larva lengthens as it grows due to the extension of its anterior end (see Figure 42). The maximum size of the larval shell is 300–315 μm.

Ecology

In Vostok Bay (Peter the Great Bay) and in Busse Lagoon (southern Sakhalin), this species reproduces from July to September at 17–24°C. In other parts of its area of distribution, reproduction of the species also occurs in the warmer part of the year — in spring and summer. Along the Danish coast, the veligers of *M. balthica* are found (Jørgensen, 1946) in the plankton from April-May to mid-August. In the Great Salma Strait, macoma larvae are found in July at 7–11°C (Mileikovskii, 1960).

The larva of *M. balthica* has been described by Werner (1939), Jørgensen (1946), and Sullivan (1948).

TALL SILIQUA, *SILIQUA ALTA* (BRODERIP AND SOWERBY)

(Cultellidae)

Veliconcha

The description of this species corresponds to that given for the family. The shell is pale yellow, almost white, its surface smooth, and the anterior part thinner than the posterior. The shell is slender, semitransparent, and not broad. The shoulders are straight and slope somewhat ventrally. The maximum length of the larval shell is 380 μm (see Figure 50).

Ecology

In Busse Lagoon (Sea of Okhotsk), *S. alta* larvae appear in the plankton mid-July. Their number is maximum in August. Mass settling of larvae occurs

from the end of August to early September. Their size at this time varies from 300 to 380 μm. The temperature at which *S. alta* larvae are found in the plankton ranges from 11–22°C. Mass settling coincides with autumn cooling of waters. In Vostok Bay, development of larvae occurs in the same period at a similar temperature.

Hayashi and Terai (1964) have described the morphology of larvae of this species.

RAZOR CLAM, *SOLEN KRUSENSTERNI* SCHRENCK

(Solenidae)

Veliconcha

The description of this species is similar to that given for the family. The shoulders of the larva are roundish and merge smoothly with the line of the anterior and posterior margins of the shell. The maximum shell length of a swimming larva is 350 μm (see Figure 49).

Ecology

Larvae of razor clams are found in Busse Lagoon and Vostok Bay (Peter the Great Bay) at the beginning of summer (May–June).

No data on the morphology and ecology of larvae of this species were found in the literature.

CHINESE MACTRA, *MACTRA CHIENENSIS* PHILIPPI

(Mactridae)

Veliconcha

The maximum length of the larval shell is 260–270 μm. The shell is oval-triangular and somewhat truncate from the posterior end. The umbones are high and somewhat shifted to the posterior end. The shoulders are round and high (see Figures 46 and 60). The hinge system comprises one rectangular tooth on the right valve and two on the left. The ligament is situated at the posterior end of the hinge line. The anterior part of the dorsal edge of the left valve has one lobate tooth. The lateral teeth along the hinge resemble tubercles on both valves.

Ecology

In Peter the Great Bay, larvae of *Mactra chinensis* appear in large numbers in July. Settled juveniles are found in shallow sandy open inlets well-warmed by the sun.

The shell of juveniles of *M. chinensis* is lustrous yellow and trihedral. The posterior part of the body has two transparent siphons and a well-developed foot that enables the mollusk to move quickly over the seabed.

Miyasaki (1933) has described the development of *Mactra chinensis*; however, data are quite fragmentary. Larvae and juveniles of this species are described by Hayashi and Terai (1964), including the hinge of the planktonic larva and its external appearance. The early development of *Mactra chinensis* has been described by Medvedeva and Malakhov (1983).

SPISULA SACHALINENSIS (SCHRENK)

(Mactridae)

Veliconcha

The larva attains this stage at a shell length of 300 μm. The shell is equivalve, ovate, and obtuse at the posterior end; the anterior part is flattened. The anterior end is larger than the posterior. The umbones are low, broad, and shifted to the posterior end. The shoulders slope gently (Figure 61). The hinge begins to form in the larva when the umbo appears. Initially, the hinge consists of two primary plates with small denticles separated by a deep pit. Later, the denticles on the primary plates disappear and the plates become massive. A lobate tooth is present in the anterior part of the hinge of the left valve. The

A

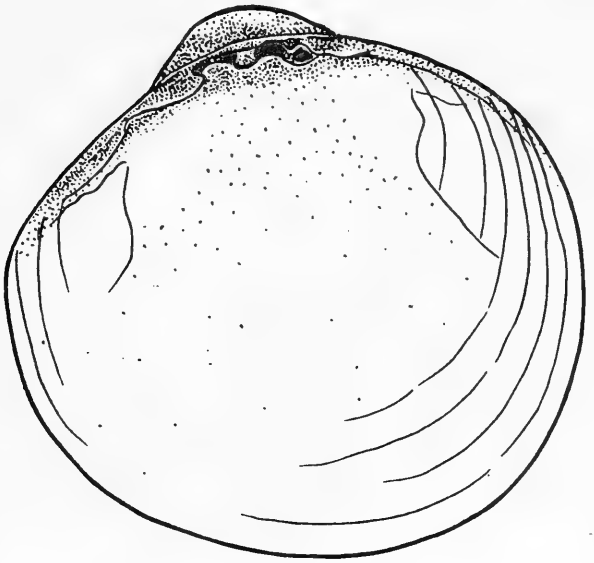


Figure 60: Veliconcha of *Mactra chinensis*.
A — right valve; B — hinges of right (1) and left (2) valves.

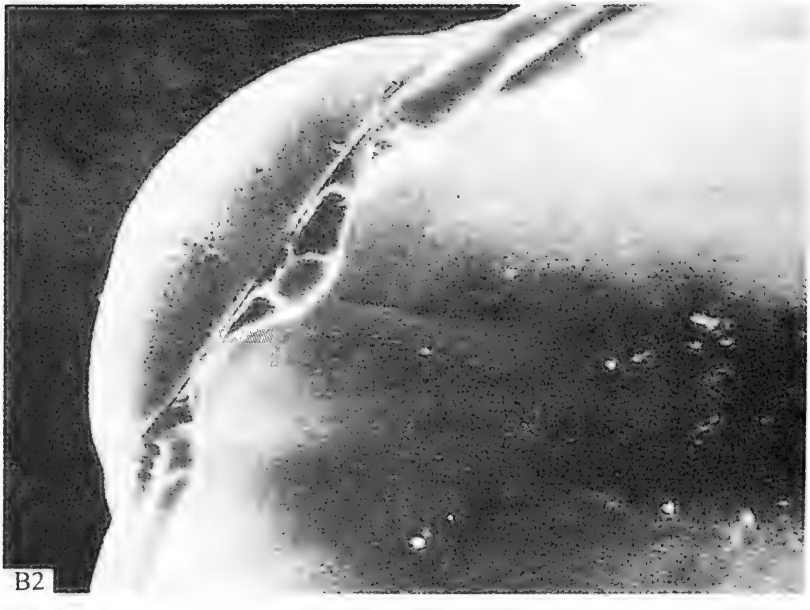


Figure 60 contd.

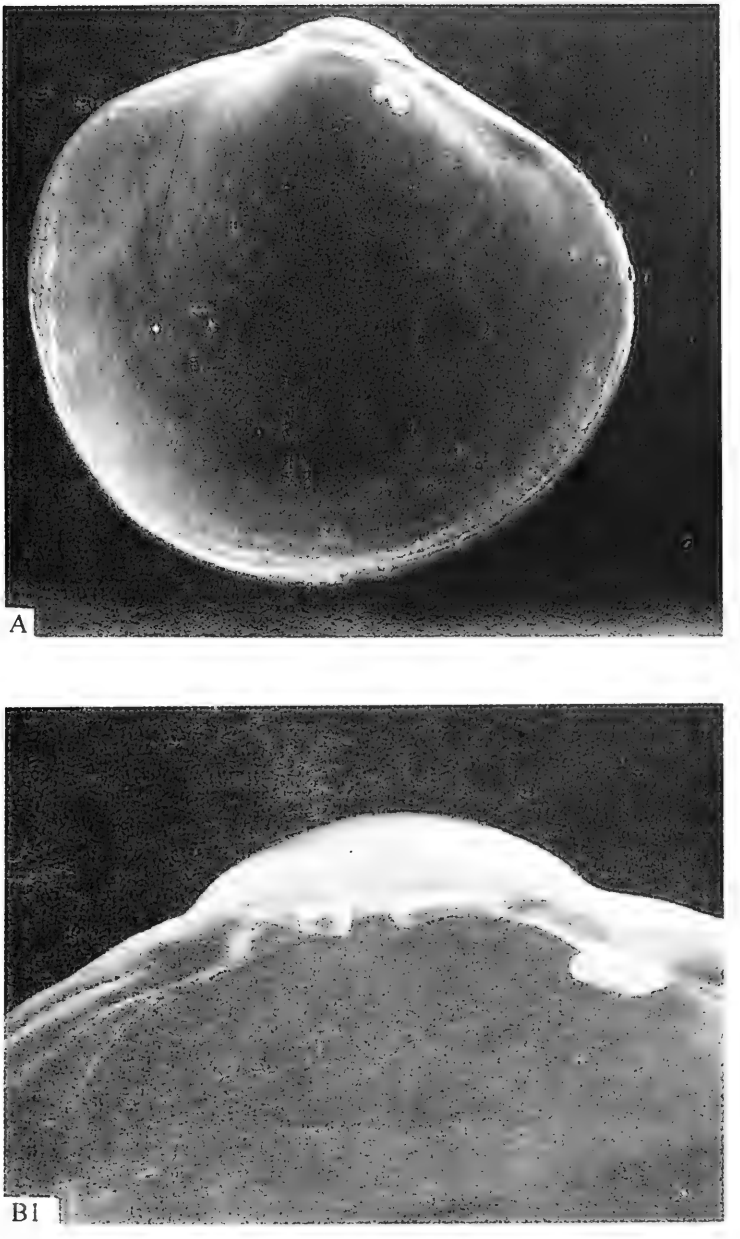


Figure 61: Veliconcha of *Spisula sachalinensis*.
A — left valve; B — left hinge (1) and right valve (2).

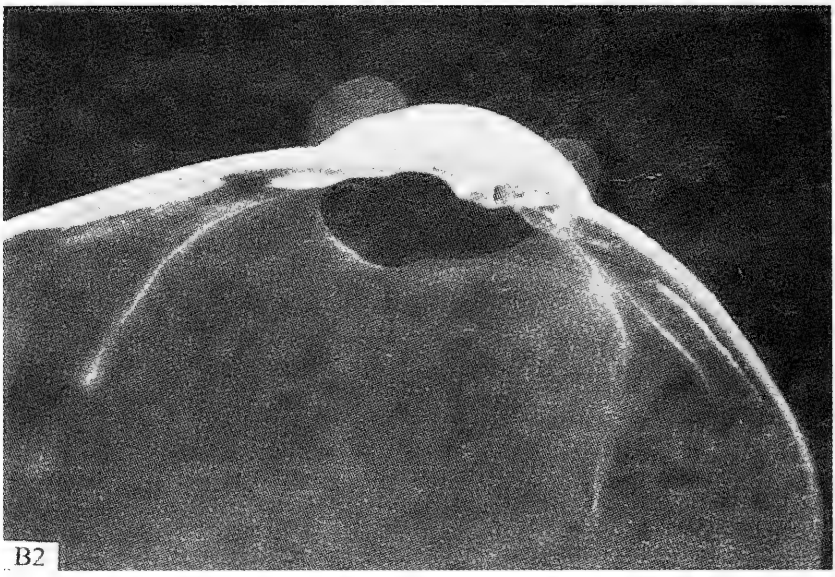


Figure 61 (contd.).

lateral teeth resemble tubercles on both sides of the hinge. The right valve has two indentations corresponding to the primary plates of the left valve. The ligament is triangular and posterior.

Ecology

In Peter the Great Bay, larvae of *Spisula sachalinensis* appear at the end of June and are most numerous in mid-July. Larvae settle in shallow water, sandy inlets, well-warmed by the sun. Freshening of water adversely affects the young of the year population (Tabunkov, 1971).

Hayashi and Terai (1964) have described external changes in the pediveliger after settling. Medvedeva (1981) gives a brief description of changes in the hinge during larval growth. Some information is also available on rearing larvae of *S. sachalinensis* in the work of Imai and coworkers (1950).

PHILIPPINE RUDITAPES, *RUDITAPES PHILIPPINARUM* (ADAMS AND REEVE)

(Veneridae)

Veliconcha

The anterior end of the shell is slightly longer than the posterior. The shoulders are straight, slope steeply, and reach almost up to the middle of the anterior and posterior margins. The umbones are broad and triangular-roundish (see Figure 47). Concentric striation is distinct. The hinge system of the larva at the veliconcha stage is represented by a row of denticles, generally numbering 12–14. The ligament is large and posterior. The length of the veliconcha shell increases with the growth from 160 to 244 μm; its height is slightly less than its length. The maximum length of the hinge line is 85 μm.

Ecology

In Vostok Bay (Peter the Great Bay), the larvae of this species are found in July–August, and in Busse Lagoon (southern Sakhalin), in August–early September, at a temperature of 15–23°C and 10–20°C respectively.

The larvae of *Ruditapes* have been described by Yoshida (1935).

MYA JAPONICA JAY

(Myidae)

Veliconcha

The shell is equivalve, with the posterior end somewhat shorter than the anterior. The posterior margin is broad and slopes from the shoulders in a straight line to the ventral margin. The anterior margin is narrow and round. The shoulders are straight, broad, and slope downward. The shell length is almost equal to its height. The umbo is initially indistinct and appears triangular, its line margin with the line of the shoulders. Later, before the larva settles, the umbo becomes roundish and distinct. The hinge system is weakly differentiated. One provincular tooth is present on each valve. The ligament is posterior. Weak concentric striation is distinguishable on the hollow valves of the shell of the veliconcha. One of the main distinguishing characters of the veliconcha of *M. japonica* is the presence of dark pigmentation on the soft parts of the body in the region of the anterior and posterior muscles (retractors) and along the velar margin (see Figure 45). Along the coasts of Primor'e, the shell of the swimming larvae of *M. japonica* is 85–270 μm long. Individual specimens reach 300–320 μm. Larger larvae have been recorded along the

Figure 62: Right valve of the veliconcha of *Mya japonica.*

coast of Japan (Yoshida, 1938). Larvae attain the veliconcha stage at a shell length of 150 μm and a hinge line of 50–70 μm.

Ecology

In Sakhalin (Aniva Bay, Sea of Okhotsk), the spawning period of *M. japonica* is protracted, beginning in early July and ending at the terminating end of August or early September. The major part of the *M. japonica* population usually spawns in Busse Lagoon (Aniva Bay) in July–beginning of August. Spawning commences at a temperature of 14–15°C and larvae are present in the plankton at a water temperature of 15–22°C. In Vostok Bay, larvae of *M. japonica* are found in the plankton during June–July at temperatures of 14–22°C.

Data on the morphology and ecology of larvae of this species are available in the works of Yoshida (1938, 1953).

TRUNCATE MYA, *MYA TRUNCATA* (LINNAEUS)

(Myidae)

Veliconcha

The larva of *Mya truncata* is identical to that of *M. japonica*, both in structure of hinge system and presence of dark pigmented bands along the shoulder as well as the mantle margin. The only noticeable difference between these two species is the larger size of the *M. truncata* larvae (90–320 μm) and significant elongation longitudinally (see Figure 45).

Ecology

Larvae of this species are found in Vostok Bay (Peter the Great Bay) in July–August at a temperature of 15–23°C.

The larva of *M. truncata* has been described by Jørgensen (1945) and Rees (1950).

SHIPWORM, *TEREDO NAVALIS* LINNÉ

(Teredinidae)

Veliconcha

Larvae enter the plankton at the stage of straight hinge. The veliconcha shell is equivalve, equilateral, oval, and dorsoventrally produced. The valves are so highly convex that the larva is almost spherical. The shoulders are short, round, and slope steeply. The umbones are narrow, high, and round. Striation is concentric and distinct. A dark band occurs along the entire margin of the shell and encloses a light-colored band. The shell is heavy and thick. The larva is dark, brown, and opaque. The soft body of a live larva has both red and green pigmentation. The height of the veliconcha shell is much greater than its length (*l*:*h* ratio 1.00:1.13). The left valve of the veliconcha has two teeth identical in shape and size. The right valve has three teeth, of which the median tooth is broader than the lateral ones (see Figures 40 and 63). The hinge line is 4–55 μm long and the larval shell 70–220 μm (Sullivan, 1948); Imai *et al.*, 1950; Loosanoff *et al.*, 1966; Chanley and Andrews, 1971). Veligers released by the female vary in length from 70–90 μm. The umbones appear at a shell length of 100 μm. Metamorphosis usually begins at a shell length of 200 μm but may begin at other shell sizes as well: 200 m x 231 m (Loosanoff *et al.*, 1966) and 220 μm × 250 μm (Sullivan, 1948).

Ecology

Duration of the pelagic stage of development of *T. nevalis* varies from region to region. At a temperature of 20°C, metamorphosis begins 28 days (Loosanoff *et al.*, 1966) or 24–35 days (Grave, 1928; Imai *et al.*, 1950) after fertilization.

Larvae occur in the plankton along the coast of southern Sakhalin (Sea of Okhotsk) and in Peter the Great Bay in the warmest months of the year — May to September — at temperatures of 15–23°C.

Because of its universal distribution, the morphology and ecology of larvae of *T. navalis* have been described in many works (see above).

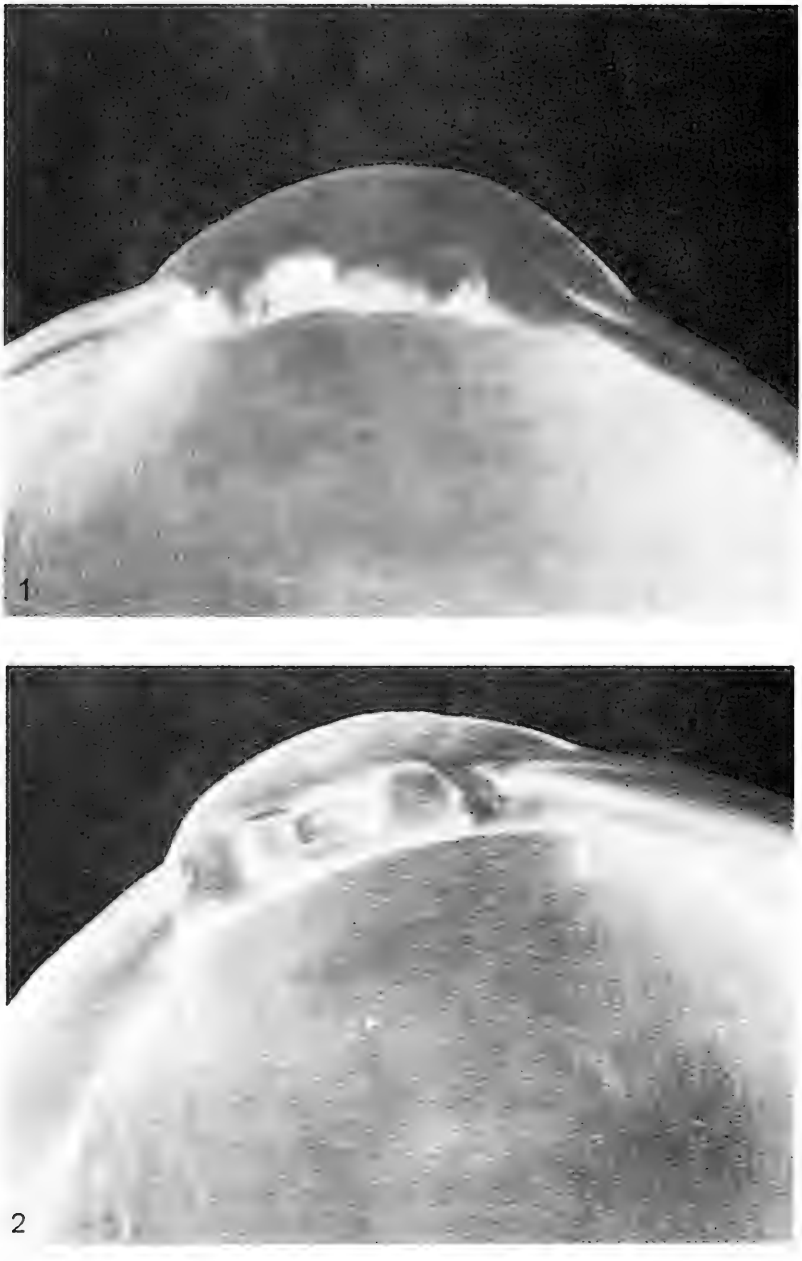


Figure 63: Hinge of right (1) and left (2) valves of the veliconcha of *Teredo navalis*.

BANKIA SETACEA (TYRON)

(Teredinidae)

Veliconcha

The veliconcha shell is equivalve and symmetric. In the initial period of this stage the larva is round; as the shell grows and the umbones become isolated, the shell expands dorsoventrally but is never as highly drawn as in *T. navalis*. Compared to the latter, the shell of *Bankia setacea* is thinner and also transparent. The larva is entirely light-colored and devoid of bright pigmentation. Dark and light bands occur along the margin of the shell. The hinge system is identical to that of *T. navalis* (Figure 64). The prodissoconch I varies in length from 100–130 μm. The larval shell before settling varies in length from 240–280 μm, with a hinge line of 100 μm (Quayle, 1953).

Ecology

In Busse Lagoon, Aniva Bay (Sea of Okhotsk), and Vostok Bay, release of gametes and development of larvae in the plankton occur in warmer months of the year (July–September) — at 14–17°C in Busse Lagoon and 15–23°C in Vostok Bay. During the autumn, as the water cools to 7–10°C, larvae settle and metamorphose. Judging from published data, *B. setacea* exhibits similar ecological characteristics in other parts of its range. Ryabchikov (1957) recorded

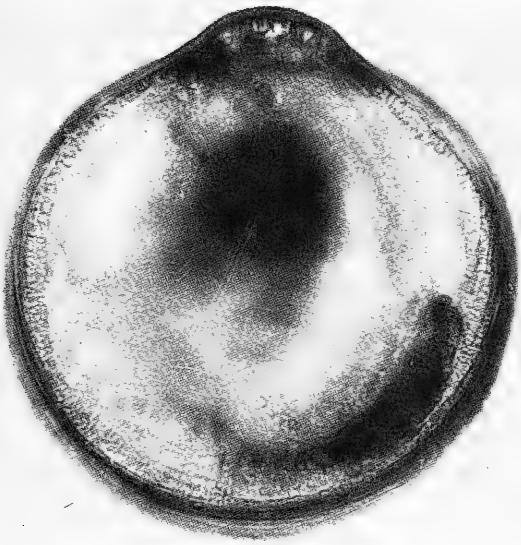


Figure 64: Veliconcha of *Bankia setacea*.

autumn settling of larvae along the eastern coast of Sakhalin at temperatures of 7–12°C. In Preobrazheniya Inlet (southern Primor'e), according to Adrianov and Vol'ter (1947), mass metamorphosis is observed twice a year: spring (March) and autumn (October–November). In southern Californian waters, Coe (1941) reported reproduction of *B. setacea* at temperatures of 10–15°C with an additional spawning period in winter and summer. In San Francisco Bay (Kofoid and Miller, 1927), the season for release of gametes begins in February at a minimum temperature of 10°C and ends, for the most part, before the beginning of summer, peaking in April–May. Northward, along the coast of Washington (USA) and Canada, the optimum temperature for settling is that in October–December, i.e., 8.0–9.5°C (Johnson and Miller, 1975). In British Columbia (western coast of Canada), this species reproduces at temperatures from 12 to 15°C, with maximum larval numbers observed at depths of more than 6.0 m, where the water is warmer (14–17°C) (Quayle, 1959). Thus, the temperature range for reproduction of this species throughout its area of distribution is 8–17°C. The pelagic stage of development of *B. setacea* in the coastal waters of British Columbia and in southern Californian waters (Quayle, 1953; Coe, 1941) continues for 20–30 days. Our observations in Busse Lagoon (southern Sakhalin) established an identical period of development.

Quayle (1953, 1955, 1959) has described the structure of larvae of *B. setacea*. The ecology of larvae of this species has been thoroughly studied (see above).

CRISPATE ZIRPHAEA, *ZIRFAEA CRISPATA* (LINNE)

(Pholadidae)

Veliconcha

Initially roundish, the shell then stretches dorsoventrally, as a result of which its height becomes slightly more than its length. The shoulders start to slope steeply and the anterior shoulder is somewhat longer than the posterior. Concentric striation is conspicuous. Before metamorphosis, a tooth on one valve and a corresponding notch on the other appear on the ventral margin of the shell, forming a firm lock (Figure 41 A, B). The hinge system is represented by two 5–10 μm broad teeth on the left valve, with a broad (20–25 μm) tooth situated between them on the right valve; a second small tooth forms at the anterior end of the right valve before metamorphosis. A fully grown larva is 300 μm long, 285 μm wide, and has a hinge line 68 μm in length.

Ecology

Larvae of *Zirfaea* are found in the plankton of Busse Lagoon (southern Sakhalin) and Peter the Great Bay in small numbers and are seen in August–October at a temperature of 10–20°C. In Sond Strait (Ersund) in Danish waters, larvae of *Z. crispata* are found in the plankton throughout the year, except in March, April, and May. The maximum number is observed at the end of summer–early autumn.

The morphology of the larvae of *Z. crispata* has been reported in many works (Werner, 1939; Jørgensen, 1945; Sullivan, 1948; Rees, 1950).

JAPANESE BARNEA, *BARNEA JAPONICA* (YOKOYAMA)

(Pholadidae)

Veliconcha

Larvae large and roundish. The shell margin is broadly oval. The shoulders are short and roundish, with the anterior shoulder slightly longer than the posterior. The umbones are narrow and high (see Figure 41 C). The hinge line is short. Concentric striation is visible on the hollow valves. A marginal band is present. The central tooth on the right valve is two to three times longer than the short front tooth. Before metamorphosis, another smaller tooth becomes distinct on the right valve behind the large tooth.

Ecology

Larvae of *Barnea* are found in the plankton of Vostok Bay (Peter the Great Bay) in the warmest months of the year, i.e., July–August, at a temperature of 15–20 °C.

The larva of this species is not described in the literature.

CHAPTER II

LARVAE OF SEA STARS (MORPHOLOGY, PHYSIOLOGY, BEHAVIOR)

EARLY DEVELOPMENT

Egg

Eggs of sea stars have a diameter ranging from 100 to 3,540 μm (see Table on p. 105). From an egg of minute diameter containing very little yolk, a definitive sea star develops after passing through larval stages of dipleurula, bipinnaria, and usually branchiolaria, with subsequent metamorphosis. Larger eggs bypass the stages of dipleurula and bipinnaria and often, in such cases, a lecithotrophic modified brachiolaria develops, followed by metamorphosis into a definitive sea star. In many species, larval stages are eliminated altogether and development is direct (*Pteraster militaris*) (Kaufman, 1968; and others). Sea star eggs with little yolk are often colorless, almost transparent. Eggs containing many nutritive substances may be yellow, pink, orange, or brown. Ovulation and shedding of eggs usually occur immediately before metaphase I maturation division. In sea water oocytes are capable of "maturation" without fertilization, i.e. proceeding from prophase I maturation division (with intact germinal vesicle) to metaphase I, and then separating polar bodies I and II. With rare execptions, the eggs of sea stars are shed directly in water.

Egg membrane : Each egg is enclosed in a thin hyaline membrane surrounding a vitalline and an exterior jellylike membrane. The jellylike membrane is 5 – 20 μm thick. In most species it is apparently present only up to the beginning of cleavage, of soft consistency, and destroyed when eggs are passed through a capron net. In some species the jellylike membrane is relatively thick and sticky, and hence a batch of eggs can adhere to the substrate.

Diameter of eggs of sea stars

Species	Diameter of eggs, μm	Source
Pentaceraster mammillatus	about 100	Mortensen, 1937
Asterias amurensis	about 100	Dautov and Kasyanov, 1981
Asterias sp.	110	Costello *et al.*, 1957
Ophidiaster guildingii	110–120	Mortensen, 1921
Pycnopodia helianthoides	120	Greer, 1962
Stichaster australis	120–140	Barker, 1978
Odontaster validus	130	Pearse, 1969
Asterias rubens	120–150	Kaufman, 1977
A. rubens	160–190	Gemmill, 1914
Concinasterias calamaria	140–160	Barker, 1978
Pisaster ochraceus	160	Strathmann and Vedder, 1977
Sclerasterias richardi	170	Falconetti *et al.*, 1978
Patiria pectinifera	170	Dautov and Kasyanov, 1981
Astropecten scoparius	230	Oguro *et al.*, 1976
Astropecten latespinosus	250–400	Komatsu, 1975
Patiriella exigua	400	Lawson-Kerr and Anderson, 1978
P. calcar	400	Lawson-Kerr and Anderson, 1978
Asterina coronata	420	Komatsu, 1975
A. batheri	430	Kano and Komatsu, 1978
A. minor	430–500	Komatsu, 1976
A. burtoni	450–500	James, 1972
A. gibbosa	500	McBride, 1896
Urasterias lincki	700	Kaufman, 1977
Crossaster papposus	700	Kaufman, 1977
Leptasterias hexactis	800	Chia, 1968
Solaster endeca	800–1,000	Gemmill, 1912
Echinaster echinophorus	800–1,300	Atwood, 1973
Fromia ghardaquana	about 1,000	Mortensen, 1937
Echinaster sepositus	1,000	Nachtsheim, 1914
Henricia sanguinolenta	1,000	Kaufman, 1977
Pteraster militaris	1,000	Kaufman, 1977
Mediaster aequalis	1,000–1,200	Birkeland *et al.*, 1971
Notasterias armata	3,540	McClintock and Pearse, 1986

Fertilization : Insemination and subsequent fertilization usually occur between the dissolution of the germinal vesicle and the separation of polar body I. The spermatozoa of sea stars are acrosomal and during fertilization an acrosomal reaction of the spermatozoon occurs, whereby the acrosomal filament of the spermatozoon penetrates the jellylike membrane and comes into contact with the egg (J.C. Dan, 1970). This is followed by a cortical reaction in the egg; one morphological manifestation of this reaction is the extrusion of the contents of cortical granules into the perivitelline space between the egg and the vitelline membrane, and the latter being modified into a fertilization membrane. The vitelline membrane detaches from the

surface of the egg in a few minutes and enlargement of the perivitelline space continues up to commencement of cleavage (Kume and Dan, 1968).

Cleavage: About 1 – 2 hr after fertilization, cleavage begins, which is usually radial in echinoderms. The first two cleavage furrows are meridional and the third equatorial (Figure 65). The somewhat unequal size of the first blastomeres in some species of sea stars, indicates weakly expressed bilateral cleavage (Field, 1892; Gemmill, 1914; Kasyanov, 1977). Although the first cleavages in general are synchronous, strict synchronization of cleavage is not observed. In sea stars the blastomeres are usually very loosely bound to each other right up to the formation of the coeloblastula. The characteristic division into macro-, meso-, and micromeres of the sea urchin embryo is absent in sea stars.

As a result of cleavage, a morula or blastula with rather loosely bound blastomeres forms (Figure 66) and then a coeloblastula with an extensive blastocoel and firmly adhering blastomeres (Dan-Sokhawa, 1977). The absence of completely radial division is a distinguishing feature of *Fromia*

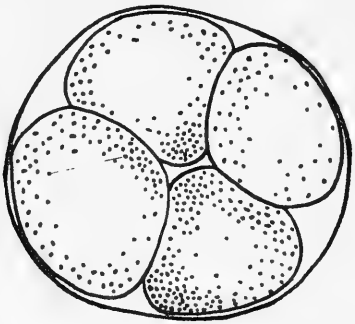


Figure 65: Cleavage of *Patiria pectinifera* into four blastomeres.

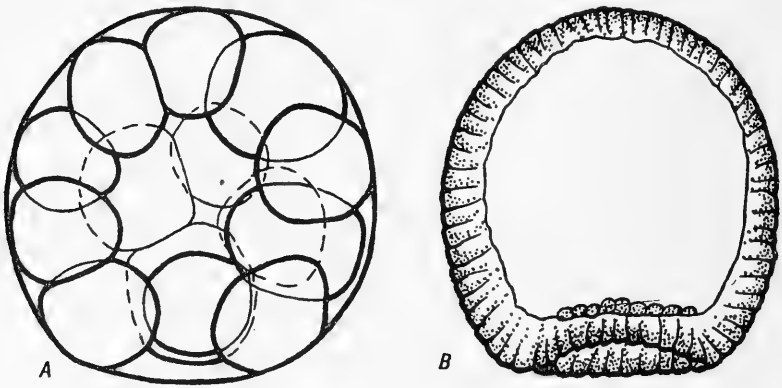


Figure 66: Blastula of *Patiria pectinifera*. A—blastomeric blastula; B—coeloblastula.

ghardaquana (Mortensen, 1938). In this sea star cytotomy (cell division) is preceded by repeated division of the nuclei; the latter then migrate to the periphery of the egg and initially form a single layer that becomes multilayered. Separation of the cellular boundaries in the embryo of *F. ghardaquana* continues for a long time. Delayed cytotomy, compared to nuclear division, characterizes the large eggs of *Henricia saguinolenta*. In the deepwater *Aspidodiadema jacobyi*, at the blastula stage the egg yolk lies under the blastoderm (Young and Cameron, 1987). In many sea stars (especially in astropectinids and many asterinids), there are surface folds on the morula or blastula which are smoothed with the emergence of the blastula from the vitelline membrane. Shedding of the membrane, i.e., changing over to a free larval life, occurs very early in echinoderms and especially in sea stars. The first larval stage is the late blastula in some species of sea stars or the early gastrula in others.

Gastrulation : Gastrulation begins soon after hatching or not long before it. It is preceded by some flattening of the blastular walls at the vegetal pole (Figure 66). Invagination of the cell layer begins at the site of flattening (Figure 67). A long narrow archenteron forms and from its base expulsion of the mesenchymal cells begins, which have long filopodia touching the cells in the wall of the blastocoel (Figure 68). Later, the archenteron becomes mushroom-shaped. The cavity of the "stalk" is lined with endodermal cells and the cavity of the "cap" (the future coelomic cavity) is bordered by mesodermal cells. The primordium of the mesoderm divides into two closed

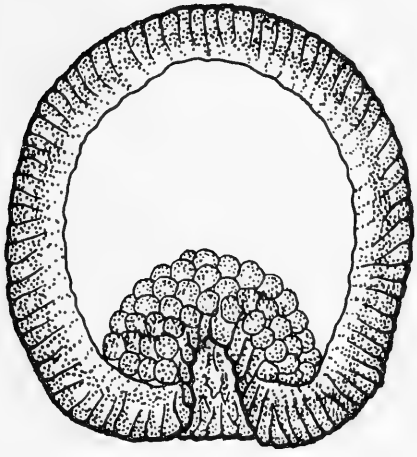


Figure 67: Gastrula of *Patiria pectinifera*.

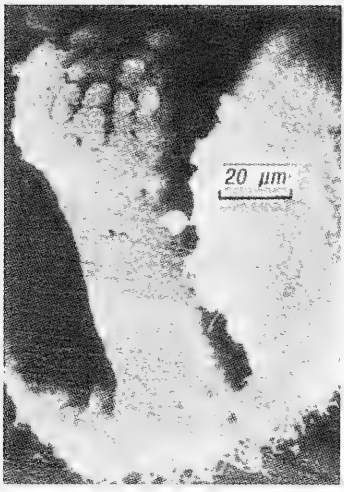


Figure 68: Archenteron of the gastrula of *Pisaster ochraceus* (from Chia, 1977).

vesicles that lie along the sides of the intestine — the left and right coeloms. Each coelom later divides into three parts — anterior (axocoel), middle (hydrocoel), and posterior (somatocoel); the left coeloms are better developed. Such is the typical picture. But in some species, the formation of coeloms may be accelerated by independent formation of the left somatocoel (in *Patiria miniata* — Heath, 1917; *Henricia sanguinolenta* — Masterman, 1902; *Solaster endeca* and *Crossaster papposus* — Gemmill, 1920). The digestive tract at this time has only one opening — the blastopore.

Dipleurula

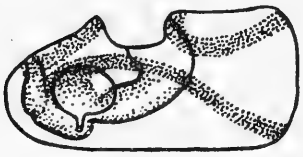


Figure 69: Early bipinnaria of *Astropecten aurantiacus* (from Hörstadius, 1939).

Before the formation of the mouth, the ectoderm of the anterior part of the ventral side of the larva flattens. A small depression forms here, i.e., the stomodeum primordium, and the tip of the gut bends in this direction. Cells of the ectoderm and endoderm merge and form the mouth opening. The blastopore becomes the anal opening and shifts position to the ventral side. The mouth opening is situated in the perioral depression and is edged with a ciliated band (Figure 69). This stage is called the dipleurula. In front of the perioral depression rises the preoral plate and behind it, the anal plate with the anal opening. These raised plates are edged with a better developed ciliary cover compared to the remaining surface of the larva. Ciliated cells lying along the edge of the preoral plate later produce the preoral ciliated band, while ciliated cells lying along the edge of the anal plate are the primordium of the postoral ciliated band that extends from the bottom upward, along the dorsolateral margins of the larva. The ciliated bands merge at the anterior end of the larva but later separate here (Figure 70).

Bipinnaria

Further development of the trapping and locomotor apparatus — the ciliated bands — transforms the dipleurula into a bipinnaria. These bands of complex configuration pass along the elongate transparent body of the bipinnaria and over numerous body projections (arms/processes) (Figure 71).

Feeding: Strathmann (1974) has noted that the body of a planktotrophic larva is primarily a temporary structure for feeding. The digestive system comprises the mouth cavity, esophagus, stomach, a very short, thin intestine, and a thick intestine that terminates in the anal opening. Like the larvae of bivalves, the larvae of sea stars feed on food particles suspended in the surrounding water. Feeding involves the creation of water currents, separation

of food particles from the water, transportation of the same to the mouth, and ingestion (Werner, 1959).

Evidently, larvae of sea stars do not possess chemoreceptors, which would discern the quality of the food ingested, since they ingest not only unicellular algae but also coal particles (Dautov, 1979). The perioral depression or the oral field participates in the capture of food but the main trapping apparatus is the ciliated bands — the small preoral band, the postoral edging the entire body (except the preoral plate), and the adoral band bordering the oral opening. The preoral band passes into the medioventral and the two preoral projections (arms), while the postoral band passes into the mediodorsal and paired postoral, posterolateral, posterodorsal, and anterodorsal projections (arms) (see Figure 71). The degree of development of any projection is considered when determining the species affinity of a larva. In some species of sea stars the ciliated band is barely discernible on the projections (arms) (*Asterias, Pisaster, Pycnopodia*); in others (*Patiria, Luidia*) it is quite distinct (Strathmann, 1971). The ciliated band reaches the maximum length in the bipinnaria of *Luidia* (Figure 72) (Meek, 1927; Strathmann, 1971; Wilson, 1978). The adoral band forms two strands passing along the ventral side of the esophagus and forms a long stretched loop. In the larvae of sea stars the entire outer surface of the body is armed with individual cilia.

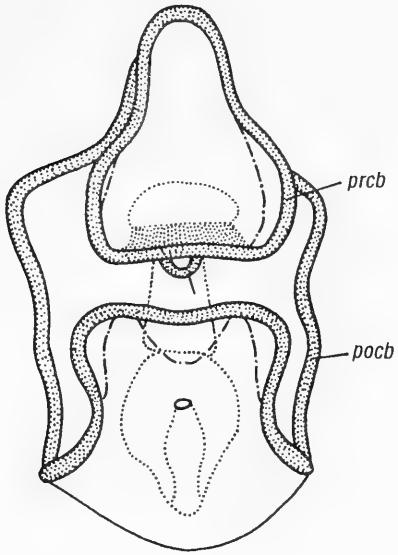


Figure 70: Bipinnaria of *Patiria miniata* (from Strathmann, 1971). pocb--postoral ciliated band; prcb—preoral ciliated band.

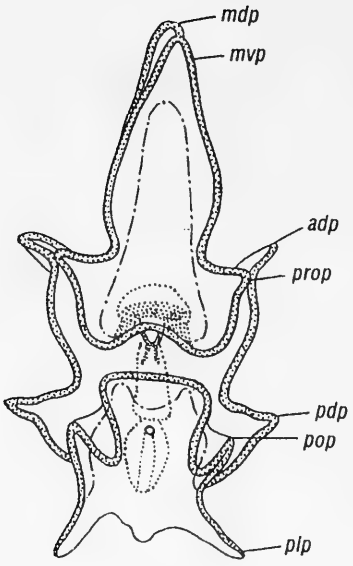


Figure 71: Bipinnaria of *Luidia foliolata* (from Strathmann, 1971).
adp — anterodorsal projection (arm);
mdp — mediodorsal projection (arm);
mvp — medioventral projection (arm);
pdp — posterodorsal projection (arm);
plp — posterolateral projection (arm);
pop—postoral projection (arm);
prop — preoral projection (arm).

Ciliated bands range from 20–30 μm in length. The band is about ten cells wide and each cell bears one cilium. Cells bordering the ciliated band secrete a mucus (Tattersall and Sheppard, 1934; Strathmann, 1971). Such cells occur on the aboral side of the band and are absent in the oral field. Cilia beating at right angles to the ciliated band create a water current directed away from the perioral field, which moves the larva forward. A flow is thereby created in front and from the sides, which is directed toward the perioral field. Food particles trapped on the ciliated band are transported by it and the cilia of the perioral field to the mouth. The mechanism of filtration of particles by the ciliated band is presumably as follows: Particles of sufficient size which touch the cilia of the band during active beating (directed from the perioral field), mechanically or chemically induce a local temporary reversal of beating of the cilia touched. The particles captured in this movement are transported to the perioral field and then to the mouth. Once these particles have been transferred to the perioral field, the initial direction of effective ciliary beating is resumed. Some particles may be trapped directly by cilia in the perioral field, bypassing the ciliated band. These particles reach the oral cavity through the upper and lateral areas of the adoral band. The cilia of these areas, like those of the esophageal loop of the band, beat in the direction of the intestine. Transportation of food particles toward the mouth is facilitated by the secretion of the mucous cells located alongside the ciliated band. Food particles entering the mouth cavity may remain there for over 20 min, congealing into a compact mass; individual particles pass through the mouth cavity without stopping and enter the esophagus (Strathmann, 1975). Coal particles added to the culture of bipinnariae of *Aphelasterias japonica* were detected in the esophagus after 50–60 sec, and in the stomach after 2 min (Dautov, 1979).

All sections of the digestive tract are lined with ciliated cells that assist in the passage of food particles. The passage of food particles through the esophagus is also aided by large circular esophageal muscles; their wavelike

contraction pushes the food into the stomach, which is separated from the esophagus by the cardinal sphincter. Food lumps are broken down in the stomach where digestion takes place. The food enters the small intestine through the open pyloric sphincter. Particles are sorted into edible and nondigestible in the stomach. Passage of food particles through the entire digestive system takes 15 – 20 min. According to Strathmann (1971), the echinoderm larva ingests particles less than 65 – 85 µm in diameter and less than 100 – 200 µm long. The rate of filtration of particles from water is 0.5 – .3 µl/min. On average, filtration proceeds at a speed of 0.3 – 0.6 µl/min per 1.0 mm of ciliated band. With an increase in concentration of algae, the rate of filtration decreases. If the concentration is very high — over 5,000 – 10,000 cells/ml — the particles cannot be handled by the ciliated band. At concentrations of algae in excess of 50,000 cells/ml, aberrations in development may occur, leading to larval mortality; the intestines of such larvae are jammed with food and many intact, undigested algal cells are present in the feces (Strathmann, 1971; Barker, 1978). During active feeding larvae cannot be

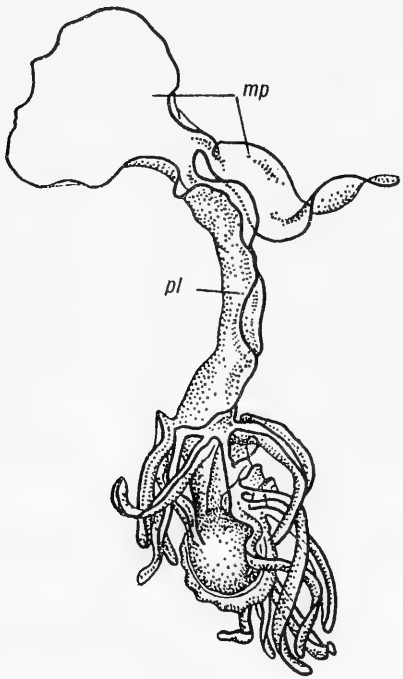


Figure 72: Bipinnaria of *Luidia ciliaris* (from Tattersall and Sheppard, 1934).
mp — medial projections (arms); pl — preoral lobe.

selective, accepting some and rejecting other species of algae; however, the rate of filtration differs for different species of algae. Moreover, one species of algae may influence the rate of filtration of another species — increasing or decreasing it (Strathmann, 1975). The nutritional value of different food particles has not been thoroughly investigated. Adequate data are not available for judging the role of bacteria and soluble organic substances in the nutrition of larvae of sea stars. But their role can hardly be important since the ciliated band poorly retains particles less than 2–3 μm in size and observations have shown that growth mainly occurs with active feeding on phytoplankton.

Like sea urchins (Chia and Burke, 1978), it has been suggested that reserve food, primarily in the form of lipids, is stored by the larvae of sea stars in cells of the digestive tract.

Respiration : As in larvae of bivalves, the intake of oxygen and removal of carbon dioxide in the larvae of sea stars occurs by diffusion. The minute size of the larvae enables them to dispense with any specialized system. Their constant motion — beating of ciliated bands, movement of other areas of the body surface, and activity of the ciliated surface of the digestive system — is conducive to gaseous exchange.

Transport of substances: In echinoderm larvae (as in larvae of other marine invertebrates), which are minute in size, there is no need for a special system for blood circulation. This function is fulfilled by extensive — primary and secondary — body cavities. Transport of substances in the primary body cavity is facilitated by contraction of the body wall and esophagus, and transportation of substances in the secondary cavity (coelom) facilitated by beating of cilia lining the coelomic cavity.

Excretion : Larvae of sea stars possess no specialized excretory system. The function of excretion, as in many lower groups of animals, is performed by the developed digestive system. Evidently, mesenchymal cells participate in the removal of metabolic products; these cells are scattered in the primary body cavity. Possibly Field (1892) is correct, as his demonstration of the excretory function of the pore canal is partly confirmed by the organized directional movement of cilia in the coelomic cavities (Gemmill, 1914), which causes a current in the direction of the pore canal. Ruppert and Balser (1986) are more specific in naming the canal-hydropore complex the nephridium.

In the course of development of sea stars the coelomic structures undergo considerable transformation. They form various organs and systems in the definitive organism, primarily its ambulacral system. We do not propose to describe the development and transformation of coeloms; rather, we shall describe only the coelomic formations of bipinnaria, since these are multi-

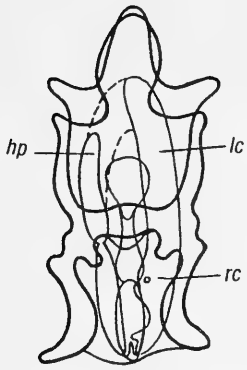


Figure 73: Development of coeloms in the bipinnaria of *Coscinasterias calamaria* (from Barker, 1978).
hp — hydropore; lc — left coelom; rc — right coelom.

functional structures performing supportive, distributive, and excretory functions. Coeloms of the bipinnaria are extensive hollow pouches situated on both sides of the digestive tract. In the early bipinnaria they are separate but in the late bipinnaria they fuse above the oral lobe and pass into the dorsomedial projection (arm) (Figure 73). The left coelom is better developed than the right. Septa (commissures) in the posterior region of the coelom partly separate the left and right coeloms (somatocoels) from the common coelom. This separation becomes complete later (Figure 74). The remaining part of the coelom is a single structure that later separates into left and right anterior and posterior coeloms, i.e., axo- and hydrocoels. The single coelom is linked with the external medium through a pore canal, which opens as a hydropore on the dorsal side, left of the median line, at the level of the lower part of the esophagus. In some species, in addition to the left pore canal, there may be a right pore canal as well, which also opens through a hydropore exteriorly (Figure 75) (Field, 1892; Gemmill, 1914, 1915). During the development of the bipinnaria, coeloms of the right and left side are connected not only in the anterior region, but also in the region of the somatocoels. The left somatocoel temporarily forms a process, termed the ventral horn, which communicates with the right axocoel ventral to the stomach, encircling the intestine from both sides. A dorsal horn also forms in the left somatocoel, which establishes contact with the left axo-hydrocoel. Thus the coeloms of the left side remain connected despite a dividing septum (Figure 76). According to Gemmill (1914), the flow of coelomic fluid is directed by cilia from the left axo-hydrocoel to the right axo-hydrocoel, from there through the ventral horn to the left somatocel, and again into the left axo-hydrocoel. In the pore canal, lined with a cuboidal ciliated epithelium, as mentioned above, a weak outward beating of the ciliated band is perceptible. Possibly, the movement of fluid in the coelomic cavities is facilitated by the pulsation of the closed madreporic vesicle (formed, probably, from the mesenchymal cells), situated alongside the left hydropore (Gemmill, 1914). This vesicle is not found in all species. Nor do all authors mention circulation of the coelomic fluid (see, for example, Barker, 1978).

Locomotion : Bipinnariae swim by means of ciliated bands, the preoral and, more so, the postoral. The structure of the ciliated bands has been

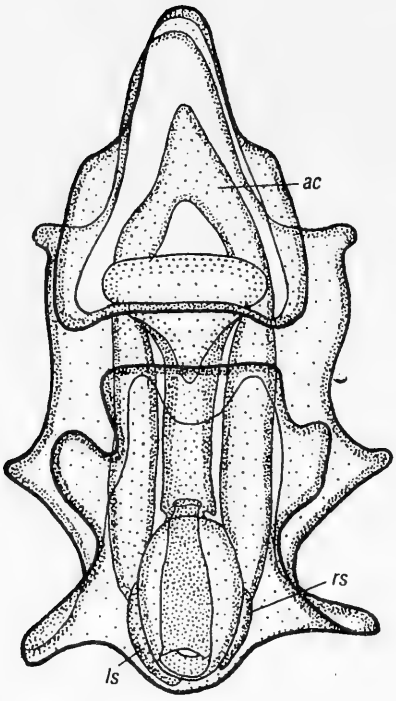


Figure 74: Development of coeloms in the bipinnaria of *Patiria pectinifera*.
ac — axocoel; ls — left somatocoel; rs — right somatocoel.

described in the section on feeding of the larva. The water current created by the cilia of these bands enables the capture of food particles and concomitantly locomotion of the bipinnaria. In this case the preoral lobe is directed forward. In the bipinnariae of sea stars of the family Asteriidae, the size of the processes increases with bipinnarial growth and they transform into long movable arms. The posterolateral and posterodorsal arms (Figure 77) become the longest (Gemmill, 1914; Kume and Dan, 1968). Since the ciliated band extends over the elongate processes of the bipinnaria, the total length of the band increases considerably. In many sea stars, however, the ciliated band on the arms is not well developed and does not participate in the capture of food; it functions only in larval locomotion. The beating of the cilia on the arms is directed from the base to the tip of the arm. The speed of movement of the bipinnaria of *Asterias rubens* is about 2.0 cm/sec (Konstantinova, 1966). Movement of the bipinnaria in a reverse direction is not performed by reversal of direction of ciliary beating (as done in the pluteus), but rather by the larva turning around. The bipinnaria executes a turn during swimming

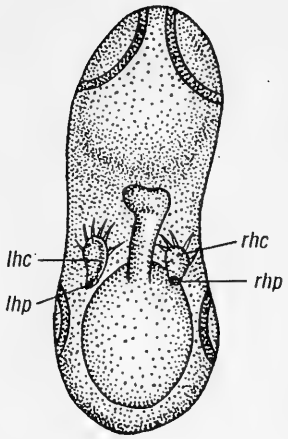


Figure 75: Left and right hydropores in the early larva of *Asterias vulgaris* (from Field, 1892).
lhc — left hydrocoel; lhp — left hydropore; rhc — right hydrocoel; rhp — right hydropore.

through contraction of the dorsal muscles, which produces considerable flexion of the larva on the dorsal side (Strathmann, 1971). Movement of the giant bipinnariae of *Luidia ciliaris* and *L. sarsi* occurs through contraction of muscles in the elongate anterior part of the larva; apparently, the ciliated bands of the larvae of these species (unlike *L. foliolata*) do not participate in locomotion (Tattersall and Sheppard, 1934; Strathmann, 1971).

Nervous system and sense organs: Earlier authors assumed that larvae of sea stars possessed a diffused nerve plexus under the epithelial cover (Gemmill, 1914; Tattersall and Sheppard, 1934). Burke (1983), while investigating the nervous system of the bipinnaria of *Pisaster ochraceus* using the glyoxalic method and electron microscopy, observed no such plexus, but demonstrated the presence of axonal tracts at the base of the ciliated band and

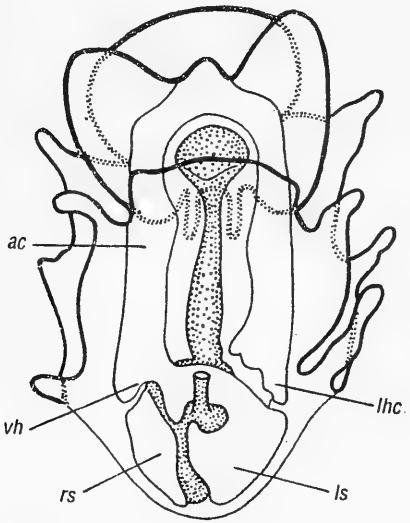


Figure 76: Development of coeloms in the bipinnaria of *Asterias rubens* (from Gemmill, 1914).
ac — axocoel; lhc — left hydrocoel; ls — left somatocoel; rs — right somatocoel; vh — ventral horn.

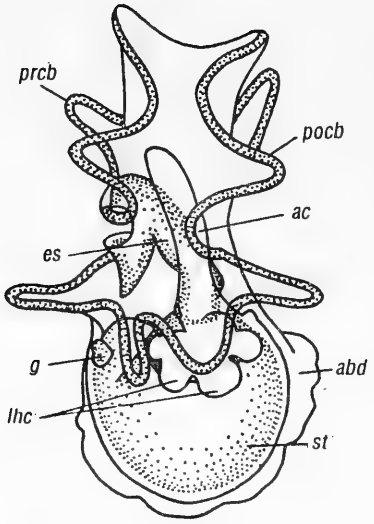


Figure 77: Bipinnaria of *Astropecten auranciacus* (from Hörstadius, 1939).
abd — aboral disk of definitive sea star; ac — axocoel; es — esophagus; g — gut; lhc — left hydrocoel; pocb — postoral ciliated band; prcb — preoral ciliated band; st — stomach.

in the esophagus, and two types of nerve cells situated in the ciliated band: one linked to the axonal tracts and the other provided with cilia. On the lower lip, in the corners of the larval mouth, clusters of nerve cells occur. In the bipinnaria of *Asterias amurensis* the presence of numerous seratonergic nerve cells has been demonstrated along the ciliated band (Nakajima, 1987). Bipinnariae do not have developed sense organs; however, it is quite possible that ciliated nerve cells of the ciliated bands perform sensory functions (Burke, 1983).

Integument : Echinoderm larvae lack a specialized protective organ, equivalent to the larval shell of bivalves — an organ that performs several functions simultaneously. Hence protection of the internal tissue of the larva against adverse effects is solely delegated to the cells of the integumentary epithelium, which bear cilia and microvilli and produce mucus.

Rudiments of definitive organs : The development of sea stars from planktotrophic larvae may proceed in two ways. In most sea stars there is a brachiolaria stage immediately following the bipinnaria stage, during which development of the organs of attachment and anchoring of the definitive body of the organism are characteristic. Metamorphosis concludes with the attachment of the larva to the substrate. In sea stars of the families Luidiidae and Astropectinidae, organs of attachment do not appear during development;

instead, the entire development of the definitive sea star and the conclusion of metamorphosis take place in the purely planktonic bipinnaria stage. Such, in particular, is the development of *Luidia ciliaris* and *L. sarsi* (Tattersall and Sheppard, 1934; Wilson, 1978); and *Astropecten auranciacus* and *A. scoparius* (Hörstadius, 1939; Oguro *et al.*, 1976). The brachiolaria stage in these sea stars is lacking. Hence, on the left side in the late bipinnariae of Luidiidae and Astropectinidae it is possible to see the rudiments of all the organs usually present in the definitive sea star. The organizing center for the formation of the definitive organism is located in the region of the middle coelom. We shall discuss metamorphosis in detail below. In other families of sea stars rudiments of definitive organs that serve no functional purpose in the larva are but slightly developed in the bipinnaria stage. These are the five lobate processes of the coelom that appear in the late bipinnaria in the region corresponding to the left hydrocoel, i.e., rudiments of radial canals of the ambulacral system (see Figure 76). At present, based on available data, it cannot be said for certain whether the definitive organs of sea stars lacking in the larva develop during metamorphosis from imaginal "silent" cells, or whether these organs differentiate from larval cells after dedifferentiation. The second course appears more probable (except for gametes, whose fate is predetermined). In the developed bipinnaria of most sea stars, rudiments of temporary organs of the brachiolaria, such as the brachiolar arms and attachment disk, appear in the preoral lobe.

Brachiolaria

The Brachiolaria differs from the bipinnaria in the presence of attachment organs, large body, and large processes, and pronounced formation of the definitive body of the sea star.

Feeding, transport of substances, respiration, and excretion: These activities take place in the brachiolaria in a manner similar to that in the bipinnaria. Barker (1977, 1978) has described the ultrastructure of the integumental epithelium and coelomic lining of the brachiolariae of *Stichaster australis* and *Coscinasterias calamaria*. In the region of the brachiolar stalk the cells of the external epithelium contain numerous vacuoles and are armed with microvilli. Under the epithelium lies the plexus of axions underlain by the basement membrane. Under the basement membrane is a connective layer of collagen fibers, fine fibrillar material, and occasional vacuolated cells. The inner basement membrane separates the coelom lining from the connective tissue. The longitudinal muscle fibers adjoin internally the inner basement membrane. The coelomic epithelium lies deepest and comprises mainly flat epithelial cells. Sometimes these cells have pseudopodial processes and long solitary cilia (Figure 78).

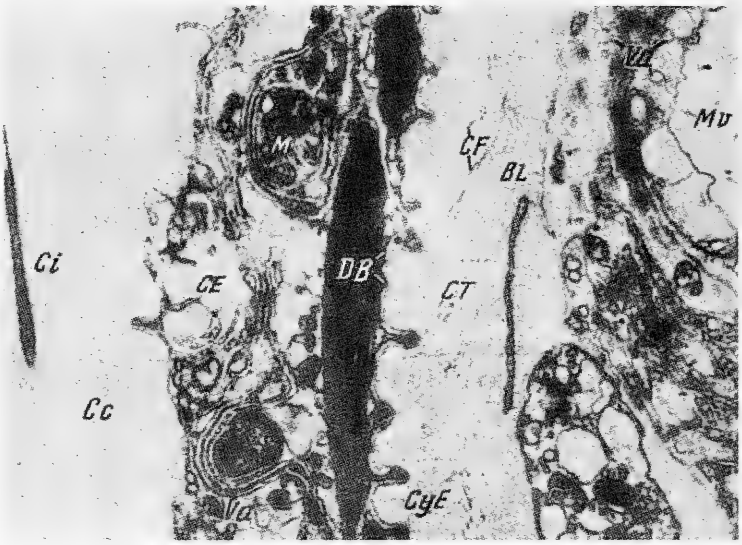


Figure 78: Structure of the brachiolar wall of the brachiolaria of *Coscinasterias calamaria* (from Barker, 1978).

ax — axons of nerve cells; bl — basement membrane; cc — coelomic lobe; ce — coelomic epithelium; cf — collagen fiber; cl — cilia; ct — connective tissue; cye — cytoplasmic processes of muscle cells; db — dense body; m — mitochondria; mv — microvilli; va — vacuolated cells.

Locomotion : This is performed by means of cilia in the ciliated band. As the body and processes grow, the size of the band increases and the processes usually become long flexible arms. The elongate ciliated band enables the brachiolaria to continue swimming as the definitive star develops. The movement of the brachiolaria becomes more rapid and more complex. The larva may reverse directions not only by describing a loop through flexion of the dorsal side of the body, but also by changing the position of its arms. On coming into contact with an obstacle, the brachiolaria extends its posterolateral, posterodorsol, and postoral arms forward, while directing the mediodorsal process ventrally. The water current generated in this action by the ciliated band, which is directed forward, moves the larva in the opposite direction. Flexion of the processes and arms of the brachiolaria occurs through contraction of the muscle fibers connecting the processes with the larval body (Figure 79) (Strathmann, 1971).

Nervous system and sense organs : In addition to the above-described nervous system of the bipinnaria, a neuropyle-axon plexus develops in the brachiolaria, which is situated apically, at the base of the brachioles and

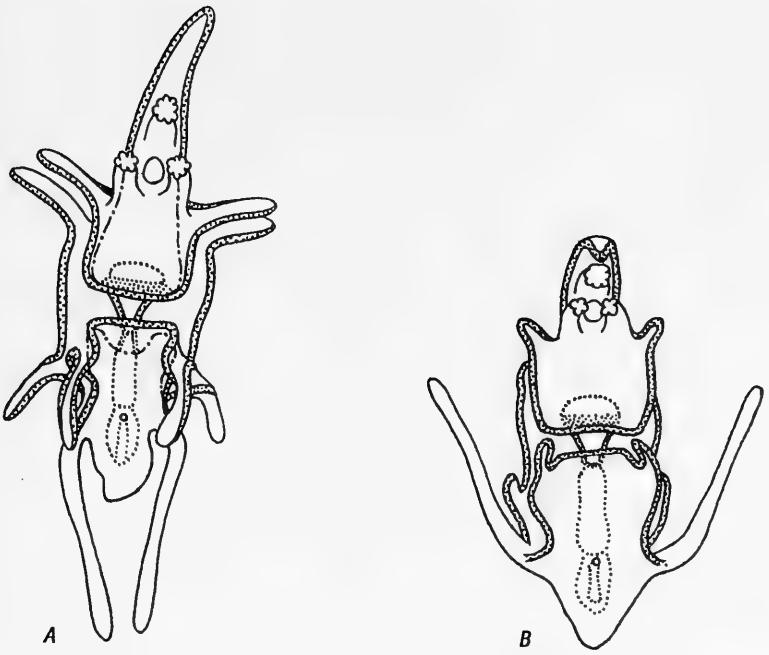


Figure 79: Flexion of processes of the brachiolaria of *Pisaster ochraceus* during reversal of movement (from Strathmann, 1971).
A — locomotion; B — reverse movement.

under the epithelium of the adhesive papillae and the disk (Barker, 1978b; Burke, 1983). Here one also finds an accumulation of serotonergic neurons (Bisgrove and Burke, 1987). The nerve cells of papillae and brachioles are connected with processes from the preoral nerve strands (Nazlin and Dautov, 1987). Among the cells of the papillae and disk, Barker identifies neurosecretory cells that presumably participate in the attachment and adhesion of the brachiolaria to the substrate. The only specialized sensory cells (if we do not consider the presumed sensory cells described in the section on the bipinnaria) are the ciliated cells of the adhesive papillae of the brachiolar arms. The basal part of such cells reaches the subepithelial axon plexus. The lone cilium surrounded by microvilli has a developed kinetochore. Probably the brachiolaria uses these cells to probe the substrate for a suitable place to settle.

Attachment system : The attachment system of a brachiolaria typically comprises three brachiolar arms, an attachment disk, and lateral papillae (Figure 80). Lateral brachiolar arms appear only in the brachiolaria stage; the medial arm is a modified medioventral process. During transformation into a

brachiole, the medioventral process in sea stars of the order Spinulosida (for example, *Acanthaster planci* — Henderson and Lucas, 1971; *Patiria pectinifera* — Mortensen, 1921; Kasyanov, 1977) is subjected to less change than in sea stars of the order Forcipulatida (for example, *Asterias rubens* — Gemmill, 1914; *Asterias amurensis* — Kume and Dan, 1968). The axocoel processes enter the brachiolar arm. The preoral ciliated band extends laterally on each brachiolar arm. The brachiolar arms are crowned by a ring of attachment papillae which serve in probing the substrate and temporary attachment to it (Figure 81). Neurosecretory and sensory cells are present in the papillary epithelium; the secretory cells predominate and produce a mucopolysaccharide-type secretion. Each such cell is armed with cilia and encircled by a ring of microvilli. Another type of secretory cell is rarely found, namely, one devoid of cilia but covered with numerous microvilli. The characteristic feature of the so-called vacuolated cells (possibly, these are actually secretory cells partially devoid of secretion) is intracellular fibrils, which extend from the basal part of the cell into the microvilli. The function of these structures is supportive. The lateral papillae, situated on each side of the attachment disk, are identical in structure.

The attachment disk is a round, slightly concave structure comprising secretory cells covered with numerous branched microvilli. The proteinic secretion of these cells acts as a cement for attaching the disk to the substrate. As in the papillary cells, supporting fibrils are located in the disk cells (Figure 82).

While probing the substrate, the brachiolaria aligns itself by its ventral side, flexes its arms covered with a ciliated band, and attaches itself by means of one or two brachiolar arms contacting the substrate with their papillary

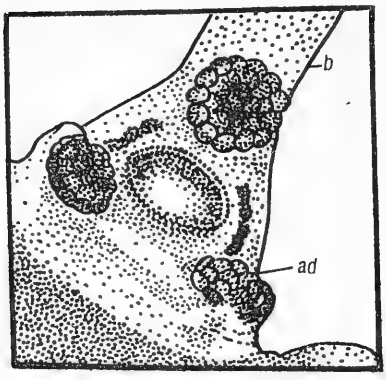


Figure 80: Attachment system of the brachiolaria of *Coscinasterias calamaria*. ad — attachment disk; b — brachiolar arm.

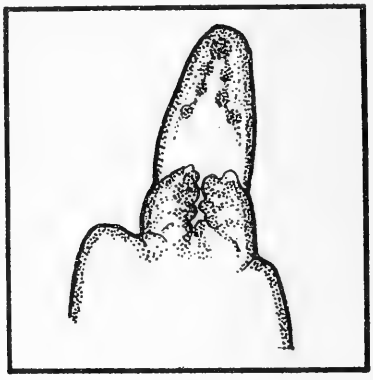


Figure 81: Brachiolar arm of the brachiolaria of *Patiria pectinifera*.

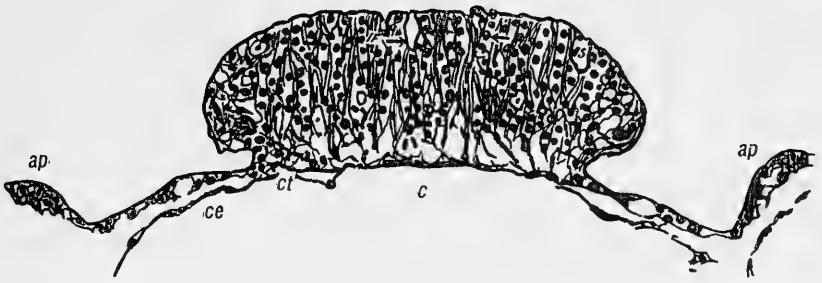


Figure 82: Structure of the attachment disk of the brachiolaria of *Coscinasterias calamaria* (from Barker, 1978).

ap — attachment papilla; c — coelom; ce — coelomic epithelium; ct — connective tissue; if — inner fibrils; is — intercellular space. Arrows indicate secretory granules.

crown. The brachiolaria, so to speak, walks along the substrate, attaching and detaching its brachiolar arms. Scouting may continue for a few seconds to one hour. If the substrate is not suitable for settling, the larva straightens its arms and swims away. If the substrate is satisfactory, the larva ceases "scouting", alternately presses its brachiolar arms to the substrate, spreads them maximally apart, then lowers the attachment disk to the substrate. A firm contact is ensured by the working of the attachment papillae situated on each side of the disk. Cementation then commences, during which the secretion of the cells of the attachment disk is discharged and binds the disk to the substrate. This process takes one to several hours. Metamorphosis, which had already begun in the pelagic period of larval life, terminates in the attached state. After six to seven days the juvenile sea star is dislodged from the larval body by means of the primary ambulacral podia and, thus freed, begins an independent life (Barker, 1978; Strathmann, 1978).

Light retards metamorphosis. Larvae of the family Asteriidae maintained in a normal daily range of illumination completed metamorphosis within ten hours at night, while larvae illuminated continuously for five days were not able to metamorphose even though they had attached to the substrate (Dautov, 1979).

Substrate selectivity is well developed in some species and lacking in others. High selectivity is typical of lecithotrophic larvae (Strathmann, 1978). The Brachiolariae of *Acanthaster planci* and *Coscinasterias calamaria*, plankton feeders, settle on almost any substrate, provided it is covered with a primary bacterial-algae film (Lucas, 1975, Barker, 1977). The microrelief of the substrate is evidently not of special importance; however, the brachiolaria in anchoring prefers, whenever possible, the lower surface of the substrate. Yet some planktotrophic brachiolariae do exhibit high substrate specificity. One such is the New Zealand sea star (*Stichaster australis*), which settles only

on coralline algae of the genus *Mesophyllum*. In the absence of a suitable substrate, the sea star can delay completion of metamorphosis and continue swimming; according to Barker (1977), its threshold of selectivity drops gradually. If the larva is unable to find a suitable substrate, it dies. Larvae of *Acanthaster planci, Culcita novaeguineae,* and *Linckia laevigata,* feeding on corals, settle on the coral algae *Porolithon* (Yamaguchi, 1973, cited by Chia *et al.*, 1984); tubes of the polychaete *Phyllochaetopterus prolifica* attract larvae of the sea star *Mediaster aequalis,* the young of which feed on these polychaetes (Birkeland *et al.*, 1971).

Larvae of the families Luidiidae and Astropectinidae possess no specialized "larval" attachment organs. For scouting the substrate and temporary attachment, the larva uses the already functional ambulacral podia of the juvenile sea star (Strathmann, 1979).

METAMORPHOSIS

The metamorphosis of sea stars from planktotrophic larvae is catastrophic in character. Intensive morphogenetic processes occur in which dedifferentiation or resorption of many larval tissues takes place. The definitive sea star forms on the left side of the larva. The oral-aboral axis of the sea star is at an angle to the principal axis of the larval body. In most sea stars the principal and concluding processess of metamorphosis are completed after the brachiolaria has settled in the attached state.

Digestive system : The ciliated band performs the function of a capturing mechanism and organ of locomotion only in the larva and, in the course of metamorphosis, is subjected, like the remaining areas of the larval epithelium, to dedifferentiation and resorption. Cells of the preoral ciliated band are part of the stalk whereby the developing sea star is bound to the attachment disk; in some species the stalk is divested after metamorphosis, while in others it is resorbed (Chia and Burke, 1978). The entire epithelium is not resorbed; the definitive integument of the juvenile sea star is differentiated from its cells (after the preceding dedifferentiation). The digestive system undergoes significant changes. The larval tissues of the mouth, part of the gut, and the anal region are resorbed. Cells of the larval esophagus constitute part of the outer epidermis and wall of the stomach. A definitive esophagus is formed, the larval stomach is reconstructed, and rudiments of the pyloric appendages appear. According to Bury (1895), the larval esophagus is directly transformed into a definitive organ. On the oral side of the juvenile sea star a mouth opening appears and on the aboral side an anal opening. A definitive gut with rectal glands forms from parts of the larval gut (Gemmill, 1914).

Respiration: The respiratory function is transferred from the larval to the definitive epithelium. In the juvenile sea star visceral coeloms formed from the larval somatocoels and the hemal and perihemal systems formed from the left somatocoel and axocoel, also participate in the *transportation of substances.*

Elimination of metabolic products: This involves several structures—spheroid bodies with phagocytes, the axial organ, and the rectal glands (Bachmann and Glodschmid, 1978; Jangoux, 1978; Höbaus, 1979). Larval coeloms are considerably transformed; with their participation, a new locomotor organ, hemal and perihemal systems, axial organ, and coelomic cavity of the definitive sea star are formed.

Locomotion: With a changeover to a benthic mode of life, the sea star loses its swimming organ — the ciliated band. The transient locomotor apparatus of the brachiolaria — the brachioles — remains for a very short time, allowing the sea star to move on the substrate. At this stage there occurs, so to speak, a testing of a new locomotor mechanism through the assistance of the apically papillate body processes, into which coelomic processes penetrate. The definitive locomotor organ — the ambulacral system, which arises during metamorphosis — works on a similar principle. The region of the left hydrocoel plays a leading role in its formation; bending, the two ends later merge and form the rudiment of the oral ring of the ambulacral system. From the arc issue hydrocoelic processes — rudiments of the radial canals of the ambulacral system (Figure 83). The terminal areas of these canals, in conjuntion with the ectoderm surrounding them, later give rise to the terminal tentacle (podia), while along the sides of the canal secondary processes form—rudiments of the ambulacral podia. The axocoel takes part in the formation of the stone canal from the larval pore canal and the hydropore (Gemmill, 1914).

Nervous system and sense organs: The larval nervous system and sense organs are replaced by definitive ones. In the opinion of Gemmill (1912), the nerve plexus of the preoral lobe of the brachiolaria participates in the formation of the oral ring of the definitive nervous system. The most developed ectoneural system in sea stars is formed from the thickened ectoderm above the circumoral ring and radial canals of the ambulacral system. In addition to sense organs scattered in the integument, numerous sensory elements are located in the terminal tentacle and ocelli at the base of the tentacle.

Integument: A variety of skin glands, spines, pedicellaria, and other elements of the skeleton of the definitive sea star perform protective functions.

Skeleton: The definitive skeleton has already begun to form in the bipinnaria. In sea stars, as in all echinoderms, the skeleton is internal and of

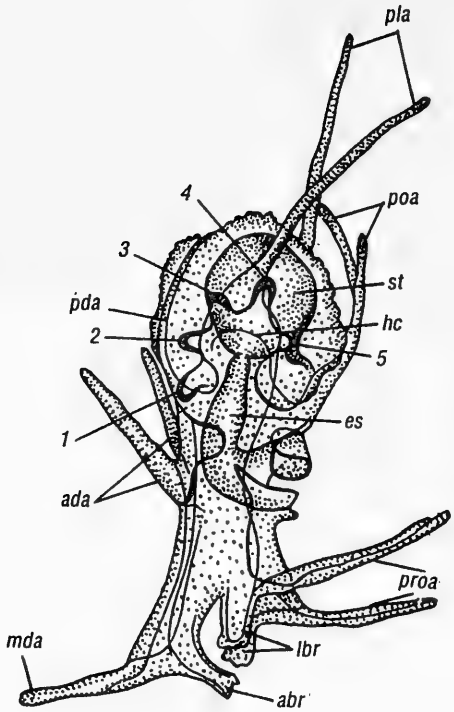


Figure 83: Initiation of radial canals of the ambulacral system in the brachiolaria of *Asterias vulgaris* attached to the substrate by brachiolar arms (Goto, 1896*).
abr — anterior brachiolar arm; ada — anterodorsal arm (projection); es — esophagus; hc — hydrocoel; lbr — lateral brachiolar arm; mda — mediodorsal arm (projection); pda — posterodorsal arm (projection); pla — posterolateral arm (projection); poa — postoral arm (projection); proa — preoral arm (projection); st — stomach; 1 to 5 — rudiments of radial canals of ambulacral system.

mesodermal origin. The first skeletal plates — central, five radial, terminal, and five interradial basal — form in the region of separation of the aboral disk of the definitive asteroid. One basal plate becomes the madreporite, which closes the outer opening of the stone canal of the ambulacral system. Other elements of the skeleton appear later (Figure 84).

Rudiments of definitive organs: In the juvenile sea star, all systems of the definitive body are found in various stages of formation; these become fully developed as the asteroid grows. Within a few days after metamorphosis, all these systems become functional except the reproductive. Development of the reproductive system has not been fully investigated. Some authors

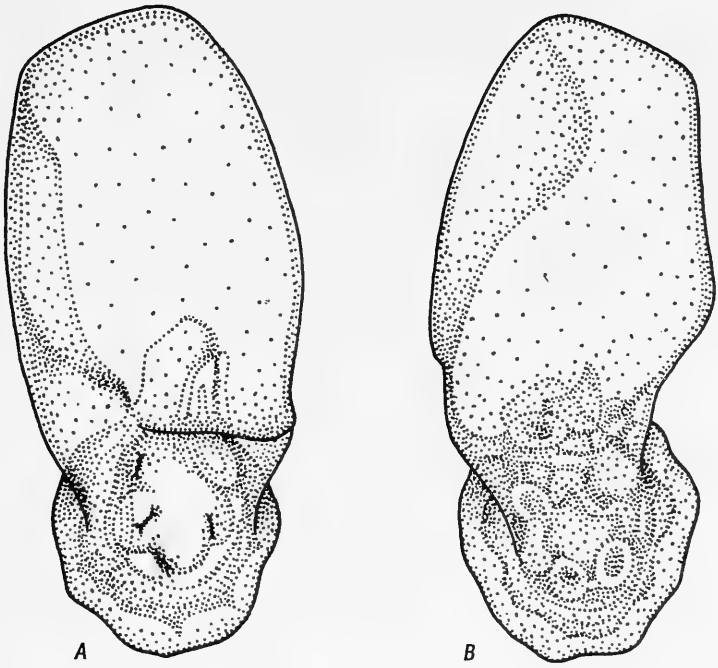


Figure 84: Lecithotrophic larva of *Astropecten latespinosus* with aboral (A) and oral (B) sides of disk of definitive asteroid (from Komatsu, 1975).

(McBride, 1896; Chia, 1968) have observed the precursors of gametes in the cellular wall separating the left and right somatocoels. Lender and Delavault (1968) were the first to identify the primary gametes in the wall of the coelom of the madreporal interradius in an 11-day-old brachiolaria of *Asterina gibbosa;* later, these were observed in the circular genital cord encompassed by the aboral perihemal ring. Processes of the genital cord in the ray of the asteroid are gonadal rudiments.

LECITHOTROPHIC LARVAE

Many species of sea stars produce large eggs — 200–3,450 μm — with a large yolk mass. The larval stages, or the bipinnaria stage, are generally bypassed in the development of such asteroids; only a highly altered brachiolaria is retained, which lacks a ciliated band and a functional digestive system. The body of such a brachiolaria is oval and provided with an attachment apparatus — brachiolar arms and disk (Figure 85), which have been partially described for *Solaster endeca* (Gemmill, 1912), *Henricia*

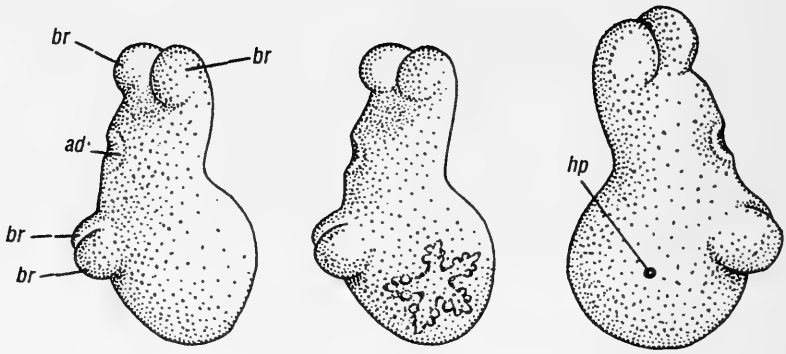


Figure 85: Brachiolaria of *Echinaster echinophorus* (from Atwood, 1973).
ad — attachment disk; br — brachiole; hp — hydropore.

sanguinolenta (Masterman, 1902), *Leptasterias hexactis* (Chia, 1966) *Patiriella exigua* (Lawson-Kerr and Anderson, 1978), and *Asterina minor* (Komatsu *et al.*, 1979). Brachiolar arms are absent in some species — *Asterina gibbosa* (McBride, 1896); in other species, they are developed but the attachment stage is absent — *Echinaster sepositus* (Nachtsheim, 1914) and *Asterina batheria* (Kano and Komatsu, 1978). The lecithotrophic larva of *Astropecten latespinosus* possesses neither brachiolar arms nor attachment disk (Komatsu, 1975), which is not at all strange since the brachiolaria stage is absent in astropectinids with planktotrophic larvae. Due to lecithotrophy, the number and degree of development of larval structures are minimal and the definitive organogenesis of such larvae proceeds in a more direct manner.

On the whole, it may be said that the secondarily acquired direct development or development lecithotrophic larva is often observed in evolutionally primitive groups of sea stars. (A similar picture is observed in many taxa of invertebrates, for example in bivalves.) In the primitive order of sea stars Paxillosida, direct development with brooding of offspring in the cavities between paxilli occurs in the genera *Ctenodiscus* and *Trophodiscus*. In *T. almus* the largest embryos are located along the margin of rays and in the interradii of the female. Embryos emerge through movement of the paxilli. Similar brooding is observed in *T. uber* (D'yakonov, 1950). Development without free-swimming larvae is also typical of *Solaster endeca, Crossaster papposus, Asterina gibbosa,* and other species of the latter genus. In *Pteraster obscurus* and *P. militaris*, fertilization and brooding of embryos occurs on the dorsal side within a special cover (Kaufman, 1977). In species of the genus *Henricia,* embryos are borne in clutches near the mouth or in the mouth of the mother. Development without planktotrophic larva occurs in the order

Forcipulatida; however, such development generally occurs in species inhabiting polar and adjacent waters, for example, species of the genus *Leptasterias* (D'yakonov, 1950) (also see Table 4 and Kasyanov, 1987).

IDENTIFICATION OF PELAGIC LARVAE OF SEA STARS (Terminology and Diagnostic Characters)

In the bipinnaria of a sea star (Figure 86) the dorsal and ventral, right and left sides, and anterior and posterior ends are well defined. On the ventral side lie the mouth and anal openings; on the left dorsal side, the hydropore leading into the coelomic cavity; usually, there is no hydropore on the right dorsal side. In the anterior part of the larva, in front of the mouth, lies the preoral lobe, which is delimited from the rest of the body by an independent preoral ciliated band. The anterior part of the preoral lobe forms the medioventral process (arm), below which the right and left preoral processes are located laterally. The lower part of the preoral band borders the preoral depression, which is hemmed by the peristomial ciliated ring girdling the mouth. The preoral depression is posteriorly bordered by the transverse area of the main postoral ciliated band, which hems the rest of the body of the bipinnaria. This ciliated band ventrally passes over the left and right postoral processes and the posterolateral processes situated in the posterior part of the larva. Dorsally, the cilited band borders (extending posteroanteriorly) the left and right posterodorsal and anterodorsal processes and finally the unpaired mediodorsal process.

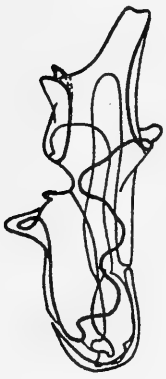


Figure 86: Bipinnaria of *Patiria miniata* (from Strathmann, 1971).

In the later larva — brachiolaria — of the sea star (Figure 87), additional projections appear on the preoral lobe, namely, the left and right brachiolar arms, which are equipped with a crown of attachment papillae. The medioventral process is also transformed into a brachiolar arm, with papillae located on its tip and/or in two rows along the ventral surface. The large attachment disk lies between the brachiolar arms.

The following parameters and characters are important in the identification of larvae of sea stars:

1. Length of larva from tip of mediodorsal process to posteriormost point of body (between posterolateral processes), measured in a larva in an extended condition.

Table 4: Types of development of sea stars.

Species	Type of Development	Source
	ORDER PAXILLOSIDA	
Astropecten auranciacus	Planktotrophic larva	Hörstadius, 1925
A. irregularis	Same	Newth, 1925
A. latespinosus	Lecithotrophic larva	Komatsu, 1975
A. polyacanthus	Planktotrophic larva	Mortensen, 1937
A. scoparius	Same	Oguro *et al.*, 1976
A. velitaris	Same	Mortensen, 1937
Ctenopleura fisheri	lecithotrophic larva	Komatsu, 1982*
Psilaster andromeda	Same	D'yakonov, 1950
Ctenodiscus australis	Brooding	Lieberkind, 1928
Leptychaster almus	Brooding	Fisher, 1917
Luidia ciliaris	Same	Tattersall and Sheppard, 1934
L. clathrata	Same	Dehn, 1979
L. foliolata	Planktotrophic larva	Strathmann, 1971
L. sarsi	Same	Tattersall and Sheppard, 1934
Luidia savignyi	Same	Mortensen, 1938
Lysasterias belgicae	Brooding	Ludwig, 1903
Trophodiscus almus	Brooding	D'yakonov, 1950
T. uber	Same	D'yakonov, 1950
	ORDER VALVATIDA	
Mediaster aequalis	Lecithotrophic larva	Birkeland *et al.*, 1971
Pentaceraster mammillatus	Planktotrophic larva	Mortensen, 1937
Porania pulvillus	Same	Gemmill, 1915
Acanthaster brevispinus	Planktotrophic larva	Lucas amd Jones, 1978
A. planci	Same	Henderson and Lucas, 1971
Asterina batheri	Pecithotrophic larva	Kano and Komatsu, 1978
A. calcar	Same	Lawson-Kerr and Anderson, 1978
A. coronata japonica	Same	Komatsu 1975
A. exigua	Same	Lawson-Kerr and Anderson, 1978
A. gibbosa	Lecithotrophic larva	Ludwig, 1882
A. minor	Same	Komatsu *et al.* 1978
Echinaster purpureus	Same	Mortensen, 1938
E. sentus	Same	Siddall, 1979
E. sepositus	Same	Nachtsheim, 1914
Fromia ghardaquana	Same	Mortensen, 1938
Linckia multifora	Planktotrophic larva	Mortensen, 1938
Ophidiaster guildingii	Planktotrophic larva	Mortensen, 1921
Patiria miniata	Planktotrophic larva	Heath, 1917
P. pectinifera	Same	Kasyanov, 1977
Patiriella obscura	Lecithotrophic larva	Dartnall, 1971
P. pseudoexigua	Same	Lawson-Kerr and Anderson, 1978
P. regularis	Planktotrophic larva	Lawson-Kerr and Anderson, 1978
P. vivipara	Brooding	Dartnall, 1971
Gymnasteria carinifera	Planktotrophic larva	Mortensen, 1921

ORDER VELATIDA		
Crossaster papposus	Lecithotrophic larva	Gemmill, 1920
Pteraster militaris	Same	Kaufmna, 1968
P. obscurus	Same	D'yakonov, 1950
P. tesselatus	Same	Chia, 1966
Hymenaster cannasus	Same	Fisher, 1940*
H. membranaceus	Same	Pain *et al.*, 1952
solaster endeca	Lecithotrophic larva	Gemmill, 1912
ORDER SPINULOSIDA		
Echinaster echinophorus	Lecithotrophic larva	Atwood, 1973
Henricia sanguinolenta	Same	Gemmill, 1916
H. abissicola	Same	Lonning, 1916
H. oculata	Same	Brun, 1978
H. hayashi	Same	Gaginskaya *et al.*, 1983
Othilia echinophora	Same	Hyman, 1955
O. senta	Same	Hyman, 1955
ORDER FORCIPULATIDA		
Anasterias antarctica	Brooding	Hyman, 1955
A. studeri	Same	Hyman, 1955
Aphelasterias japonica	Planktotrophic larva	Dautav, 1979
Asterias amurensis	Same	Dautov and Kasyanov, 1981
A. forbesi	Same	Mead,1901
A. lincki	Lecithotrophic larva	Falk-Peterson and Sargent, 1982
A. pallida	Same	Goto, 1896
A rubens	Same	Gemmill, 1914
A. vulgaris	Same	Field, 1892
Coscinasterias calamaria	Same	Barker, 1944
Distolasterias nipon	Same	Dautov (personal communication)
Cryptasterias turqueti	Brooding	Hyman, 1955
Diplasterias brandti	Same	Hyman, 1955
D. brucei	Same	Hyman, 1955
D. meridionalis	Same	Hyman, 1955
D. octoradiata	Same	Hyman, 1955
Evasterias troscheli	Lecithotrophic larva	Mortensen, 1921
E. retifera	Same	D'yakonov, 1950
Leptasterias arctica	Brooding	Fischer, 1930
L. groenlandica	Same	D'yakonov, 1950
L. hexactis	Lecithotrophic larva	Osterud, 1918
L. mulleri	Same	Ludwig, 1900
L. polaris	Same	Emerson, 1977
Marthasterias glacialis	Planktotrophic larva	Gemmill, 1916
Orthasterias leptolena	Same	Mortensen, 1921
Pisaster ochraceus	Same	Mortensen, 1921
Pycnopodia helianthoides	Same	Greer, 1962
Stichaster australis	Same	Barker, 1977
S. roseus	Lecithotrophic larva	Gemmill, 1916

2. Relative length of preoral part of larva. This part is usually less or almost equal in length to the postoral part. Exceptions are the bipinnariae of the family Luidiidae in which, as a result of growth of the medioventral and mediodorsal processes, the preoral part is longer than the postoral.
3. Relative length and movability of paired processes of bipinnaria. In bipinnariae of the families Astropectinidae, Gymnasteriidae, and Asterinidae, the processes are relatively short and less movable. In bipinnariae of the family Asteriidae and some species of the family Luidiidae, they are longer and capable of greater movement.
4. Relative length and movability of brachiolar arms. In brachiolariae of the families Gymnasteriidae, Asterinidae, and Acanthasteridae, the brachiolar arms are relatively short and less movable than in brachiolariae of the family Asteriidae.

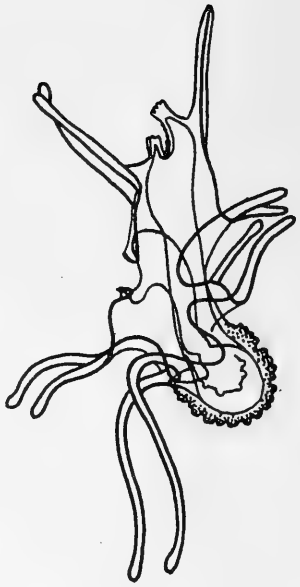


Figure 87: Brachiolaria of *Asterias rubens* (Gemmill, 1914)

5. Degree of development of unpaired brachiolar arms. In brachiolariae of the family Asteriidae, the middle brachiolar arm is similar in structure to the lateral ones. Two short lateral rows of small papillae occur on the ventral surface of the middle brachiolar arm near its base. In brachiolariae of the families Poraniidae, Asterinidae, Acanthasteridae, and some others, the middle brachiolar arm is a relatively less modified medioventral process, with two long rows of papillae on the ventral surface.
6. Color of larva and of its processes.

Identification of larvae before the late bipinnaria stage is difficult.

Key to Larvae Based on Late Bipinnaria Stage

In Peter the Great Bay sea stars belonging to five families of three orders have been found. In *Henricia* sp. (family Echinasteridae) and *Solester* sp. (family Solasteridae), development proceeds with lecithotrophic larva, and the bipinnaria stage is absent; only a modified nonfeeding brachiolaria stage occurs.

1 (4). Preoral part of larva shorter than, or almost equal in length to postoral part.
2 (3). Preoral part of larva shorter than postoral part. Processes short, less movable. Pigment absent on tips of processes. . . . . **Asterinidae**, Figures 70 and 74.
3 (2). Preoral part of larva shorter than, or almost equal in length to, postoral part. Processes long, movable, especially posterolateral and posterodorsal. Tips of processes orange. . . **Asteriidae**, Figures 76.
4 (1). Preoral part of larva longer than postoral part. . . . . **Luidiidae**, Figures 71 and 72.

Key to Planktotrophic Larvae Based on Brachiolaria Stage

In addition to the characters listed in the key above, new diagnostic characters are found in the brachiolaria stage.

1 (4). Brachiolaria stage present.
2 (3). Lateral brachiolar arms relatively short, less movable. Crown of papillae absent on middle brachiolar arms; papillae arranged in two rows on ventral surface. . . . . **Asterinidae**, Figure 80.
3 (2). Lateral brachiolar arms relatively longer, movable. Middle brachiolar arm with crown of papillae. . . . . .**Asteriidae**, Figure 87.
4 (1). Brachiolaria stage absent. . . . . **Luidiidae**, Figure 71.

CHARACTERS OF LARVAE ACCORDING TO FAMILIES

Luidiidae

In some species the bipinnaria is giant in size — 15–30 mm in length. The preoral part of the larva is very long, and curved. Larval locomotion is powered in some species by beating of the cilia bordering long arms, in other species by contraction of the muscles in the preoral part. Branching of the paired arms may be observed. The bipinnaria stage with characteristic attachment organs is absent. Metamorphosis occurs in the planktonic period of life. The larval body is resorbed or discarded. In the latter case, it may exist independently in the plankton for over a month.

Luidia quinaria bispinosa Djakonov is found in Peter the Great Bay. The larva of *Luidia quinaria* von Martens has been described (Komatsu *et al.*, 1982).

Asterinidae

The bipinnaria is relatively small, up to 1,000 μm in length, the arms (especially the preoral and postoral) are short, less movable, and devoid of pigment. Locomotion is performed by beating of the ciliated band. The brachiolaria stage is present. The brachiolar arms are relatively short; the middle brachiolar arm has no papillary crown but has two lateral rows of papillae on the ventral surface. Metamorphosis begins in the planktonic stage and terminates in the attached stage. In species with lecithotrophic larvae the bipinnaria is absent and the brachiolaria is modified.

Patiria pectinifera (Müller and Troschel) is found in Peter the Great Bay and its larva has already been described (Mortensen, 1921; Kasyanov, 1977; Dautov and Kasyanov, 1981).

Asteriidae

The processes of the late bipinnaria are long, movable, and orange at the tips. Locomotion is mediated by the beating cilia of the ciliated band and flexion of the processes. The brachiolaria stage is present and the brachiolaria are 3–4 mm long. The brachiolar arms are relatively long and the middle brachiolar arm is identical in structure to the lateral ones. The brachiolariae of different species of the family Asteriidae can be distinguished by the disposition and number of papillae at the base of the attachment disk. Metamorphosis begins in the planktonic stage and ends in the attached stage. In species with lecithotrophic larvae, the bipinnaria is absent and the brachiolaria is modified.

The following species are found in Peter the Great Bay; *Lysastrosoma anthostricta* Fisher, larva not described; *Distolasterias nipon* (Döderlein), larva not described; *Lethasterias fusca* Djakonov, larva not described; *Aphelasterias japonica* Bell, larva not described; *Asterias amurensis* Lütkén, larva described (Kume and Dan, 1968; Dautov and Kasyanov, 1981); *Evasterias retifera tabulata* Djakonov, larva not described; and *Evasterias echinosoma* Fisher, larva not described.

PATIRIA PECTINIFERA (MÜLLER AND TROSCHEL)

(Asterinidae)

Egg

The eggs of the *Patiria* are yellow, 170 μm in diameter, and surrounded by vitelline and jellylike membranes. Cleavage is radial, with weakly expressed bilaterality, and somewhat asynchronous (see Figure 65). The stage of 4 – 16 blastomeres is attained 2 – 3 hr after fertilization at 18 – 22°C. A

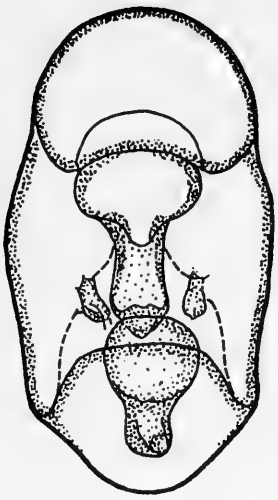


Figure 88: Bipinnaria of *Patiria pectinifera.*

typical coeloblastula forms with a unilayered blastoderm and an extensive blastocoel; rotating by means of cilia in its envelope, the coeloblastula then exists from it (see Figure 66). Gastrulation begins 16–20 hr after fertilization; it occurs by invagination accompanied by slight unipolar immigration of the mesenchymal cells. The gastrula is 250 μm × 200 μm in size. Coeloms grow faster than in larvae of the family Asteriidae. After a relatively short dipleurula stage, the larva becomes a bipinnaria.

Bipinnaria

The bipinnaria of *Patiria* is characterized by relatively undeveloped and less movable processes (Figure 68). Pigment is absent in the distal ends of the processes. The left and right axocoel grow forward and merge and the single axo-hydrocoel encompasses the oral cavity with

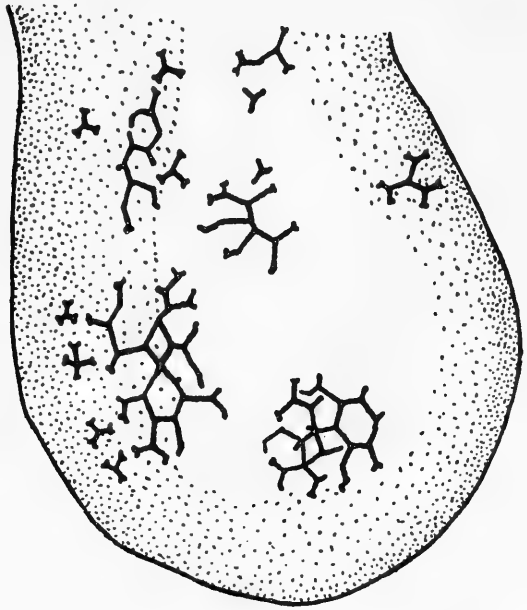


Figure 89: *Patiria pectinifera.*
Formation of definitive skeleton.

collar, extending ventrally to the midline of the stomach. The left and right somatocoels lie lateral to the stomach. The first plates of the definitive skeleton (Figure 89) begin to form in the middle and late bipinnaria. The early bipinnaria is formed by the 2nd – 3rd day of development and the completely formed late bipinnaria by 13th – 15th day at 14 – 16°C.

Brachiolaria

As in other asterinids, the brachiolaria of *Patiria* bears two lateral brachiolar arms with terminl papillae. The brachiolar arms are smaller in size than in the asteriid brachiolaria. The medioventral process performing the function of a third brachiolar arm is relatively larger than the lateral brachiolar arm, bearing two rows of small papillae (3 – 7 in each row) and one large papilla at the tip of the process. The other processes remain almost unaltered (Figure 90). The brachiolaria is about 700 μm long.

Ecology

Larvae of *Patiria pectinifera* are found in the plankton of Vostok Bay from the second half of July to September. *Patiria* spawns in Vostok Bay from the second half of July to early September (Kasyanov *et al.*, 1976, 1980). According to Novikova (1978), a second spawning is possible in November. In Sagami Bay (Pacific Coast of Japan), *Patiria* spawn from April to May (Kume and Dan, 1968).

ASTERIAS AMURENSIS LÜTKEN

(Asteriidae)

Asterias amurensis belongs to the order Forcipulaida. The development of most species of this order proceeds from a pelagic planktotrophic larva stage through subsequent metamorphosis. Most species of this order exhibit development with the pelagic larva stage followed by metamorphosis.

Egg

The eggs of *A. amurensis* are about 100 μm in diameter and colorless. Cleavage is radial, with some signs of bilaterality, and somewhat asynchronous. Division by cleavage results in a smooth blastula stage 14 – 16 hr after fertilization (at 19°C).

In the blastula stage, the embryo exists from the fertilization membrane and begins active swimming by means of cilia that uniformly cover the body surface.

Gastrulation occurs through invagination. During gastrulation the larva is stretched slightly along the animal-vegetal axis. At the end of gastrulation, rudiments of the left and right coelom form. The gastrula is 100 μm × 150

μm in size. The gastrula is flattened somewhat on the 3rd day and in the middle of the ventral surface of the larva an investigation appears that comes into contact with the bottom of the archenteron. At the site of this contact, a secondary mouth forms. In front of the mouth on the ventral side, an elevation forms, the preoral plate. The intestinal tract initially looks like a thin tubule, but later differentiates into sections. The blastopore, which becomes the anal opening, shifts to the ventral surface. At this stage the larva is called a dipleurula (Figure 91). It begins to feed. The dipleurula stage is very brief.

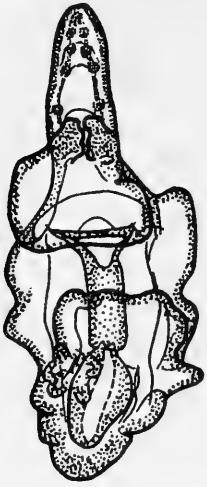


Figure 90 : Brachiolaria of *Patiria pectinifera.*

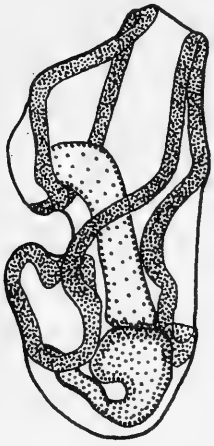


Figure 91: *Asterias amurensis.* Dipleurula; coelom rudiments visible.

Bipinnaria

The ciliated epithelium of the larva forms two ciliated bands. One of them, the preoral, borders the preoral plate. The second or postoral band proceeds posteriorly along both sides of the larva, passes onto the dorsal side, and extends anteriorly to terminate at the tip of the larval body. The cilia on the rest of the body surface either disappear or are very sparse. However, two other ciliated bands form, which are intimately associated with feeding. A preoral depression forms in the mouth region. The peristomal ciliated ring passes along the margin of the mouth, thereby separating it from the preoral depression. The adoral ciliated band originates from the peristomal ring, which passes with two branches deep into the esophagus and forms a loop there. The preoral depression extends laterally along both sides of the larva, bordered by ciliated bands. Thus the larval digestive apparatus is formed (Figure 92).

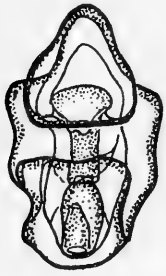


Figure 92: *Asterias amurensis.* Early bipinnaria.

By the 7th – 8th day of development the bipinnaria is about 350 μm long (Figure 93). The brachiolaria stage of *A. amurensis* has not been satisfactorily described. However, Kume and Dan (1968) present photographs of the late

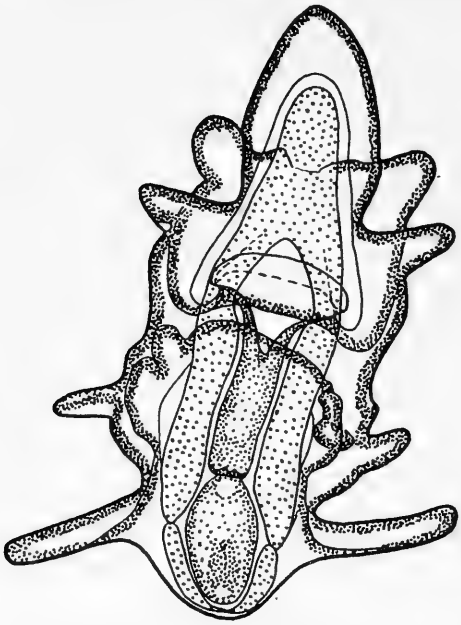


Figure 93: *Asterias amurensis.*
Late bipinnaria.

bipinnaria and brachiolaria of this sea star. Judging from these photographs, in *A. amurensis* the planktotrophic brachiolaria has three brachiolar arms, typical for the genus *Asterias*, long pigmented larval processes, and skeletal elements of the juvenile sea star in the posterior end of the body (Figure 94).

Information on the duration of larval development is lacking. The larval stage of a closely related species, *A. rubens*, extends for 8 – 9 weeks (Gemmill, 1914). One may tentatively estimate the duration of the pelagic stage of *A. amurensis* as 1.5 – 2.0 months; however, this requires verification.

Ecology

Larvae of *A. amurensis* are found in the plankton of Peter the Great Bay from the end of April to November (spawning twice a year; April – June and August – September at surface water temperatures of 12 – 16°C) Kasyanov *et al.*, 1976; Novikova, 1978).

Besides Peter the Great Bay, the spawning period of *A. amurensis* is known for some regions in Honshu: Tonkin Bay — January to June at 6 –

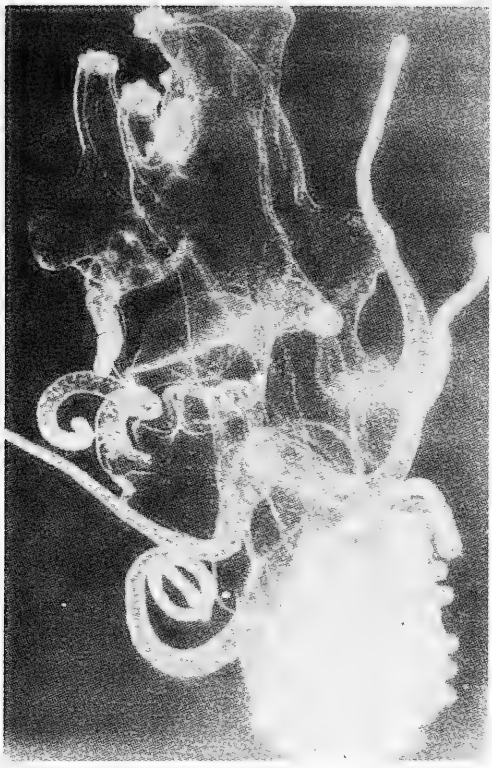


Figure 94: *Asterias amurensis*.
Brachiolaria; papillae and attachment disk visible.

14°C (Ino *et al.*, 1955) but according to other data, February to April at 14 – 15°C (Kume and Dan, 1968); Sendai Bay — January to May at 8 – 11°C (Hatanaka and Kosaka, 1958); Mutsu Bay — March to June at 5 – 10 °C (Kim, 1968); and the Pacific coast — June to October at 6–14°C (Kume and Dan, 1968).

It can be seen from these fragmentary data that *A. amurensis* spawns at a relatively wide temperature range (4 – 16°C); only seasons with very high and low temperatures are excluded. If our assumption regarding the duration of development of the larvae of this species is reliable, then the pelagic stage in *A. amurensis* is completed at relatively moderate temperatures, i.e. 5 – 20°C.

CHAPTER III

LARVAE OF SEA URCHINS (MORPHOLOGY, PHYSIOLOGY, AND BEHAVIOR)

EARLY DEVELOPMENT

Egg

The eggs of sea urchins usually do not exceed 80–100 μm in diameter. However, there are deviations from this range with diameters decreasing to 54–68 μm, as in *Stomopneustes variolaris* (Mortensen, 1931) and increasing up to 1,470 μm. In the yolk-rich floating eggs of the bathyal sea urchins *Araeosoma fenestratum* (Cameron *et al.*, 1987) and for the eggs of the brooding Antarctic sea urchin *Abatus nimrodi* (McClintock and Pearse, 1986). Two species, e.g. *Prionocidaris baculosa* (Mortensen, 1938) and *Echinostrephus molaris* (Onoda, 1936) may be mentioned in which the diameter of the egg is 150 μm. Eggs are still larger in *Peronella japonica* — 300 μm (Mortensen, 1921; Okazaki and Dan, 1954) and *Heliocidaris erythrogramma* — 500 μm (Mortensen, 1921). Egg size is not a distinguishing species characteristic. According to Hagström and Lonning (1961), egg size may differ among individuals of the same population as also in the same individual.

Yolky large-sized eggs are less transparent than small eggs and are more intensely colored. Situated mostly in the cortical layer, the pigment granules containing echinochrome impart an orange color to the eggs of *Hemicentrotus pulcherrimus* and *Asthenosoma ijimai*, yellowish-brown to the eggs of *Echinostrephus molaris*, green to the eggs of *Heliocidaris crassispina*, chocolate-brown to the eggs of *Temnopleurus hardwicki*, and red to the eggs of *Arbacia punctulata*. In the eggs of *Paracentrotus lividus* from some habitats, the reddish pigment forms a ring below the equator (Selenka, 1883; Boveri, 1901).

Ovulation and shedding of eggs in water occur upon completion of the

maturation divisions. Among echinoderms, the shedding of eggs which have completed meiosis is observed only in sea urchins and sea lilies.

Egg membrane : The unfertilized egg of sea urchins is surrounded by a vitelline membrane adjoining the plasma membrane and a jellylike membrane. The jellylike membrane consists of sulfomucopolysaccharides secreted by the egg in the later stages of oogenesis. It usually has the same refractive index as water and cannot be seen without staining. Staining reveals the micropyle in the jellylike membrane, in which polar bodies can then be identified (Boveri, 1901; Lindahl, 1932; Harvey, 1956; Piatigorsky, 1975; Schmekel, 1975). In the sand dollars *Echinarachnius brevis* (Onada, 1938), *E. parma,* and *Scaphechinus mirabilis,* the jellylike membrane contains pigment cells (Chia and Atwood, 1982), has a fine fibrillar structure, and is clearly visible under a microscope. The thickness of this membrane is 20–60 μm.

Fertilization : As in most animals, contact of the spermatozoon with the mature egg produces an acrosomal reaction in the spermatozoon and a cortical reaction in the egg. It is generally believed that the spermatozoon can penetrate the egg at any point. At the site of sperm penetration, a fertilization cone is produced, which usually disappears in a few minutes. As a result of the release of the cortical granules of the egg in the space between the plasma membrane and the vitelline membrane, the latter separates from the egg and is transformed into the fertilization membrane. The content of cortical granules takes part in the formation of the fertilization membrane and the hyaline membrane, which is a thin transparent fibrillar structure, a few microns thick, that directly borders the plasma membrane of the zygote.

Cleavage : A definitive typical radial cleavage is observed in sea urchins (Figures 95–97). In *Paracentrotus lividus* (Boveri, 1901) the disposition of individual blastomeres is distinctly visible in the early stages of development. The first two divisions of the egg occur in a meridional direction, giving rise to four equal blastomeres. The third division is equatorial. After this, in *Paracentrotus lividus* four nonpigmented animal and four pigmented vegetal blastomeres are formed. Eventually, the animal blastomeres divide meridionally, giving rise to eight mesomeres, while the vegetal blastomeres divide longitudinally, giving rise to four pigmented macromeres and four nonpigmented vegetal micromeres. Mortensen (1938) observed that in *Prionocidaris baculosa* the fourth division occurs in the meridional plane in all the blastomeres, as a result of which two coronas of eight cells each are formed. In a large majority of sea urchins, cleavage proceeds according to that described by Boveri in *Paracentrotus lividus* and the 16-blastomere stage leads to formation of micro-, meso-, and macromeres. The fourth division is

often asynchronous, i.e., blastomeres of the vegetal quadrant divide a few minutes earlier than the blastomeres of the animal quadrant and form a brief 12-cell stage.

Thereafter, during the fifth division the mesomeres divide in the latitudinal plane and the macromeres in the meridional plane; the division of the micromeres proceeds with some delay in the latitudinal plane and the stage of 32 blastomeres is preceded by 20- and 28-blastomeres stages. After the sixth division, the order of disposition of the blastomeres and the synchrony of their division are disturbed; only the macromeres form two regular crowns.

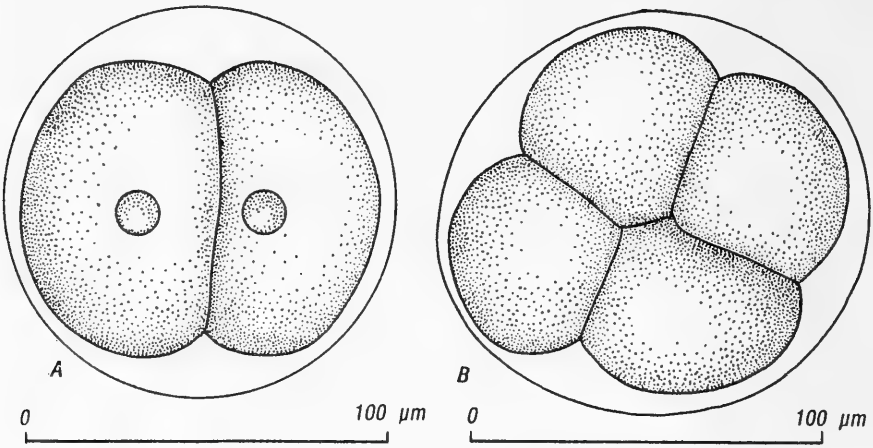


Figure 95: Beginning of cleavage in *Scaphechinus griseus*.
A—two blastomeres; B—four blastomeres.

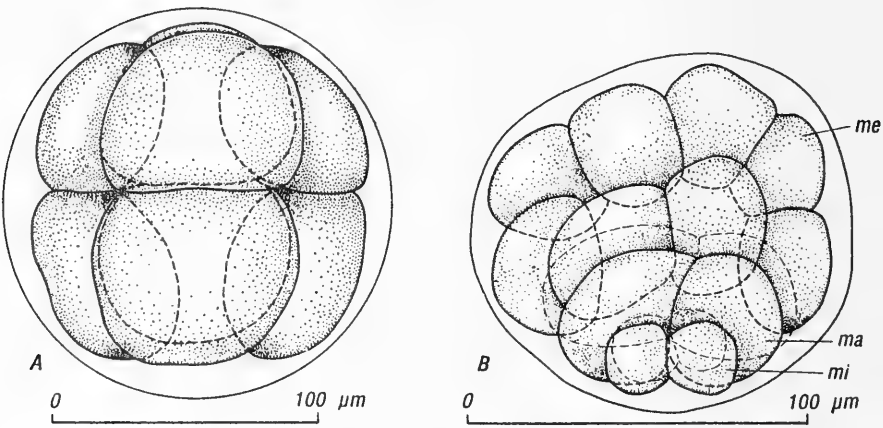


Figure 96: Early cleavage in *Strongylocentrotus intermedius*.
A— stage of 8 blastomeres; B—stage of 16 blastomeres; ma—macromere; me—mesomere; mi—micromere.

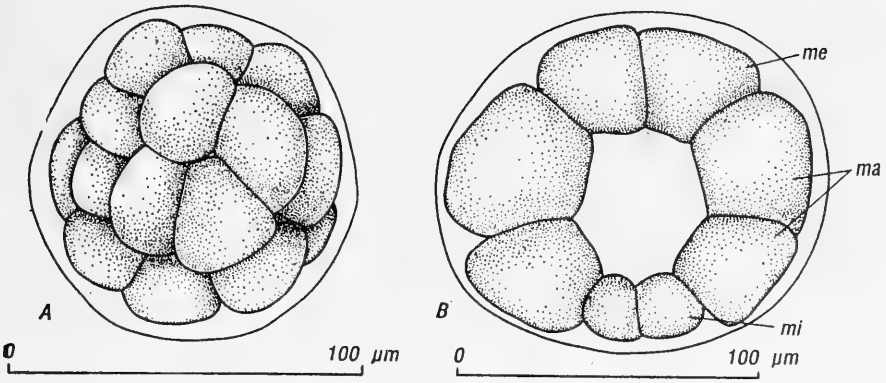


Figure 97: Stage of 32 blastomeres: view from the animal pole.
A—*Scaphechinus mirabilis*; B—*Strongylocentrotus intermedius* Optical section. Legend same as in Figure 96.

In subsequent divisions the differences in size of blastomeres gradually disappear (Selenka, 1880; Fewkes, 1893). In sea urchins with direct development, micromeres are not formed during division and the fourth division is uniform (Raff, 1986).

Blastula

In many species of sea urchins the blastula is formed on the first day of development. According to Onoda (1938), blastula of *Astriclypeus manni* hatches 4.5 hrs after fertilization. According to our data, in *Scaphechinus mirabilis* the blastula also leaves the membrane after 4.5 hrs. In urchins of the genus *Strongylocentrotus*, the blastula appears after 10 hrs in *S. nudus* and *S. intermedius* (Buznikov and Podmarev, 1975) and after 13 hrs in *S. pulcherrimus* (Onoda, 1936). The slowest blastula development occurs in *Scaphechinus griseus* (16 hrs) and *Echinocardium cordatum* (28 hrs), though for the latter species McBride (1918) has given a duration of 10 hrs.

Possibly, this is because he investigated the development of *E. cordatum* on the coast of Scotland, where the species spawns at much lower temperatures than in the Sea of Japan, where we conducted our observations. On the average, the development of sea urchins from fertilization to the blastula stage takes 5–8 hrs (Onoda, 1931, 1938; Aiyar, 1936). The blastula is spherical and possesses an extensive blastocoel (Figure 98). In most species, in the early blastula stage the contact between the blastomeres is relatively weak. Only in the apicolateral areas they are joined by desmosomes. Later, the blastomere contact strengthens and the wall of the blastula consists of densely arranged cells. The inner surface of these cells, facing the blastocoel, is lined with a thin 0.1 μm layer of protein and polysaccharide material, which had the function of the basal membrane (Okazaki, 1975). The

blastocoel contains mucopolysaccharides secreted by the blastomeres (Monne and Harde, 1951). Cilia form on the blastula before it leaves the membrane; each blastomere bears a single cilium. Some time after formation of cilia, the blastula is immobile; then the cilia begin to move and the blastula initially starts to rotate slowly inside the membrane. The blastula is capable of rotating both in a clockwise and an anticlockwise direction around the animal-vegetal axis. The direction of movement changes at brief halts (Fewkes, 1893). During rotation the blastula veers to the margin and begins to "rub" it. The blastula hatches after the 10th division due to the action of a hatching enzymes secreted by the blastomeres beginning from the 8th division. After hatching, the vegetal wall slightly flattens, and the region of the animal pole thickens and forms an apical organ with long immovable cilia (Selenka, 1880; Okazaki, 1975). The blastula swims with its animal pole forward while rotating around the animal-vegetal axis (Maruyama, 1981).

Thus, in sea urchins the embryo leaves the membrane in the blastula stage to commence its free-swimming mode of life.

Gastrula

Within a few hours after the blastula has hatched, the cells of the mesenchyme lose their cilia and begin to migrate from the region of the vegetal pole into the blastocoel; these cells later produce the spiculogenous syncytium. This is followed by gastrulation. Its mechanism in sea urchins has been described in detail by Gustafson (1963, 1964, 1975). In the course of gastrulation, the cells of the vegetal pole invaginate inside the blastocoel, to form

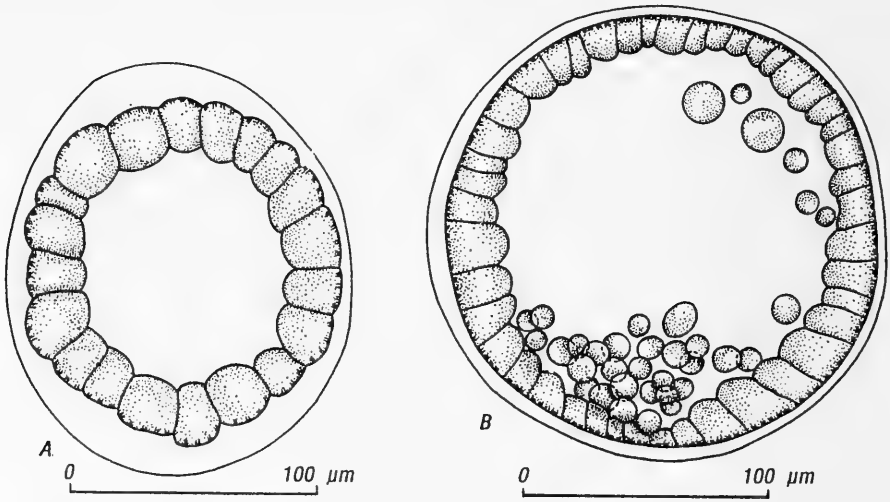


Figure 98: Blastula before leaving the membrane.
A—*Scaphechinus mirabilis*; B—*Strongylocentrotus nudus*.

the primary gut (archenteron) which in sea urchins is located at an angle to the animal-vegetal axis. At the place of the vegetal pole a blastopore forms (Figures 99, 100). The process of formation of an early gastrula in sea urchins proceeds at a variable rate. In the sand dollars *Echinarachnius parma* and *Scaphechinus mirabilis,* it takes just 8 hrs from the moment of hatching of the blastula, while a slow rate of development, 2 days, has been reported for *Echinus esculentus* (McBride, 1903). The late gastrula appears in *Echinarachnius* and *Scaphechinus mirabilis* 12 hrs after hatching of the blastula; a similar time has been reported for *Echinostrephus molaris* (Onoda, 1936). In other species of sea urchins the process of gastrulation is completed within 14–19 hrs (Onoda, 1931, 1936, 1938; Fenaux and Fenaux, 1974), in still others only after 23–32 hrs (Aiyar, 1936; Onoda, 1936, 1938; Kryuchkova, 1977).

After the formation of the archenteron, the cells of the primary mesenchyme begin to accumulate at two sides of its base. Soon one can distinguish a small calcareous granule in the center of each such cluster which gradually acquires the shape of a triradiate spicule. From this moment, the formation of the larval skeleton begins (Figure 100). The formation and growth of the skeletal rays were thoroughly studied by Okazaki (1960, 1963). Simultaneously with the formation of the calcareous granules, the coelomic sac separates from the upper end of the archenteron. This process is accompanied by the expulsion of the cells of the secondary mesenchyme (Gustafson and Wolpert, 1967). The coelomic sac soon divides into right and left parts. After this, in the region of the future esophagus an invagination forms, which gradually deepens and reaches up to the upper end of the archenteron, causing the walls of the archenteron and ectoderm of the esophagus to rupture, which leads to the formation of a through gut. From this moment the blastopore assumes the function of an anus. Soon the region of the vegetal pole of the gastrula flattens and the animal pole region inclines somewhat towards the future dorsal side (Figure 101). The larva, still entirely covered with cilia, acquires the shape of a prism. This process has been studied in detail by Onoda (1931) in *Heliocidaris crassispina.*

Prism Stage

Duration of this stage, corresponding to the dipleurula in sea stars, has seldom been observed.

Differentiation of the intestinal tube into the esophagus, stomach and small intestine occurs in the prism stage. As a result of contraction of the apical areas of the presumptive cells of the sphincters, two constrictions occur in the digestive tract, which become the cardiac and pyloric sphincters of the stomach (Burke and Chia, 1980). The regions forming the esophagus, stomach and small intestine do not differ in intensity of cell proliferation; the total

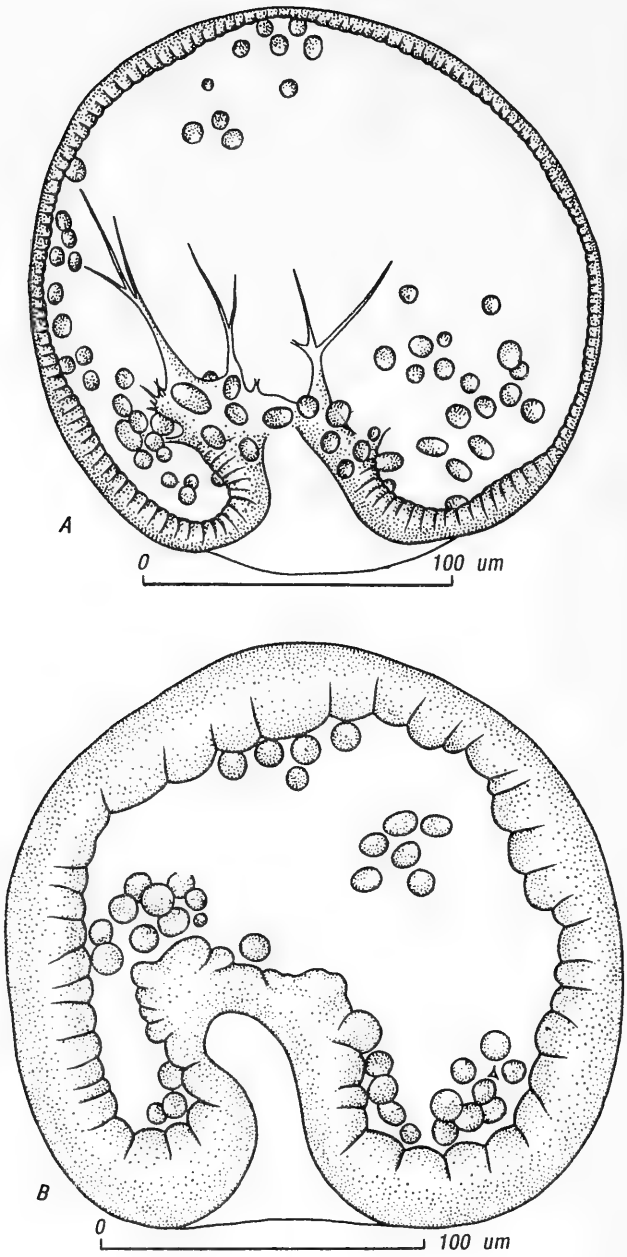


Figure 99: Early gastrula.
A—*Strongylocentrotus nudus;* B—*Scaphechinus mirabilis.*

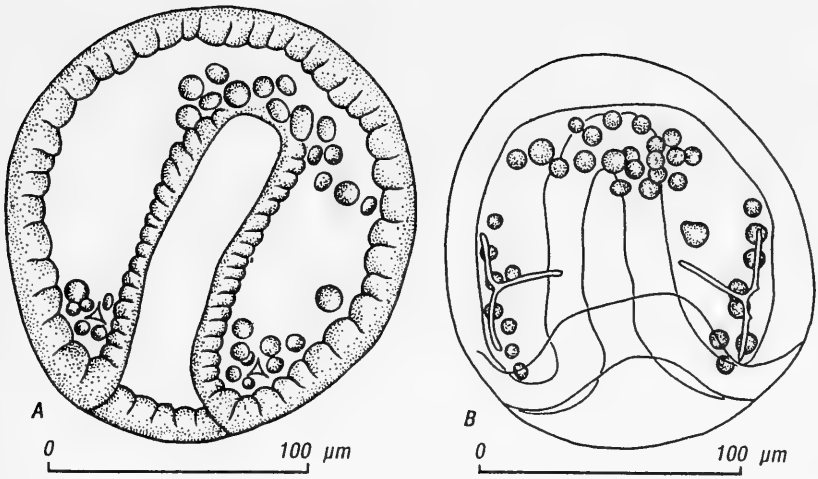


Figure 100: Midgastrula.
A—*Strongylocentrotus nudus;* B—*Scaphechinus mirabilis.*

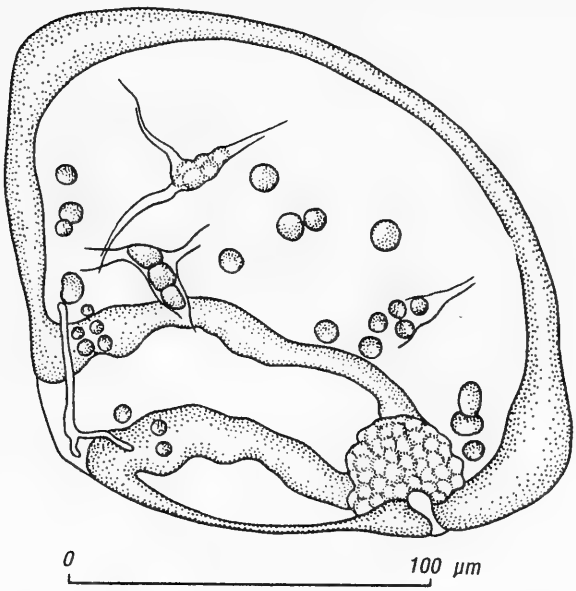


Figure 101: Flattening of the vegetal pole and inclination of the animal-vegetal axis of the larva in *Strongylocentrotus intermedius.*

number of cells of the digestive tract in the prism stage is about 100 (Burke, 1980).

On both sides of the larva, at the level of the esophagus, two tubercles form — the rudiments of the first pair of arms. The entire ciliary cover gradually reduces to a single ciliated band running along the margin of the preoral depression and the rudiments of the arms. The ectoderm under the ciliated band is thick and the cells of the ciliated epithelium are cylindrical.

The triradiate spicules formed in the gastrula stage now increase in size and each ray transforms into a rod of the larval skeleton (Figure 102). The coelomic sac enlarges somewhat but is still not differentiated. The rudiments of the arms gradually enlarge, and the larva acquires the shape typical of the early pluteus.

Pluteus I stage

In sand dollars, larval development up to the pluteus I stage proceeds rapidly, during only 20 hrs in *Astriclypeus manni* (Onoda, 1938) and 34 to 36 hrs in *Echinarachnius parma*, *Scaphechinus mirabilis* and *Scaphechinus griseus* (Kryuchkova, 1977). On an average, the pluteus I stage is attained by the 2nd–3rd day (McBride, 1914; Aiyar, 1936; Onoda, 1936, 1938). While inves-

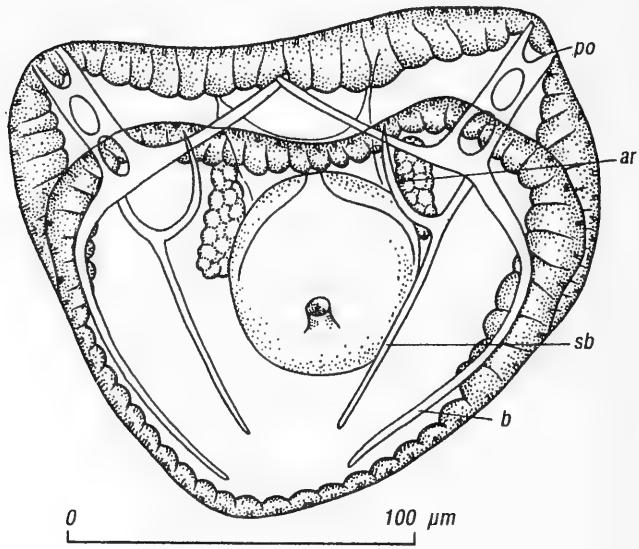


Figure 102: Prism stage in *Scaphechinus mirabilis*.
ar—anterolateral rods; b—basal rods; po—postoral rods; sb—secondary basal rods.

tigating the development of *Tripneustes gratilla* in Japan, Onoda (1936) established that the pluteus I stage formed by the fourth day. For this very species in the Mediterranean Sea, Fenaux and Fenaux (1974) found that at a temperature of 21°C the pluteus I stage develops within 40 hrs. The longest period of development required for attaining this stage, 8 days, was observed in *Heliocidaris crassispina* (Onoda, 1931). All the structures of the larva are formed in the pluteus I stage and simply grow in size in later stages.

Skeleton : The distinctive feature of the larvae of sea urchins is the larval skeleton, which provides support for the larva. The pluteus I stage has two pairs of arms — anterolateral and postoral. The anterolateral arms are almost parallel to each other and support the apical part of the pluteus — the oral lobe; the postoral arms diverge at an obtuse angle to each other. The anterolateral rods of the larval skeleton are always simple while the postoral ones in some species may be complex triradiate and perforated. The basal rods are situated at the base of the larval body, they often join to form complex structures. Sometimes, besides the principal basal rods, one or two pairs of secondary basal rods also develop. Above the stomach, from the base of the basal rod to the center of the larva, there may be an inner transverse rod. In heart urchins another unpaired aboral rod is seen (Figure 103). The skeleton structure is of systematic importance and many researchers are engaged in its study.

Feeding : Unlike larval sea stars, the body of sea urchin larvae is bordered by a single ciliated band. The length of the outer cilia is 25–30 μm. The width of the band is 3–5 cells and each cell contains one cilium. Few secretory cells are found only on the tips of the arms (Strathmann, 1971).

In the larvae of sea urchins the ciliated band between the anterolateral arms makes a ventral loop to the side of the transverse section of the postoral part of the general ciliated band (Figure 103). In the region of the peristome water currents are created by beating of the cilia of the ventral loop and the transverse part of the postoral band. Two currents are generated: an incurrent into the peristome and an excurrent from it. As in the larvae of sea stars, the region of the peristome in plutei bears cilia.

The mechanism of capture of food particles by cilia of the ciliated band and transport of these particles to the oral opening in planktotrophic larvae is common to all classes of sea urchins (see above). In echinoplutei the speed of movement of the food particles along the ciliated band is 0.5 mm/sec at 13°C. As soon as the food particles are trapped by the cilia, they are moved along the ciliated band to the peristomal field. In this region they move at a speed of almost 0.5–1.4 mm/sec. Cilia of the peristomal field transfer the food particles to the adoral band, which forms a loop that extends along the

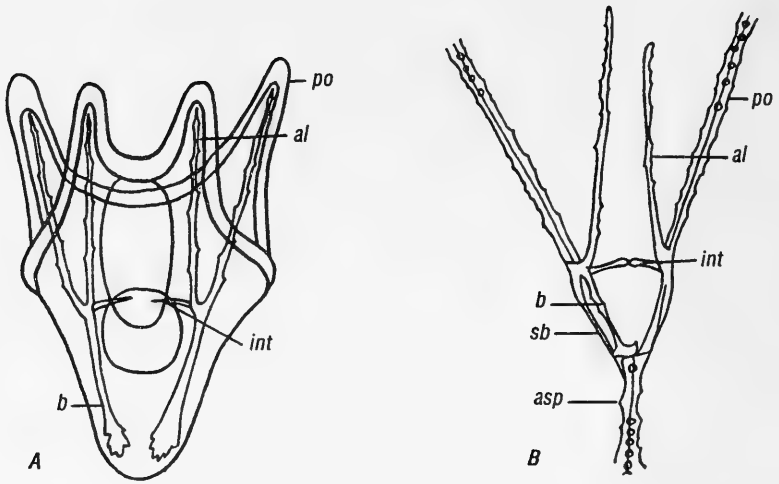


Figure 103: General appearance of the pluteus I stage.
A — *Strongylocentrotus pulcherrimus* (Onoda, 1936); B — *Spatangus purpureus* (Fenaux, 1972).
al — anterolateral rods; asp — aboral spicule; b — basal rods; int — inner transverse rods; po — postoral rods; sb — secondary basal rods.

ventral side of the esophagus. Cilia of the aboral band transport food particles into the oral opening, where they reach the esophagus.

To remove inedible food particles and, possibly, to ingest large particles, the oral opening in the echinopluteus I stage can be broadened through the action of a pair of special muscles — the posterior dilators. One end of these muscles is attached to the upper ventral part of the esophagus and the other end to the larval skeleton at the place of divergence of the anterolateral and inner transverse rods.

Numerous cilia line the esophagus and pass the food particles to its posterior part where they are stored until the circular esophageal muscles begin to contract and the cardiac sphincter opens up. The food mass enters the stomach where sorting takes place. Two types of cells have been observed in the stomach: cells secreting digestive enzymes and absorbing and sorting nutrients, and cells phagocytizing food particles as a whole (Burke, 1981). Experiments conducted by Strathmann (1971) have shown that when carmine and crystals of calcium carbonate together with algal culture reach the stomach, the algae remain in the stomach while the carmine and calcium carbonate pass through it unobstructed to the small intestine and are egested. The separation of particles is observed until they reach the lower part of the stomach. Clumps of algae circulate in the stomach for a long time. The time of passage for the food through the digestive tract is, on average, 30 min.

When the pyloric sphincter is opened, the food particles from the stomach enter the small intestine. Defecation is accompanied by a contraction of the intestine, which happens when the pyloric sphincter is closed and the anal sphincter is open (Figure 104). The larvae of sea urchins feed on various species of microalgae whose diameter does not exceed 85 μm, namely, species of *Amphidinium, Phaeodactylum, Dunaliella,* and others.

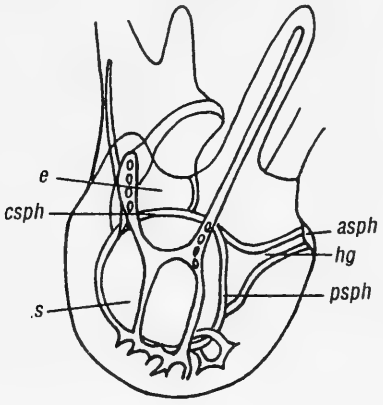


Figure 104: Division of the intestinal canal into sections in *Echinarachnius parma* (Fewkes, 1893).
asph — anal sphincter; csph — cardiac sphincter; e — esophagus; hg — hind gut; psph — pyloric sphincter; s — stomach.

Although phytoplankton is the main food of sea urchin larvae, the plutei of the heart urchin *Echinocardium cordatum* can obtain a large part of their daily ration from soluble organic matter even at its fairly low concentration in water (Vyshkvartsev and Sorokin, 1978). The pluteus of *Dendraster excentricus* stores nutrients in the cells of the stomach wall (Chia and Burke, 1978).

Respiration, transport of metabolites, and excretion: The larva has no special organs of respiration. Respiration is performed by the entire body surface. Hemal and excretory systems are also absent. Transport of nutrients within the larval body occurs through the primary and secondary body cavities. Excretion of metabolic products, after formation of the madreporic pore, apparently proceeds with the participation of coelomic sacs.

At this stage in the larvae of sea urchins, the coelomic sacs enlarge along the esophagus and divide into two: the anterior — axohydrocoel and the posterior — somatocoel. The left axohydrocoel broadens anteriorly, becomes thin-walled, and forms an ampulla in which the stone canal opens. The madreporic pore opens on the left side of the larva and connects the axohydrocoel with the external medium (McBride, 1903) — Figure 105.

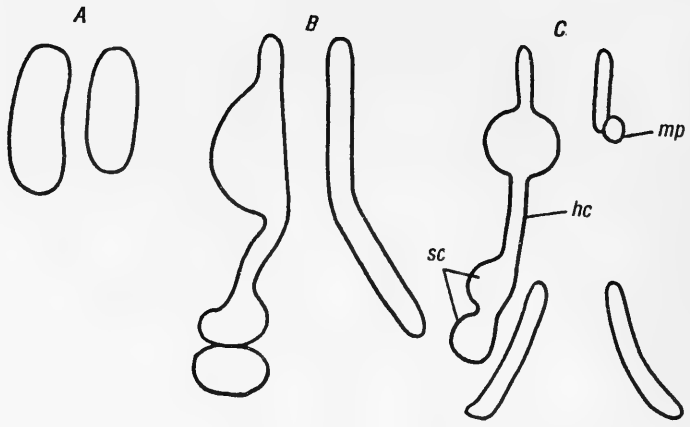


Figure 105: Scheme of development of coelomic sacs in *Echinus esculentus* (McBride, 1903).
A — prism stage; B — pluteus I stage; C — pluteus II stage.
hc — hydrocoel; mp — madreporic pore; sc — stone canal.

Locomotion : The ciliated band performs a locomotor function. At this stage, locomotion occurs along the anterolateral and postoral arms and the peristomal depression. When the larva moves, the cilia in some sections of the band remain erect while those in other areas bend to one side or the other. Thus, a wave is created which traverses the entire ciliated band. The larva can change the direction of its movement and turn; in this process a change in the direction of beating of the cilia occurs, which is preceded by a brief pause. The direction of water currents created by beating of the ciliated band is opposite to the direction of movement of the larva. When moving forward with the arms, the current is directed by the wave motion of sections of the band on the outside of the arms to the base of the larva. When the larva is motionless, beating of the right sections of the band is directed in the direction opposite to beating of the left sections of the band. When the larva turns, beating of the cilia is noticeable only on the outer side of the direction of turning. Movement of the pluteus in a reverse direction is accomplished by beating of the cilia of the ciliated band in a forward direction.

The speed of horizontal movement of the larvae of *Strongylocentrotus dreebachiensis, S. purpuratus,* and *Dendraster excentricus* is 0.3–0.5 mm/sec at 10–15°C (Strathmann, 1971; Strathmann *et al.*, 1972).

Nervous system and sense organs : The first mention of the presence of nervous elements in the larvae of sea urchins is found in the work of McBride (1903), who speaks of nerve fibrils situated above the adoral band. However, no information whatsoever on the structure of the larval nervous system was

available until histochemical methods and electron microscopy made identification of the nervous elements possible. Some works devoted to this problem have recently been published. Ryberg (1973, 1977) and Ryberg and Lundgren (1977) described the cells forming the ectodermal nerve network and the network surrounding the digestive tract as nerve cells of the sea urchin larvae. However, it later became clear that the ultrastructure of these cells nerve is different. The true nervous system of the larva is associated with the ciliated band and muscle elements. The nerve cells are situated along the ciliated band under which pass the axonal tracts — Figure 106 (Burke, 1978, 1983a, b). The nervous system of a pluteus develops from the cells of the animal place of the gastrula containing catecholamines (Burke, 1983a, b).

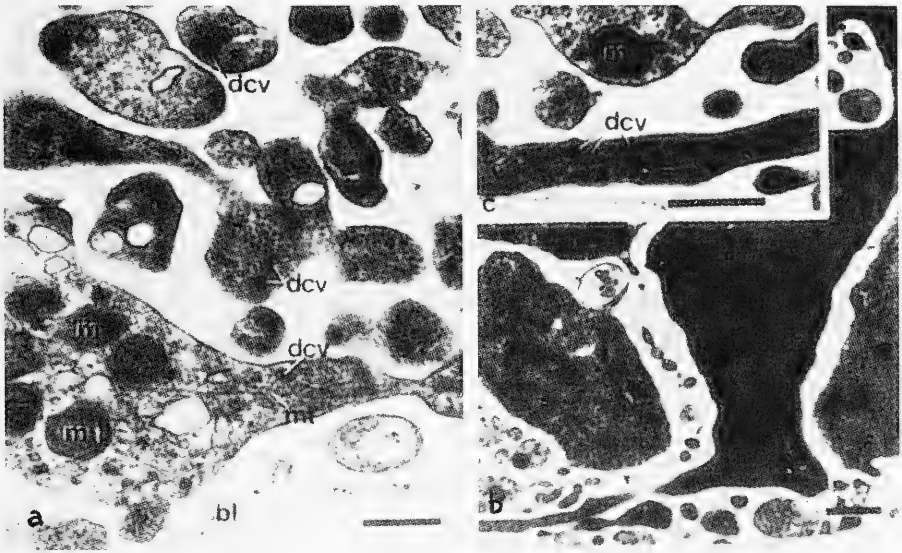


Figure 106: (a) axonlike projections of cells of the ciliated band of a 60-hr pluteus of *Dendraster excentricus*, Bar = 0.5 µm; (b) cells of the ciliated band of a 72-hr pluteus; arrow indicates an axonlike projection from the base of one cell, Bar - = 1 µm; (c) higher magnification of the axonlike process in (b), Bar = 0.5 µm.
bl — basal lamina; dcv — dense core vesicles; m — mitochondria; mt — microtubules (Burke, 1983).

Pluteus II Stage

The rate of development up to the pluteus II stage may differ significantly in various species. Thus *Astriclypeus manni* (Onoda, 1938) requires only 45 hrs to attain this stage from the moment of fertilization. The development of stage II in the sand dollars *Echinarachnius parma, Scaphechinus mirabilis*, and *Scaphechinus griseus* takes three to five days. *Echinarachnius*

brevis takes 15 days for this process (Onoda, 1938). McBride (1903) noted that sea urchins of the genus *Echinus* require 7–8 days to complete the pluteus II stage. A similar period is necessary for *Salmacius bicolor* (Aiyar, 1936). Fundamental changes in the skeleton of the larvae of sea urchins occur at this stage.

Skeleton : In addition to the anterolateral and postoral arms, posterodorsal arms, develop in the pluteus II stage on the dorsal side between the anterolateral and postoral arms. In some sea urchins the rods in the pairs of arms are simple but in others complex and fenestrated. The rudiment of the dorsal arch is situated at the level of the upper third of the stomach. In the heart urchins the ends of this arch elongate very quickly, providing the beginning for the rods of the preoral arms. These rods are simple in all sea urchins (Figure 107).

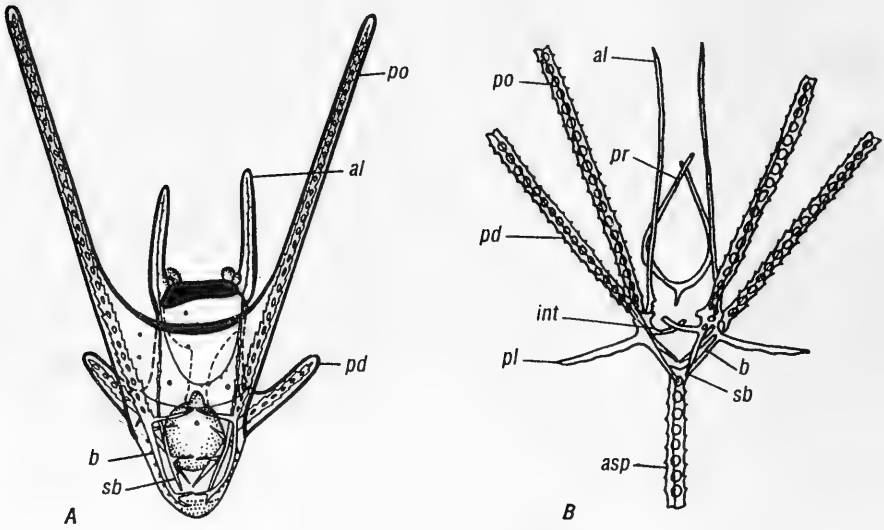


Figure 107: General view of pluteus II stage.
A —*Parasalenia gratiosa* (Onoda, 1938); B — *Echinocardium mediterraneum* (Fenaux, 1972).
al — anterolateral rods; asp — aboral spicule; b — basal rods; int — inner transverse rods; pd — posterodorsal rods; pl — posterolateral rods; po — postoral rods; pr — preoral rods; sb —secondary basal rods .

Respiration, transport of metabolites, and excretion : At this stage a further complication in the structure of the coelomics sacs occurs in the larvae. In particular, the left axohydrocoel divides into the axocoel and hydrocoel — rudiment of the ambulacral system of the definitive sea urchin (McBride, 1903).

Locomotion: With increase in the number of arms, the ciliated band elongates. After the complete development of the posterodorsal arms, the larva can spread the postoral and posterodorsal arms and thereby come to a stop. The arms are moved by muscles which appear at the site of joining of the postoral and posterodorsal rods with the basal rods. These muscle fibers were observed by McBride (1903) in larvae of the genus *Echinus*. Grave (1902) found muscle fibers in larvae of *Mellita testudinata* at the posterior end of the body, which were situated between the rods proceeding from here (Figure 108). On contraction, the postoral and posterodorsal arms diverge to the sides.

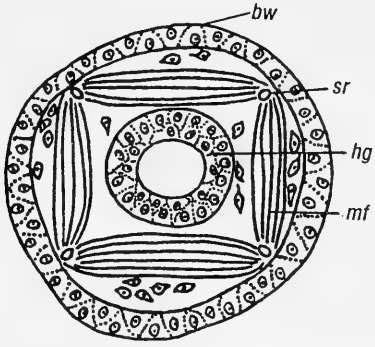


Figure 108: Arrangement of muscle fibers in the posterior end of the *Mellita testudinata* pluteus (Grave, 1902).
bw — body wall; hg — hind gut; mf — muscle fibers; sr — skeletal rods.

Nervous system and sensory organs: The nervous system remains unchanged. In some species, pigment granules which perform a photosensory function begin to accumulate in the cells at the tips of arms. According to Ryberg and Lundgren (1979), localization of the pigment cells can be observed in the regions of active morphogenetic processes. Histochemical methods revealed a carotene-protein complex in the pigment cells. The most common carotenoid in the sea urchins is echininon, which is similar in its function to the provitamin A. The pigment cells work as photoreceptors and play an important role in the vertical migration of larvae.

Pluteus III Stage

Complete development of the larvae of sea urchins, according to many investigators, requires different time spans. Larvae of the sand dollars *Astriclypeus manni* (Onoda, 1938), *Echinarachnius parma, Scaphechinus mirabilis,* and *Scaphechinus griseus* require only 5–7 days while *Echinarachinus brevis* needs 38 days (Onoda, 1938); completely developed larvae appear in sea urchins of the genus *Echinus* in 18–20 days (McBride,

1903). The average time requirement for attaining the pluteus III stage is 12–15 days from the commencement of development.

As in the previous stage, the maximum changes are observed in the larval skeleton and coelom.

Skeleton : In most species the basal part of the larval body is broadened; sometimes a transverse rod of very complex structure is situated here. A fourth pair of arms, the preoral, develops in which the rods are a continuation of the ends of the dorsal arch. These rods are always simple. In some heart urchins, anterior to the preoral arms on the dorsal side, another pair of arms, the anterodorsal, develops, whose rods initially arise as processes of the dorsal arch. These, like the preoral rods, are simple in shape. In other species yet another pair of arms, the posterolateral, emerges, whose rods originate from the upper ends of the arcuate rods serving as the base of the aboral rod (Figure 109).

Feeding : After the appearance of the preoral arms, the system of ciliated bands in the peristomial field becomes complicated. The ventral loop of the anterodorsal band no longer participates in filtration of feed particles from the water. It is replaced by a preoral transverse band. An adoral band likewise develops. The water currents created by these bands become complex.

Enlargement of the oral opening, priorly effected by the posterior dilater muscles, is now enhanced by a pair of anterior muscles, the dilaters, situated between the body wall in the region of the anterolateral arms and the preoral transverse band. The rods of the preoral arms pass through these muscles (Strathmann, 1971).

According to Burke (1981), at this stage in the pluteus of *Dendraster excentricus* the esophagus is surrounded by muscle fibers, which are circular in the upper part and longitudinal in the lower. The stomach sphincters consist of myoepithelial cells with transversely striated fibers. The stomach wall is lined with secretory cells and cells absorbing and storing nutrients. The intestinal wall is made of epithelial nonspecialized cells.

Respiration, transport of metabolites, and excretion : At this stage, the coelom of the right side remains unchanged. The left coelom enlarges, particularly the hydrocoel, in which five primary protuberances appear.

Respiration : The ciliated band enlarges with the increase in the number of arms. To support the larval body in water and to ensure locomotion at this stage, in some species additional ciliary fields develop — the epaulettes, which may comprise several pairs. Sometimes they are so closely disposed to one another that an additional annular ciliated band is formed (Figure 110). The length of the cilia on the epaulettes may vary in different species of sea

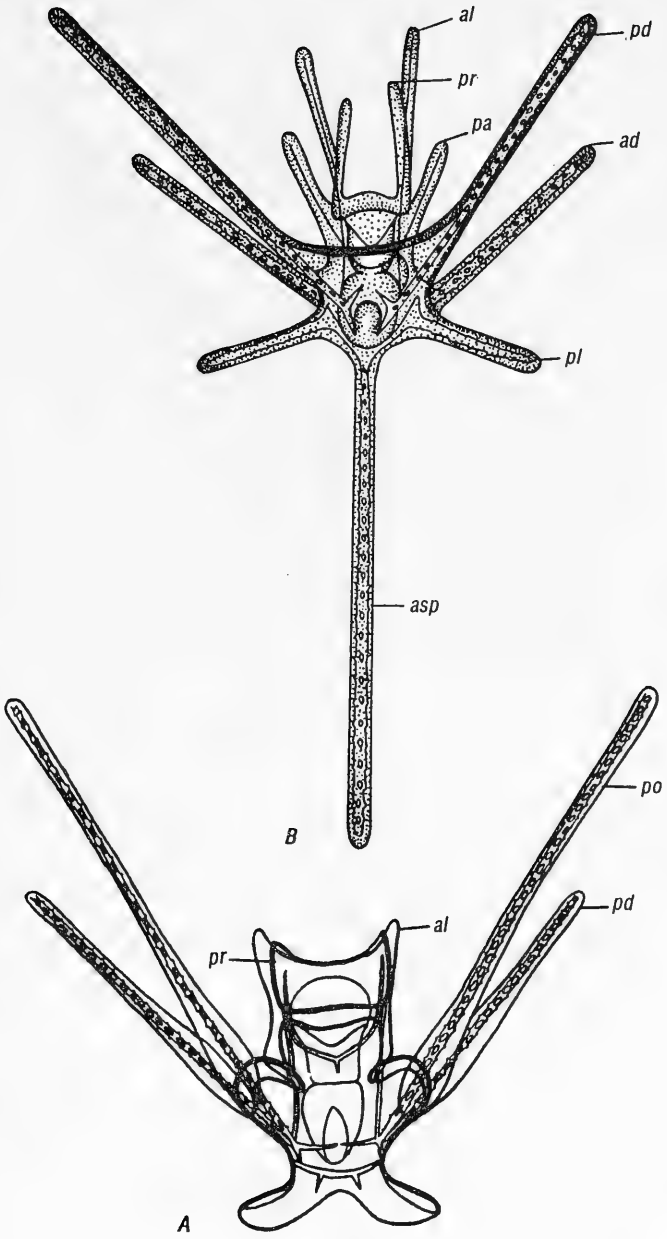


Figure 109: General view of the pluteus III stage.
A — *Prionocidaris baculosa* (Mortensen, 1938); B — *Lovenia elongata* (Mortensen, 1937).
ad — anterodorsal arm; al — anterolateral arm; asp — aboral spicule; pd — posterodorsal arm; pl — posterolateral arm; po — postoral arm; pr — preoral arm.

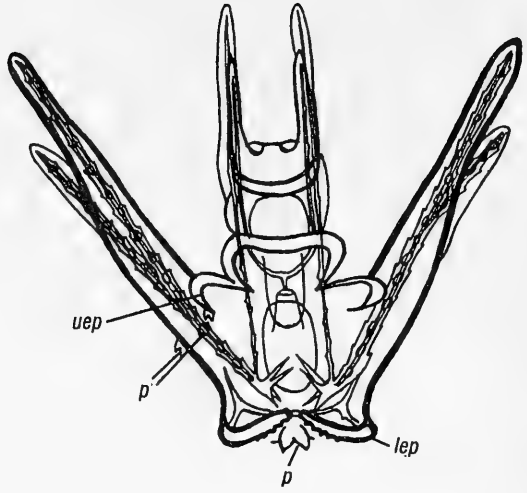


Figure 110: Epaulettes and pedicellaria in the pluteus of *Echinometra mathaei* (Onoda, 1936).
lep — lower epaulettes; p — pedicellaria; uep — upper epaulettes.

urchins; in Strongylocentrotids it is 35 μm. On the epaulettes, as also at the base of the ciliated band, beating of the cilia is undulatory (Strathmann, 1971). In other species, in place of the epaulettes between the postoral and posterodorsal arms, the integument and corresponding areas of the ciliated band become stretched and vibratile lobes are formed (Figure 111).

The beating wave of cilia on the epaulettes of strongylocentrotids and lobes of *Dendraster* is directed toward the median line of the larva. Such an unusual direction of beating possibly counteracts rotation of the larva, created by the beating of the ciliated band (Strathmann, 1971). Neither the cilia of the epaulettes and various lobes nor the cilia of the bands bordering the aboral rod of the pluteus of heart urchins participate in the seizure of food particles; they serve only for locomotion.

Nervous system and sense organs: The nervous system of the larvae remains unchanged. Pigmentation intensifies on the arms and new pigment centers appear. Especially intensive pigmentation is observed in the region of the stomach, coelom and amniotic sac; the latter appears at this stage (Figure 112).

Attachment apparatus: Settling, searching the substrate, and temporary attachment to it are ensured in the metamorphosing larvae of sea urchins by the five primary plates formed during metamorphosis at the base of the

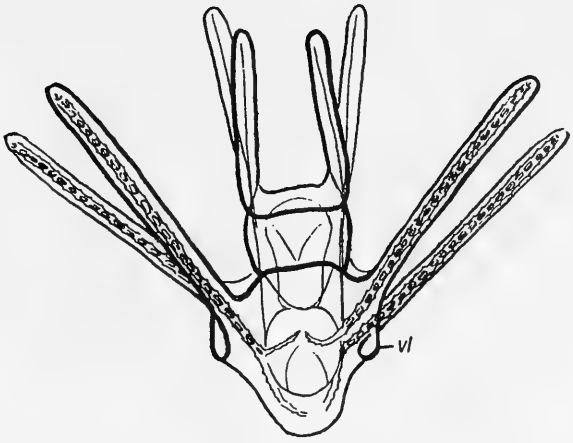


Figure 111: Vibratile lobe in the pluteus of *Laganum depressum* (Mortensen, 1938).
vl — vibratile lobe.

ambulacral system of the definitive urchin. Hence, the attachment apparatus and the act of settling are described at the end of the section on metamorphosis.

METAMORPHOSIS

As soon as the larva attains complete development, invagination of the ectoderm takes place from the left side between the postoral and posterodorsal rods. This invagination advances and acquires the shape of a small sac, which separates from the body wall. Its formation was reported earlier by Fewkes (1893), who called it the "Vasoperitoneal sac". McBride (1914) designated this structure the "amniotic sac". It grows and descends toward the stomach up to its contact with the left hydrocoel. A single complex is formed, which comprises the hydrocoel and two-layered wall of the amniotic sac. McBride (1914) noted that in *Echinocardium cordatum* the amniotic sac does not communicate with the external medium, whereas in larvae of the genus *Echinus* it forms a narrow canal opening externally. Aiyar (1936), based on McBride, indicated that in larvae of the genus *Echinus* the coelomic wall is always separated from the stomach by a space, while in *Salmacis bicolor*, whose development was investigated by Aiyar, the coelomic wall firmly adjoins the stomach.

Formation of the definitive juvenile occurs in the amniotic sac. This is accompanied by the disintegration of reorganization of larval structures.

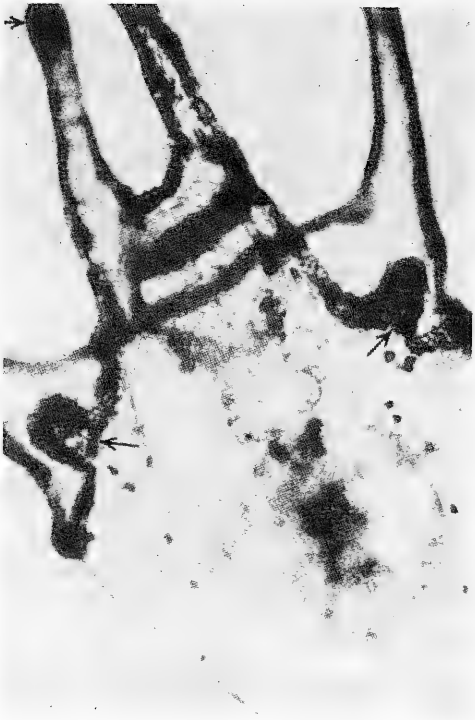


Figure 112: *Psammechinus miliaris* (Ryberg and Lundgren, 1979). Arrows show disposition of pigment cells in the pluteus.

Thickening of the floor of the amniotic sac constitutes the imaginal disk of organs of the oral half of the definitive urchin. As in sea stars, the oral-aboral axis of the definitive animal lies at an angle to the principal axis of the larva. Metamorphosis in sea urchins is markedly catastrophic in nature. Cidaroid sea urchins might be an exception to this rule (Emlet, 1988).

Skeleton : Development of the definitive test in the amniotic sac is accompanied by resorption of rods of the larval skeleton beginning, first of all, with rods supporting the larval body. The resorption of rods supporting the arms is observed only after the juvenile individual has settled on the substrate and moves rapidly for a few hours (Fewkes, 1893; McBride, 1903, 1914, 1918; Ubisch, 1913; Onoda, 1931; Aiyar, 1936).

During the development of the definitive test the coronal elements develop first, i.e., the interambulacral and ambulacral plates and spines. Formation of the oral and aboral sides terminates only after the juvenile individuals have settled on the substrate (Gordon, 1926a, b, 1928; Onoda, 1931; Kryuchkova, 1979a, b, c).

Formation of test in regular sea urchins (subclass Regularia): In *Strongylocentrotus nudus* and *Strongylocentrotus intermedius* the interambulacral plates and their spines appear first. Following the development of the first interambulacral plates, the twin rudiments of the first ambulacral plates appear (Figure 113). Then the ocular plates develop: four of them independent of the larval skeleton, with the first one around the fragment of the left posterodorsal rod. Development of the genital plates is associated more closely with the larval skeleton. As in *Arbacia pustulosa (= A. lixula), Strongylocentrotus lividus* (Ubisch, 1913), and *Heliocidaris crassispina* (Onoda, 1931), in *Strongylocentrotus nudus* genital plates 1, 4 and 5 are also modified from the plate constituting the base of the pedicellariae, which remain on the juvenile individual for some time after it settles. In *Strongylocentrotus intermedius* the plates that developed in the larvae III stage around the left posterodorsal and

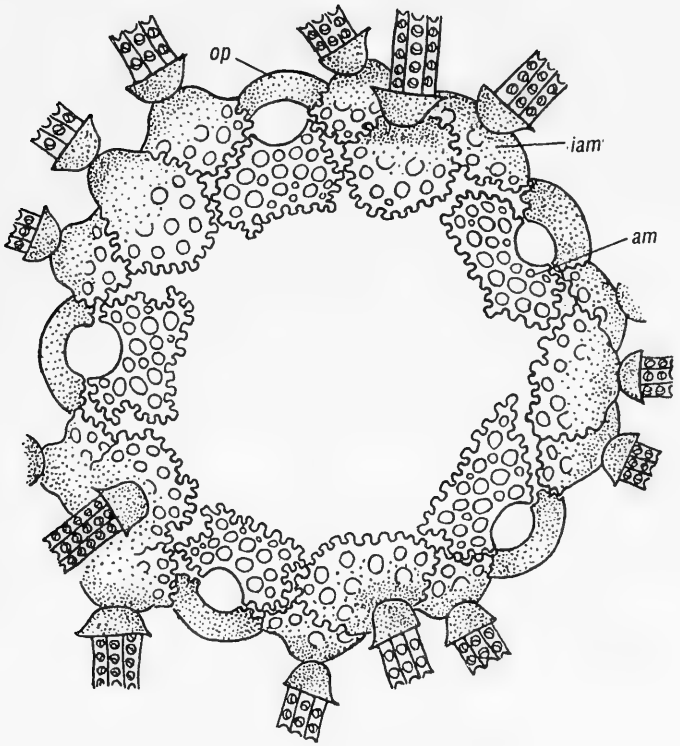


Figure 113: Arrangement of the ambulacral and interambulacral plates in *Strongylocentrotus intermedius*.

am — ambulacral plate; iam — interambulacral plate; op — ocular plate.

left postoral rods as well as the plate which appeared at the base of the larval body, are transformed into genital plates. In all regular urchins the madraporic or second genital plate forms around the appendage of the dorsal arch. Only one genital plate, the third, is not associated in its development with the larval skeleton (Figures 114 and 116).

As described above, in the larvae some species of regular urchins, at the place of connection of the rods supporting the arms and at the base of the larval body, growing pedicellariae are attached by their bases to the skeletal plates. These are complex capitate formations attached to the plate by a short stalk. The bulb is composed of three articulating blades with a dentate margin. The stalk is similar in structure to the rods of the juvenile individual and has a tetrahedral base (Figure 116). These pedicellàriae have a special system of muscles for opening the blades. On the surface of each blade sensory cells occur among the epithelial; each sensory cell bears one cilium surrounded by a ring of microvilli. In structure and function these pedicellariae are quite similar to those of the adult, although their development is completed in the larva much before the rapidly developing processes of metamorphosis. The larval pedicellariae, in all probability, perform a defensive function in the settling individual (Burke, 1980). The mesenchymal cells of the rudiment of the pedicellariae are differentiated into skeletogenic and myogenic cells. The ectodermal cells of the rudiment produce the covering epithelium of the pedicellariae, nerve, and sensory cells. The larval pedicellariae begin to function very early in the larva. During metamorphosis they are shifted to the aboral surface of the definitive individual. The plates, or future bases, as already mentioned, are transformed into genital plates. The juvenile spines present on the settling urchins perform a defensive and partly locomotor function, then later disappear (Ubisch, 1913).

The mouth apparatus and its skeleton form in regular urchins after the juvenile has settled.

Formation of test in the sand dollars (subclass Irregularia, order Clypeasteroida): In the development of *Echinarachnius parma* (Gordon, 1928; Kryuchkova, 1979a), *Scaphechinus mirabilis*, and *Scaphechinus griseus* (Kryuchkova, 1979a), the second and third interambulacral plates and their spines are the first to appear (Figure 117). Subsequently, the ambulacral plates develop. The ocular plates develop independent of the larval skeleton.

The genital plates, except for the second, that is, the madreporite, appear after settling and are not associated with the larval skeleton. The madreporite forms around the projection of the dorsal arch of the larva. Besides the five genital plates, two additional ones develop on the aboral side. These plates, like the genital ones, fuse to form the single complex madreporic plate of the adult (Figure 118).

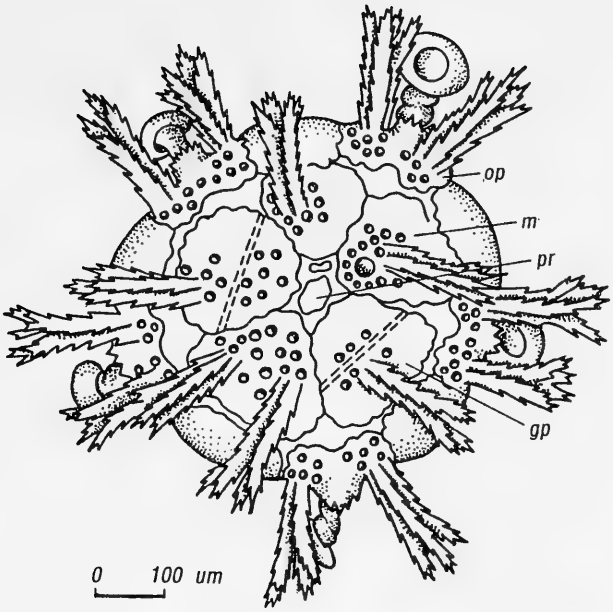


Figure 114: Aboral view of the young urchin *Strongylocentrotus intermedius*. gp — genital plate; m — madreporic plate; op — ocular plate; pr — periproct.

The skeleton of the oral apparatus (Aristotle's lantern) begins to form very early. Dental cones appear after the emergence of the first ambulacral plates. Rudiments of the alveoli and epiphyses appear before settling (Figure 119).

Formation of test in the heart urchins (subclass Irregularia, order Spatangoida): According to Gordon (1926a) and Kryuchkova (1979a), in *Echinocardium cordatum* during the development of the definitive test, interambulacral plates and their spines are the first to appear (Fig. 120).

The ocular plates are not associated with the larval skeleton. The third, first and fifth ocular plates appear before settling while the second and fourth plates appear after the juvenile individual settles.

Development of the genital plates is associated with the remains of the larval skeleton. The second plate, as in all urchins, develops around the process of the dorsal arch. The third, fifth and fourth plates appear around fragments of the left posterodorsal, left postoral, and aboral rods respectively. Only the first genital plate develops independent of the larval skeleton (Figure 121).

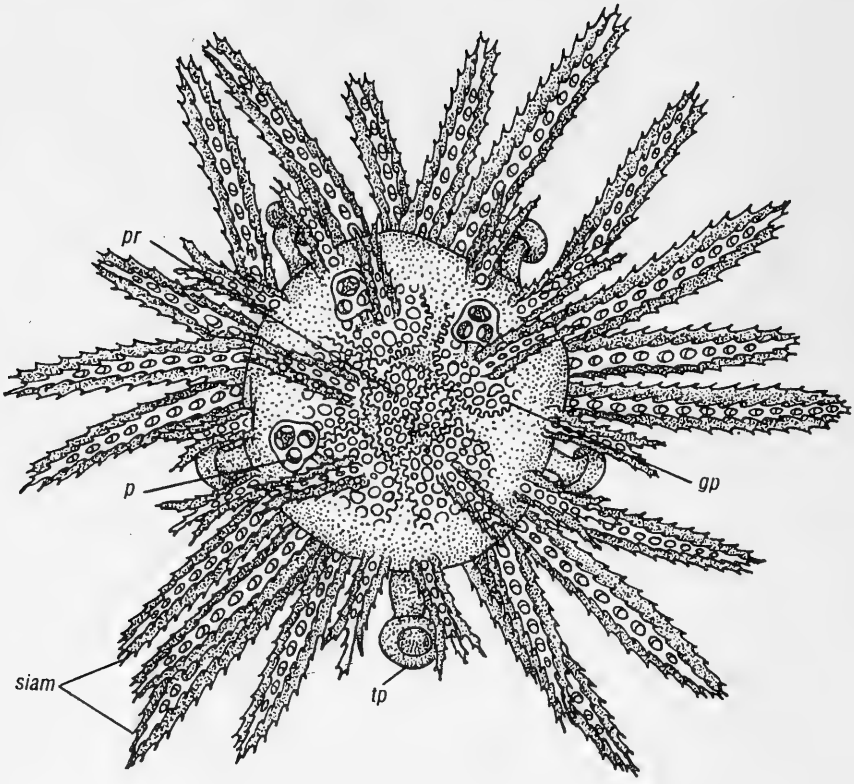


Figure 115: Aboral view of the young urchin *Strongylocentrotus nudus*.
gp — genital plate; p — pedicellaria; pr — periproct; tp — terminal podium; siam — spines of the interambulacral plates.

No rudiments of the oral apparatus are formed in heart urchins. The oral field is gradually furnished with plates. On the oral side there are five sphaeridia and five buccal podia.

Feeding: After metamorphosis the nature of urchin feeding changes sharply. Hence the trapping and digestive apparatuses are considerably restructured. The trapping apparatus of the larvae — the ciliated band — is completely destroyed. Cells of the ciliated band, like the cells of other regions of the larval epidermis, are dedifferentiated, disassociated from one another, and subsequently phagocytized by the cells of the larval digestive system (Chia and Burke, 1978). In the sea urchin *Lytechinus pictus* the larval arms bend, rudiment of the definitive individual makes contact with the surface, and the former lining of the amniotic sac surrounds the tissues adjoining the

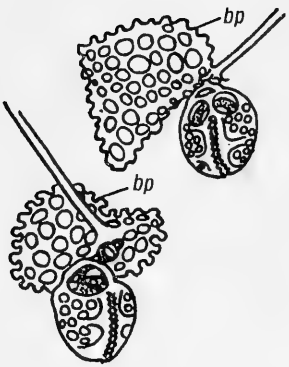


Figure 116: Structure of pedicellariae in the pluteus of *Strongylocentrotus nudus*.
bp — base of pedicellaria.

oral surface and forms the definitive epithelium (Cameron and Hinegardner, 1974, 1978). After metamorphosis, in most sea urchins the special oral apparatus functions to capture food; it is called Aristotle's lantern.

During the development of the definitive digestive system the larval mouth and anus close before settling, and the tissues of the larval digestive system are completely reorganized. The definitive esophagus consists of two parts; investigation of the floor of the amniotic sac (ectodermal part) and investigation of the stomach wall (endodermal part). The mouth initially opens in the epineural sac bound by the primary floor of the amnion below and the epineural fold above; the mouth opens outside, in *Salmacis bicolor* for example, 10–12 days after the juvenile urchin settles (Aiyar, 1936). The intestinal canal, earlier monolayered, now becomes multilayered. The stomach and a part of the intestinal canal become folded. The larval stomach transforms in the anterior

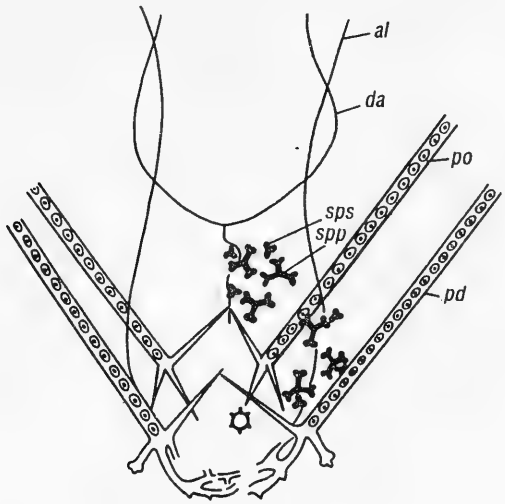


Figure 117: Diagram of disposition of spicules — the forerunners of interambulacral plates in the sand dollars.
al — anterolateral rod; da — dorsal arch; pd — posterodorsal rod; po — postoral rod; spp — spicule-forming plate; sps — spicule-forming spine.

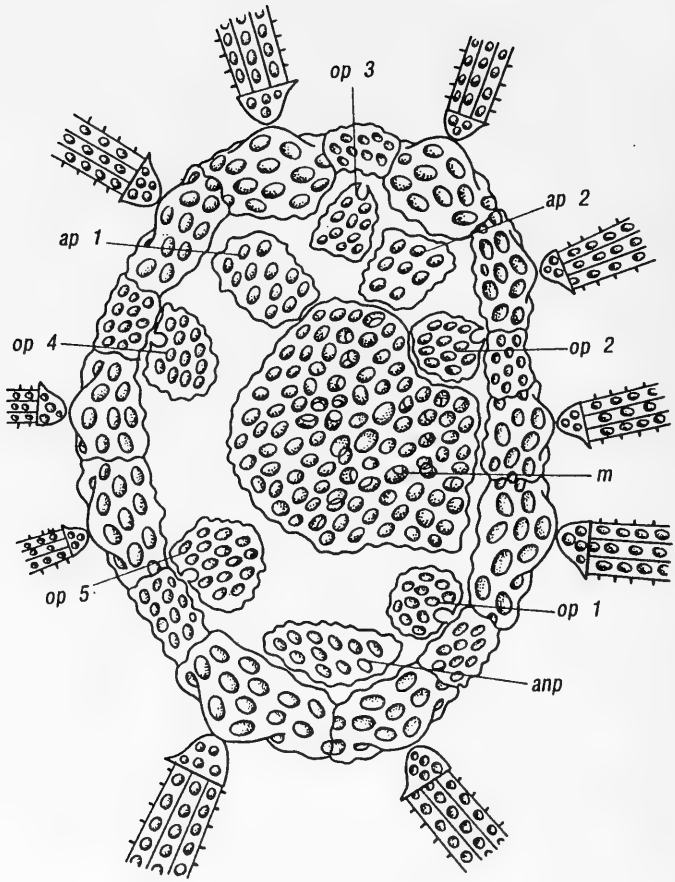


Figure 118: Aboral view of the sand dollar.
anp — anal plate; ap (1, 2) — additional plates; m — madreporite; op (1, 2, 3, 4, 5) — ocular plates.

section of the definitive intestine, describing a loop, and the larval intestine produces a counterloop in the definitive intestine. The definitive anus opens again (Figure 122).

As in sea stars, the function of *respiration* is passed on to the definitive epithelium and *transport* of metabolites to the hemal/perihemal systems and visceral coelom, while *excretion* of products is passed on to the coelomocytes.

Locomotion : One of the most important functions of the larval ciliated band is locomotion. During metamorphosis the ciliated band is replaced by a new — the embulacral — system, specialized for performing this function.

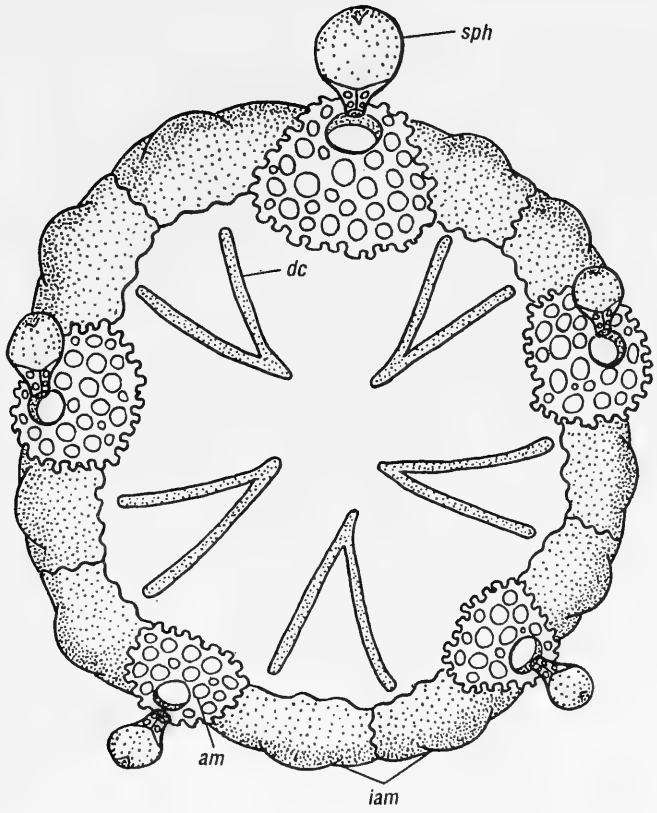


Figure 119: Arrangement of the first dental cones and sphaeridia in the sand dollar.
am — ambulacral plate; dc — dental cone; iam — interambulacral plate; sph — sphaeridium.

As in all echinoderms, the main rudiment from which it develops is the hydrocoel. Long before larval settling, the hydrocoel begins to form the first five processes that will become the radial canals of the ambulacral system of the adult urchin. After this, the hydrocoel bends and takes the shape of a ring, forming the ring canal of the ambulacral system (Figure 123). Soon the coelomic processes are seen to rest upon the bottom of the amniotic sac. In the opinion of McBride (1914), these processes in *Echinocardium cordatum* are rudiments of the radial canals of the future urchin. A similar picture was observed by Fewkes (1893) during the development of *Echinarachnius parma* by Aiyar (1936) for *Salmacis bicolor* (Figure 124), and by other investigators for various urchins. By the time of settling, or soon after it, the first ambulacral plates have formed. Aiyar (1936), while describing the metamorphosis

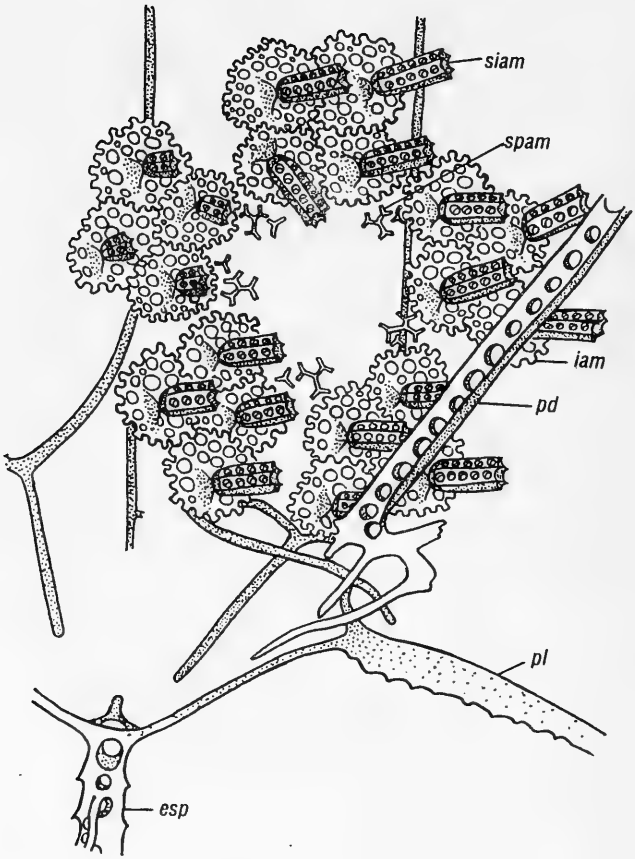


Figure 120: Arrangement of ambulacral and interambulacral plates in *Echinocardium cordatum*.
asp — aboral spicule; iam — interambulacral plate; pd — posterodorsal rod; pl — posterolateral rod; siam — spicules of the interambulacral plates; spam — spicules forming an ambulacral plates;.

of *Salmacis bicolor*, mentioned that epaulettes remained for some time after resorption of all the rods and continued to function even though the young urchin had already begun to move using the spines and podia.

Rudiments of the nervous and reproductive systems appear. Their further development, like that of the ambulacral system, occurs after settling.

Settling : During development of the juvenile in that period when larvae are still to be found in the plankton, five primary ambulacral podia develop in some urchins, which are usually much larger than the normal ambulacra

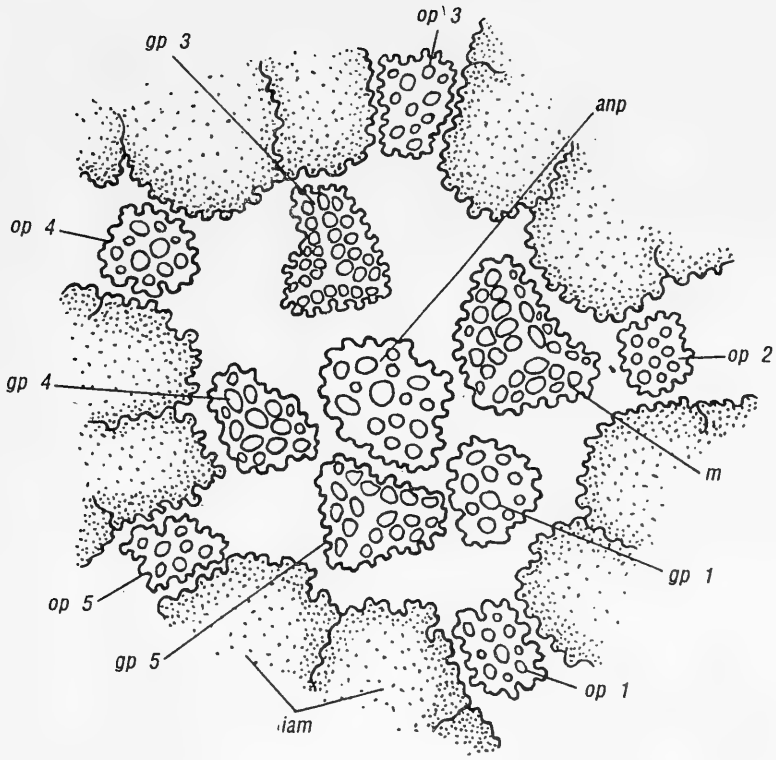


Figure 121: Aboral side of the young heart urchin *Echinocardium cordatum*.
anp — anal plate; gp (1, 3, 4, 5) — genital plates; iam — interambulacral plates; m — madreporite; op (1, 2, 3, 4, 5) — ocular plates.

(McBride, 1903; Ubisch, 1913; Onoda, 1931, 1936, 1938; Aiyar, 1936; Kryuchova, 1979b). Primary podia do not form in the sand dollars (Kryuchova, 1979b). McBride (1903) noted many years ago that after the primary podia had developed, the larvae of sea urchins of the genus *Echinus* begin to touch the container well with them as though seeking an attachment site in order to complete metamorphosis.

The larvae of the sea urchin *Strongylocentrotus purpuratus* settle mostly on coralline algae (Rowley, 1987). Cameron and Hinegardner (1974) identified the factors responsible for settling and demonstrated that for *Lytechinus pictus* and *Arbacia punctulata* one of the factors was the bacterial film formed on the walls of the containers holding larvae during metamorphosis. The larvae of sea urchins generally prefer the bacterial-algal film common in the sea as a substrate for settling (Chia *et al.*, 1984). *Parechinus angulosus*

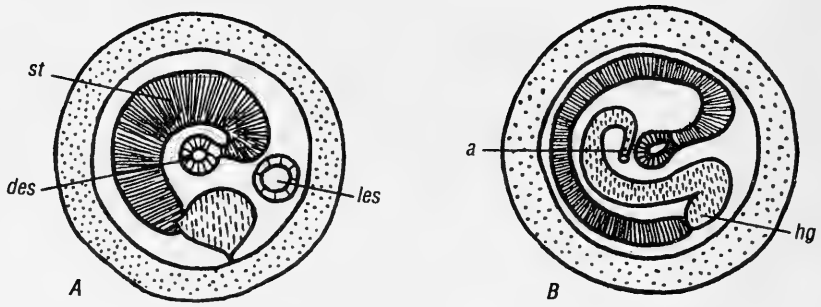


Figure 122: Development of the definitive digestive system in *Echinus esculentus* (McBride, 1903).
A — larva III stage; B — juvenile; a — anus, des — definitive esophagus; hg — hind gut; les — larval esophagus; st — stomach.

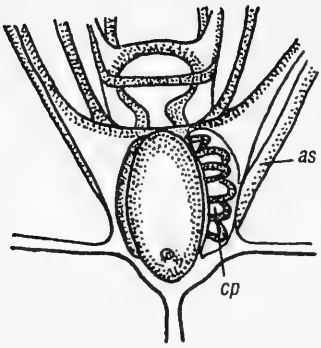


Figure 123: Formation of processes in the amniotic sac in *Echinocardium cordatum* (McBride, 1914).
as — amniotic sac; cp — coelomic processes.

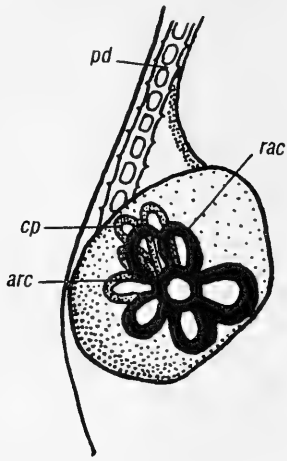


Figure 124: Formation of ambulacral ring canals and radial canals upon branching of hydrocoel in *Echinarachnius parma* (Fewkes, 1893).
arc — ambulacral ring canal; cp — coelomic processes; pd — posterodosal rod; rac — ambulacral radial canal.

requires the presence of shell fragments previously attached to the adult animals. Mortensen (1921) observed a delay in settling of the larvae of *Mellita sexiesperforata* in the absence of a sandy substrate. A peptide responsible for the metamorphosis of larvae has been isolated from the tissue ex-

tracts of the adult sea urchin *Dendraster excentricus* (Burke, 1984, 1986). Probably, this protein serves as the active agent at induction of metamorphosis in larvae using water from the aquarium in which the adult individuals are held; in nature, or using sand from natural habitats (Highsmith, 1982). Even before some of this corroborative data was available, Strathmann (1978) had concluded that the primary podia ought to perform the function of attachment and consequently possess secretory and sensory cells capable of receiving mechanical and chemical stimuli. In 1980, Burke investigated the morphology of the primary podia of urchins and demonstrated that sensory and secretory cells actually are present on the surface of the suction disks of the podia. Sensory cells occur over the entire surface of each disk and lie in groups of 3–5 cells along its margin. Apically, each cell bears a simple cilium. The basal ends of the sensory cells taper to the axonal process, which constitutes the subepithelial nerve plexus (Figure 125). Thus, the presence of sensory and secretory cells in the attachment of primary podia disks plays an important role in scouting the substrate, settling, and successful completion of metamorphosis of the urchin.

LECITHOTROPHIC LARVAE

Among the present-day "regular" sea urchins only a few species exhibit brood care. They are representatives of the order Cidaroida, including *Austrocidaris canaliculata* (Hyman, 1955), *Ctenocidaris nutrix*, and *Stereocidaris nutrix* (Baranova, 1968) from the Antarctic waters. They have special brood chambers — dermal outgrowths — situated in the buccal field or the periproct. The developed young is later transferred to the aboral side of the test where it remains for some time before undertaking independent existence. Besides cidaris, *Hyrsiechinus coronatus* (Mortensen, 1903) seems to be the only known regular urchin with brood care. The young in this species are transferred to the apical system of plates around the raised periproct.

In "irregular" urchins, the brood chambers are situated in the female petaloids. Such urchins, are *Fibularia nutriens* (Mortensen, 1948; Hyman, 1955) from the order Clypeasteroida (sand dollars), which have a small inflated test and are found in the Pacific. Among the heart urchins (order Spatangoida), there are also species in which the young develop in brood chambers. One such urchin, *Abatus (Hemiaster) cavernosus* (Meisenheimer, 1921; Kilias, 1969), occurs around Kerguelen Island in the Southern Indian Ocean.

The presence of brood chambers is usually observed in species living either in Antarctic waters or at great depths where the water temperature is low. Yet, in some sea urchins inhabiting waters of low temperatures, brood chambers are absent. This is observed in *Pourtalesia jeffreysi* (order

Spatangoida) living in the Atlantic Ocean and having an egg diameter of 3.2 mm (Thorson, 1936). On the other hand, sea urchins with large eggs and lecithotrophic larvae occur in the tropical zone of the Pacific Ocean. They belong to the following three orders: Echinothurioida — *Asthenosoma ijimai;* Cidaroida — *Heliocidaris erythrogramma*, and Clypeasteroida — *Peronella japonica*. The development of these three species has been fairly well studied.

In *Peronella japonica* (Mortensen, 1921; Okazaki and Dan, 1954) the egg diameter is 300 μm. Already in the late gastrula stage, invagination appears in its anterior end which enlarged to form the amniotic sac between the archenteron and ectoerm. In the pluteus the arms are sometimes not at all developed, but usually one pair of arms may be present. After 60 hrs, the amniotic sac in which development of the definitive individual takes place is everted and the young urchin begins to move on the substrate by means of the ambulacral podia. Remains of the larval body are retained for some time (Figure 126).

In *Heliocidaris erythrogramma* (Mortensen, 1921) the egg diameter is 500 μm. About 42 hrs after fertilization, the amniotic invagination appears, which remains open. It lies in the posterior part of the larva, is covered with cilia, and occupies three-fourths its circumference. On the fourth day of development, the oral disk of the definitive individual appears on the outer surface and the ends of the larval body bend to the aboral side. The developing young urchin feeds on the yolk present in the larval body. According to the data of Mortensen, the development of this urchin takes two days (Figure 127).

The largest eggs, 1.2 mm in diameter, have been described in *Asthenosoma ijimai* (Amemiya and Tsuchiya, 1979). The blastula hatches after 27 hrs. The gastrula is formed after 48 hrs. By the third day of development, the late gastrula has become flattened in a dorsoventral plane. After 4–5 days, two tubercles appear on the ventral side of the larva. At this stage, the larva remotely resembles the early bipinnaria of the sea stars. Four strongly reduced arms appear in the larva after five days, which are devoid of rods and differ in position from the arms in planktotrophic larvae (Figure 128). At this time, the rudiments of organs of the juvenile also appear but the amniotic sac does not develop. By the end of the fourth week, metamorphosis has been completed and the juvenile settles on the substrate (Figure 128).

IDENTIFICATION OF PELAGIC LARVAE OF SEA URCHINS (Terminology and Diagnostic Characters)

The larvae of sea urchins have an elongate body that may taper in the basal part. At the level of the esophagus, several pairs of processes are seen, the so-called arms. The characteristic feature of the larvae of sea urchins is the

Table 5: Type of development of sea urchins

Species	Type of development	Source
	Order Echinothurioida	
Asthenosoma ijimai	Lecithotrophic larva	Amemiya and Tsuchiya, 1979
	Order Cidaroida	
Aporocidaris milleri	Brood care	Mortensen, 1927; Hyman, 1955
Ctenocidaris nutrix	Same	Thomson, 1878; Hyman, 1955
Ctenocidaris spinosa	Same	Baranova, 1968; Koehler, 1926; Hyman, 1955
Ctenocidaris geliberti	Same	Mortensen, 1950; Hyman, 1955
Ctenocidaris perrieri	Same	Mortensen, 1950; Hyman, 1955
Austrocidaris canaliculata	Same	Thomson, 1878; Hyman, 1955
Goniocidaris umbraculum	Same	Mortensen, 1925; Hyman, 1955
Notocidaris gaussensis	Same	Mortensen, 1909; Hyman, 1955
Rhynchocidaris triplopora	Brood care	Mortensen, 1909; Hyman, 1955
Stereocidaris nutrix	Brood care	Baranova, 1968
	Order Echinoida	
Heliocidaris erythrogramma	Lecithotrophic larva	Hyman, 1955; Mortensen, 1921
	Order Temnopleuroida	
Hypsiechinus coronatus	Brood care	Mortensen, 1903; Hyman, 1955
	Order Clypeasteroida	
Fibularia nutriens	Brood care	Mortensen, 1948; Hyman,1955
Peronella japonica	Lecithotrophic larva	Mortensen, 1921; Okazaki and Dan, 1954
	Order Cassiduloida	
Anochanus sinensis	Brood care	Grube, 1868; Hyman, 1955
Tropholampas loveni	Same	Clark, 1923; Hyman, 1955
	Order Spatangoida	
Abatus cordatus	Brood care	Thomson, 1878; Hyman, 1955
Abatus cavernosus	Brood care	Meisenheimer, 1921; Kilias, 1969
Plexechinus nordenskjöldi	Same	Mortensen, 1950; Hyman, 1955
	Order Holasteroida	
Pourtalesia jeffreysi	Same	Thorson, 1936

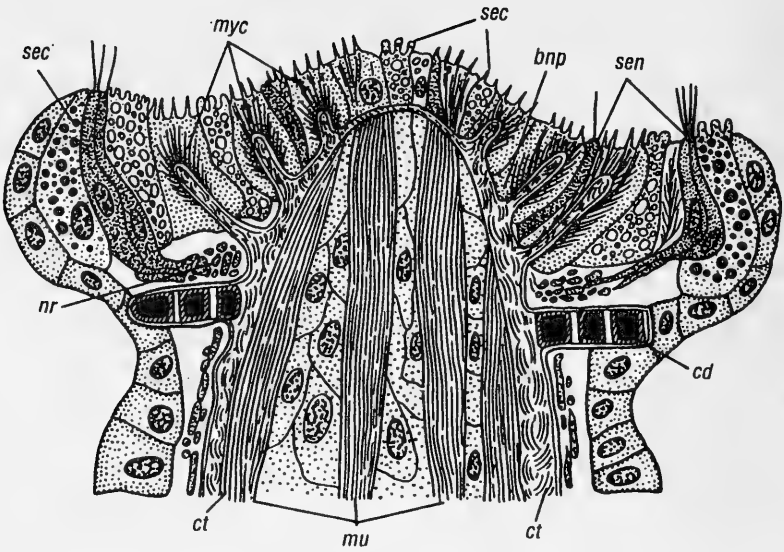


Figure 125: *Strongylocentrotus droebachiensis* (Burke, 1980). Sagittal section through the terminal podium of a juvenile.

bnp — basiepithelial nerve plexus; cd — calcified disk; ct — connective tissue; mu — muscle layer of the podium; myc — myoepithelial cells; nr — nerve ring; sec — secretory cells; sen — sensory cells.

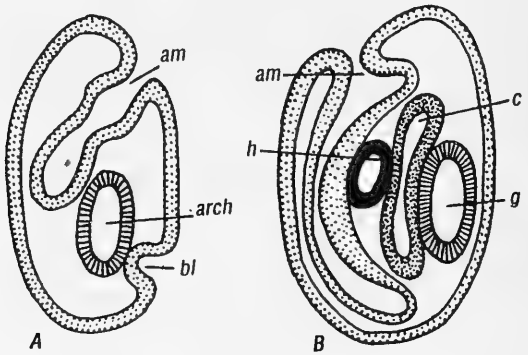


Figure 126: Sagittal section of the primordium of *Peronella japonica* (Okazaki and Dan, 1954).

A — early larva; B — late larva.

am — amniotic sac; arch — archenteron; bl — remains of blastopore; c — coelom; g — rudiment of gut; h — hydrocoel.

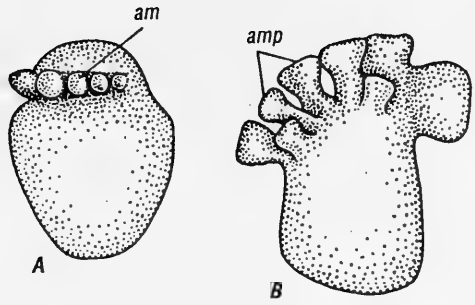


Figure 127: Development of primordium of *Heliocidaris erythrogramma* (Kaestner,* 1963).
A — early larva; B — late larva.
am — amniotic sac; amp — ambulacral podia.

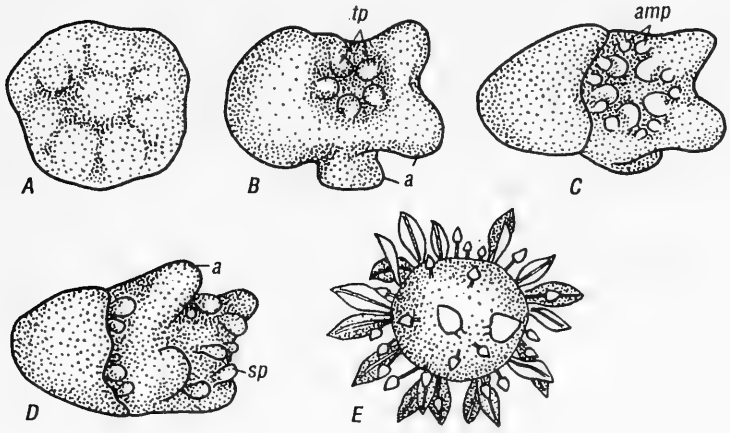


Figure 128: Development of *Asthenosoma ijimai* (Amemiya and Tsuchiya, 1979).
A — blastula; B — 4-day-old larva; C — 14-day-old larva; D — same, aboral view; E — juvenile.
a — arms; amp — ambulacral podia; sp — spine of interambulacral plates; tp — terminal podia.

presence of an endoskeleton consisting of rods, which differ in structure in different groups of these animals. These rods may fuse or simply be contiguous. Rods proceeding from the esophagus and descending to the edge of the body of the larva are called basal and usually comprise one pair. In addition to these rods, in some species of sea urchins there may be one or two more pairs extending parallel to the basal rods and often joining them. These are the secondary basal rods. From the basal as well as secondary basal rods, transverse rods are directed inward. These may be in two pairs, anterior and posterior, and both pairs may not be present simultaneously in every species.

The rods extend inside, and lend support to, the arms. Their number varies from species to species. Thus, in the regular urchins and sand dollars the fully formed larva has four pairs of arms, while the larva of heart urchins has six pairs. Moreover, in heart urchins the presence of an unpaired posterior rod is characteristic; equipped with complex perforations, it is termed the aboral rod.

Rods passing in direct proximity to the mouth of the larva from the dorsal side are termed the preoral rods. They are simple in all species of sea urchins. The rods situated behind the esophagus on the ventral side are called postoral, while those lying behind the preoral ones are known as the anterolateral. The anterolateral rods are always simple but the postoral ones are often complex, triradiate, and with numerous perforations. The structure of the postoral rods is of taxonomic significance.

The next pair of rods, the posterodorsal, is also rather frequently complex in structure; these rods are situated on the dorsal side and basally adjoin the base of the postoral rods. The structure of this pair of rods is likewise of taxanomic significance.

In heart urchins, in front of the preoral rods on the dorsal side, one more pair of rods develops. These rods are the anterodorsal pair and, like the preoral rods, they are simple in structure. Further, in some species of heart urchins yet another pair of rods, the posterolateral, may form, which diverge from the upper ends of the archlike rod.

The basal and secondary basal rods in the larvae of some groups of sea urchins are fused, and form in the basal part of the larva the so-called "basket structure".

In many species of sea urchins the pluteus III stage has one or several pedicellariae, also of taxonomic importance.

1. In sea urchins the number of arms in the larvae is a diagnostic character. In larvae of the order Spatangoida there are six pairs of arms in the pluteus III stage, while in those of the orders Camarodonta and Clypeasteroida there are four pairs.
2. Structure of the rods forming the skeleton: In species of the Superorder Camerodonta, found in the Sea of Japan, all the skeletal rods are simple. In species of the orders Clypeasteroida and Spatangoida both simple and complex perforated rods occur.
3. Presence of pedicellariaes in larvae: These are characteristic of the larvae of some species of the Superorder Camarodonta.
4. Presence of ciliated epaulettes or vibratile lobes: Ciliated epaulettes are found in larvae of the Superorder Camarodonta while vibratile lobes are found in larvae of the order Clypeasteroida.
5. Distribution and color of the pigment.

6. Formation of fenestrated plates in the larvae of later stages. Such plates are characteristic of larvae of the Superorder Camarodonta.
7. Length of larva: Measured from the body base to the arm tip in a perpendicular plane.
8. Angle of bending of the dorsal arch.

Key to Species Based on Larvae in the Pluteus Stage

1 (6). Aboral rod present. . . . . **Loveniidae**
2 (3). Two pairs of arms. . . . . **Echinocardium cordatum,** pluteus I stage (Figure 144).
3 (2). More than two pairs of arms.
4 (5). Three–four pairs of arms. Transverse rod present between the basal rods, above the aboral rod. . . . . **Echinocardium cordatum,** pluteus II stage (Figure 145).
5 (4). Five–six pairs of arms. Transverse rod absent between the basal rods, above the aboral rod. . . . . **Echinocardium cordatum,** pluteus III stage (Figure 146).
6 (1). Aboral rod absent.
7(18). All skeletal rods simple. . . . . **Strongylocentrotidae**
8(11). Two pairs of arms.
9(10). Basal rods which processes at the distal end. . . . . **Strongylocentrotus nudus,** pluteus I stage (Figure 129).
10 (9). Basal rods clavate, one with a spine, the other with a depression. . . . . **Strongylocentrotus intermedius,** pluteus I stage (Figure 132).
11 (8). More than two pairs of arms.
12(15). Three pairs of arms.
13(14). Secondary basal rods fused above the basal rods. . . . . **Strongylocentrotus nudus,** pluteus II stage (Figure 130).
14(13). Secondary basal rods are absent. Inner transverse rods present. . . . . **Strongylocentrotus intermedius,** pluteus II stage (Figure 138).
15(12). Four pairs of arms.
16(17). Three pedicellariae on the inner part of the arm rods; no fenestrated plates. . . . . **Strongylocentrotus nudus,** pluteus III stage (Figure 131).
17(16). Pedicellariae absent. Perforated plates on the inner part of the arm rods. . . . . .**Strongylocentrotus intermedius,** pluteus III stage (Figure 134).
18 (7). Skeletal rods simple and complex. . . . . **Echinarachniidae and Dendrasteridae.**
19(24). Two pairs of arms.

20(21). Basal and secondary basal rods form a basket. Single fenestrated plate present under the basket. . . . . **Echinarachinus parma,** pluteus I stage (Figure 135).

21(20). Basket different in shape.

22(23). Basal and secondary basal rods fused in pairs, forming two plates with numerous spines on the lower side. . . . . .**Scaphechinus mirabilis,** pluteus I stage (Figure 138).

23(22). Distal ends of the basal and secondary basal rods thickened, bearing numerous spines, but not fused . . . . . **Scaphechinus griseus,** pluteus I stage (Figure 141).

24(19). Three-four pairs of arms.

25(26). Basket height three-fourths basal width. Angle of bending of the dorsal arch 180°. . . . . .**Scaphechinus mirabilis,** pluteus II and III stages (Figures 139, 140).

26(25). Basket height greater than basal width. Angle of bending of the dorsal arch 120°.

27(28). Red pigment at ends of arms. . . . . **Echinarachnius parma,** pluteus II or III stage (Figures 136, 137).

28(27). Larva light green. . . . . . **Scaphechinus griseus,** pluteus II or III stage (Figures 142, 143).

CHARACTERS OF LARVAE ACCORDING TO FAMILIES

Strongylocentrotidae

The larva has four pairs of arms. All the skeletal rods are simple. The basal rods are clavate. In *S. nudus* and *S. franciscanus* the basal rods bear numerous spines at their ends, which interlock the rods. Secondary basal rods are also present but only in *S. nudus* and *S. franciscanus*. In the pluteus III stage the ends of the basal rods are reduced and the base of the larval body is broadened. Upper and lower epaulettes appear. In *S. nudus* and *S. franciscanus* pedicellariae are present.

Three species of the genus *Strongylocentrotus* are found in Peter the Great Bay: *S. nudus, S. intermedius,* and *S. pulchellus*. Descriptions of the larvae are available for *S. nudus* (Kawamura, 1970; Kryuchkova, 1976), *S. intermedius* (Kawamura, 1970; Krychkova, 1976), and *S. pulchellus* (Kryuchkova, 1976).

Scutellidae, Dendrasteridae and Echinarachniidae

The larva has four pairs of arms. The rods of the postoral and posterodorsal arms are fenestrated. The basal and secondary basal rods are fused, forming

a single fenestrated plate at the base of the larva. In *Scaphechinus mirabilis* the single plate is not formed but the basal and secondary rods are fused in pairs. In *Scaphechinus griseus* these rods are not fused, only contiguous.

Three species are found in Peter the Great Bay: *Echinarachnius parma,* (Echinarachniidae), *Scaphechinus mirabilis,* and *S. griseus,* (Dendrasteridae).

Descriptions of the larvae are available for *Echinarachnius parma* (Fewkes, 1893; Kryuchkova, 1976), *Scaphechinus mirabilis* (Kryuchkova, 1976), and *Scaphechinus griseus* (Kryuchkova, 1976).

Loveniidae

The larva has six pairs of arms and an aboral rod. The rods of the postoral and posterodorsal arms as well as the aboral rod are fenestrated. In the pluteus II stage the base of the aboral rod enlarges and assumes the shape of an inverted arch with a long process in the middle. Fenestration in the aboral rod commences from its base.

One sea urchin of this family is found in Peter the Great Bay, namely, *Echinocardium cordatum.*

The larvae have been described by Selenka (1880), McBride (1914, 1918), and Kryuchkova (1976).

STRONGYLOCENTROTUS NUDUS AGASSIZ

(Strongylocentrotidae)

Eggs of the mature female before they are shed in water are perfectly spherical, nontransparent, and grayish. Their size varies from 90 to 100 μm in diameter. The fertilization membrane begins to separate 2–3 min after penetration of a spermatozoon. The first division occurs 40 min later at a temperature of 20–21°C. The free-swimming blastula develops after 32 hrs and the pluteus I stage develops two days after fertilization.

Pluteus I stage

The larva is transparent, with a slightly bluish tinge. The endoskeleton is visible through the tissue and is composed of simple rods. At this stage, the larva has two pairs of arms: anterolateral and postoral. The body is supported by thickened basal rods which, at the basal end, are somewhat flattened and bear large spines that interlock the rods. Short inner transverse rods arise from the site of fusion of the postoral and basal rods. Secondary basal rods are attached to the inner transverse ones, they are shorter and do not fuse with each other. The length of the larva at this stage is 200–400 um (Figure 129).

Pluteus II stage

From the time of appearance of the third pair of arms, the posterodorsal, the larva enters the pluteus II stage. A calcification center arises on each side at the base of the postoral arms and forms a single triradiate rod that later transforms into a short rod. As it grows, a projection develops alongside the postoral arm on the dorsal side of the larva. This projection is the posterodorsal arm. Simultaneous with the development of the new pair of arms, the inner transverse rods begin to interconnect. The secondary basal rods also begin to enlarge but do not attain the full length of the basal rods; approximately midlength of the latter they bend inward and cross. A short dorsal arch arises on the dorsal side above the stomach. The basal part of the body gradually enlarges and the spines at the distal ends of the basal rods break off. This process becomes perceptible when the third pair of arms reaches the size of the two earlier pairs and the larva is as long as 500–700 μm (Figure 130).

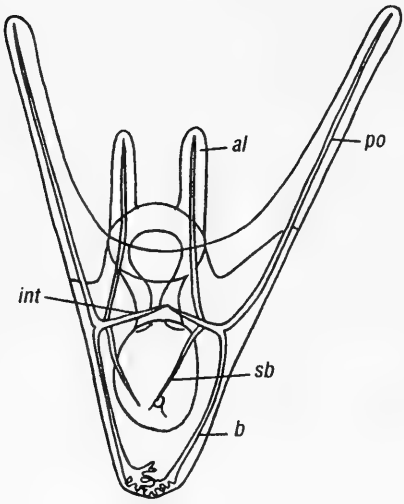


Figure 129: *Strongylocentrotus nudus*.
Pluteus I stage.
Legend same as in Figure 103.

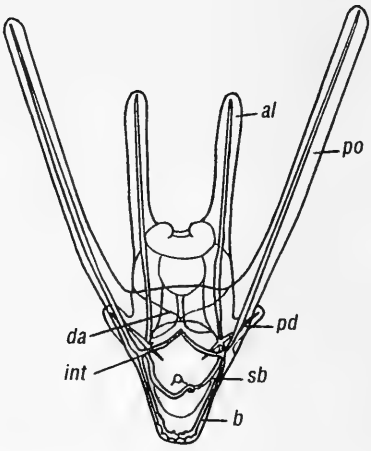


Figure 130: *Strongylocentrotus nudus*.
Pluteus II stage.
da — dorsal arch.
Remaining legend same as in Figure 107.

Pluteus III stage

The ends of the basal arch elongate into a pair of new rods, which support the processes appearing above the oral opening. These rods are termed the preoral. With their appearance, formation of the larval skeleton terminates and the larva enters the pluteus III stage. In the dorsal and ventral views, at the level of the esophagus, dense ciliated bands of the ectoderm gradually

become discernible. The upper epaulettes appear. Slightly later, the lower epaulettes appear, which are situated in the lower part of the larval body. At this stage, three larval pedicellariae form, one between the lower epaulettes and the other two on the dorsal and ventral sides of the larval body. By the end of the pluteus III stage, the larva has accumulated crimson pigment, which is initially evenly distributed over the entire body. This pigment gradually concentrates at the tips of the arms and in the region of formation of the definitive test, which develops in the amniotic sac on the left side of the larval body. The stomach becomes bright green. The length of the larva reaches 900 μm before metamorphosis (Figure 131).

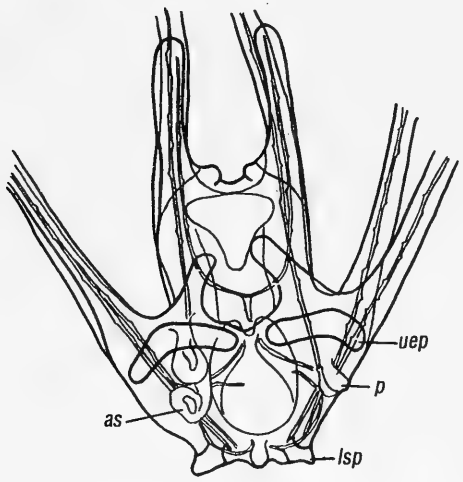


Figure 131: *Strongylocentrotus nudus*.
Pluteus III stage.
as — amniotic sac; lep — lower epaulettes; p — pedicellariae; uep — upper epaulettes.

Ecology

The larvae of *S. nudus* appear in the plankton of Peter the Great Bay in the middle ten days of July when the water temperature in the surface layer is 18.5°C. The pluteus I stage is found up to August 20th. At August end, the pluteus III stage can be seen undergoing metamorphosis. By mid-September, the larvae of *S. nudus* have disappeared from the plankton, although in some favorable years they are seen up to the end of September. According to Fuji (1960a, b), spawning of *S. nudus* in southern Hokkaido is observed from mid-August to mid-December.

STRONGYLOCENTROTUS INTERMEDIUS (AGASSIZ)

(Strongylocentrotidae)

The mature eggs of this species are smaller than those of *S. nudus*; their diameter does not exceed 90 μm. The eggs are nontransparent and grayish. The fertilization membrane appears 5 min after penetration by the spermatozoa. The first division occurs 45–50 min after fertilization at a temperature of 20–21°C. The pluteus I stage develops two days later.

Pluteus I stage

The larval body is transparent, slightly bluish, with evenly scattered granules of crimson pigment. The basal part of the body is highly elongate and contains the basal rods whose ends are clavate. One of the rods terminates with a small depression while the other bears a spine that fits into this depression. Secondary basal rods are absent. The inner transverse rods are very short. The rods supporting the anterolateral and postoral arms are two-thirds of the length of basal rods. The larva at this stage is 250–400 μm long (Figure 132).

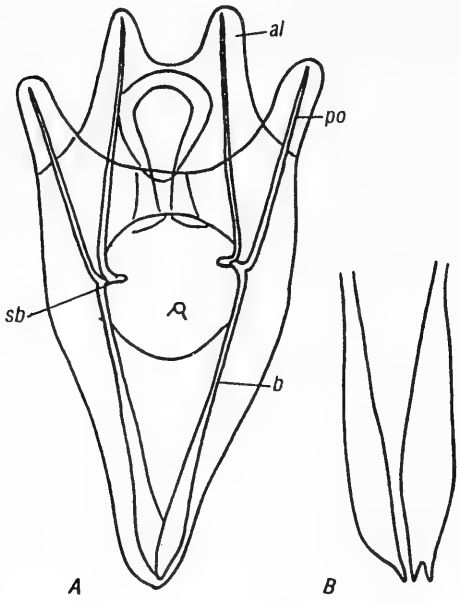


Figure 132: *Strongylocentrotus intermedius*.
Pluteus I stage.
A — general view of the larva; B — basal rods.
Legend same as in Figure 103.

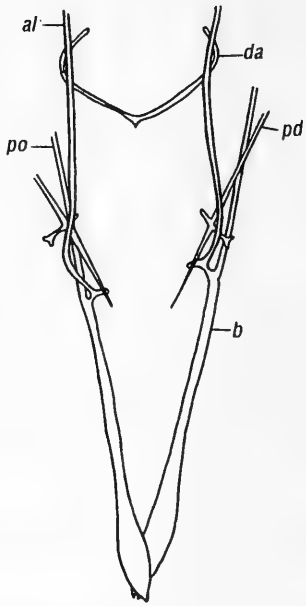


Figure 133: *Strongylocentrotus intermedius*.
Pluteus II stage.
da — dorsal arch.
Remaining legend same as in Figure 107.

Pluteus II stage

Similar to *S. nudus*, the third posterodorsal pair of arms develop during stage II in this species also. The dorsal arch becomes discernible and is much narrower than in *S. nudus*. By the end of stage II, the clavate tips of the basal rods break off but the position of the rods remains the same; hence the hind end of the larva appears almost unaltered (Figure 133). On the 8th–9th day of development, the ends of the basal arch elongate, giving rise to the preoral rods. The pluteus II stage then becomes the pluteus stage III.

Pluteus III stage

The base of the larval body gradually enlarges and parts of the basal rods contained therein gradually reduce. Ciliated epaulettes appear, which are denser than in *S. nudus* and lie closer. The larva looks as if it has two powerful ciliated bands. Pedicellariae do not form in *S. intermedius*. The larval body is high set, resembling a truncated cone from which four pairs of arms arise. All the skeletal rods are simple and armed with numerous short spines. The larva soon loses its transparency, becoming bright red. This change of color is due to the disappearance of the earlier scattered crimson pigment granules, which are replaced by more numerous red granules. Now the tips of the arms and the larval body are so filled with red granules that the skeletal rods are no longer discernible. However, at higher microscopic magnification, the reticular structures can be seen underneath the layer of pigment on both sides of the stomach and at the base of the larval body. On removal of the soft tissue, these structures are found to consist of lattice plates, which have formed around the dorsal arch and left and right posterodorsal and postoral rods. Another small plate is situated at the base of the larval body. The fate of these plates was discussed above in the section on metamorphosis and formation of the definitive test. At the time of plate formation, the length of the larva is 750–900 μm (Figure 134).

Ecology

In Peter the Great Bay, larvae of the pluteus I stage begin to appear in mid-July, when the water temperature in the surface layer is 16.5°C, and continue to be found until early September with some interruptions. The first juvenile individuals are found in early August. Large-scale settling is observed in mid-August. In southern Hokkaido, according to Fuji (1960b), spawning of *S. intermedius* is observed from mid-August to late December. According to Kawamura and Taki (1965), who investigated the population of these urchins near Rebun Island, spawning in this region occurs from early August to mid-September.

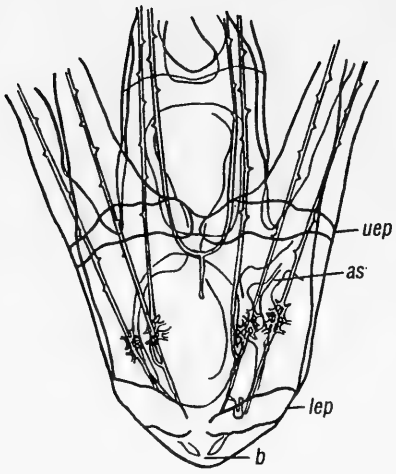


Figure 134: *Strongylocentrotus intermedius*. Pluteus III stage.
b — basal rods.
Remaining legend same as in Figure 109.

ECHINARACHNIUS PARMA (LAMARCK)

(Echinarachniidae)

Mature eggs of this sand dollar species are encased in an envelope densely speckled with crimson pigment granules. The eggs are 130–140 µm in diameter and the membrane 60 µm thick. Development proceeds fairly rapidly. The early pluteus stage is formed within 36 hrs after fertilization at a water temperature of 20–21°C.

Pluteus I Stage

The larval body is short with a slightly tapering base. The body is transparent, bluish, and devoid of pigment granules. Two pairs of arms develop — the anterolateral and the postoral; the former is represented by simple rods with short spines, while the latter contain complex perforations. From the bases of these rods arise the inner transverse rods, which are connected above the stomach and bear numerous small spines distally. The larval body is supported by a pair of basal rods and a pair of secondary basal rods. All these rods join in the basal part of the larval body; their distal ends are greatly enlarged and form fenestrated plates, which are so tightly fused that traces of their fusion are not visible in later stages. The secondary basal rods extend to this plate and are likewise slightly enlarged at the site of connection. Such

a formation is known as a "basket". It is completely formed in larvae 300–400 μm long. The width of the "basket" base is three-fourths of its height (Figure 135). The length of the larvae is 250–300 μm.

Pluteus II Stage

New arms, the posterodorsal, which also have a complex fenestrated structure, appear as two small triradiate rods lying at the base of the postoral arms. From the time of their appearance, the pluteus enters stage II. In this stage the rudiment of the dorsal arch of about 120°C develops above the stomach. From the posterodorsal rods, small secondary transverse rods are directed inward. At this time, the first granules of crimson pigment begin to appear at the tips of the arms. The length of the larva increases up to 500–600 μm (Figure 136).

Pluteus III Stage

The preoral arms appear in stage III; their supporting rods are simple because they are extensions of the dorsal arch. *E. parma* have neither pedicellariae nor ciliated spaulettes. The epidermal vibratile plates form between the posterodorsal and postoral arms. By the 7th–8th day of

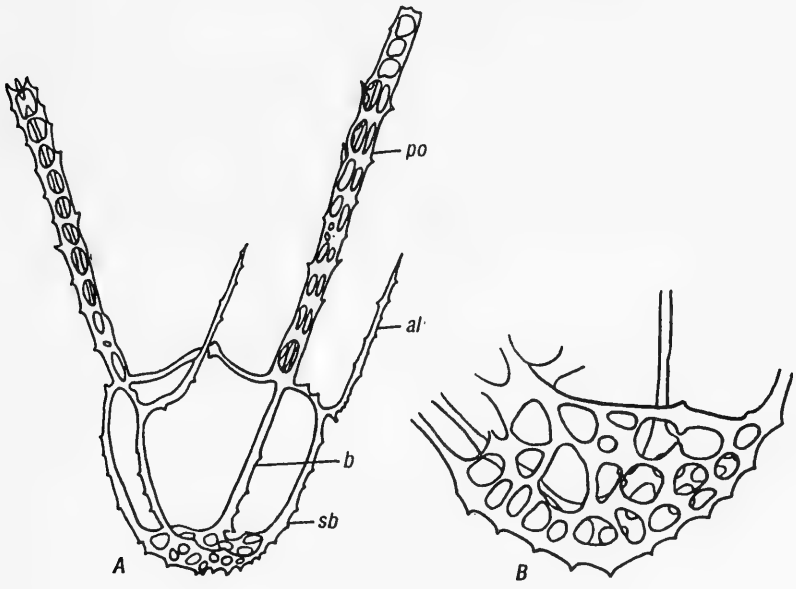


Figure 135: *Echinarachnius parma*. Pluteus I stage.
A — general view of the larval skeleton; B — basket structure.
Legend same as in Figure 109.

development, the first signs of resorption of the larval skeleton becomes evident. The basal plate in "the basket" disintegrates. The quantity of pigment increases but only slightly. A fairly outstanding feature of the larva of this stage is its change in color when placed in 70° alcohol. The red in the pigment granules disappears and is replaced by green, which evenly colors the entire larval body (Figure 137). The length of the larva is 700–800 μm.

Ecology

Pluteus I stage begins to appear in the plankton of Peter the Great Bay in early July, when the water temperature in the surface layer is 16.5°C. Under conditions favorable for spawning, they may be found even in the second ten-day period of June. The maximum density of pluteus I stage larvae is observed in mid-July. The first individuals of settling juveniles are seen after July 10.

According to Costello and coworkers (1957), spawning of *E. parma* along the Atlantic coast of America (Woods Hole, Massachusetts) is observed from late February to mid-August.

SCAPHECHINUS MIRABILIS (AGASSIZ)

(Dendrasteridae)

Mature eggs have a secondary envelope with inclusions of red pigment. The eggs are 90–100 μm in diameter and the envelope 40 μm thick. Free-swimming blastulae were found 13 hrs after fertilization in cultures at a temperature of 20–21°C. Four hours later gastrulation was observed, and in the 20th hr the first triradiate calcite spicules appeared in the gastrulae. The early plutei developed 34 hrs after fertilization.

Pluteus I Stage

The larval body is transparent, shortened with a broad and flat base, and slightly tapering. Two pairs of arms are present; anterolateral and postoral. The structure of the rods supporting these arms is the same as in *Echinarachnius parma*. The inner transverse rods join medially but unlike in *E. parma* do not bear spines. The basal and secondary basal rods fuse in pairs. Each rod thereby enlarges somewhat to form a small plate or lobe and basal and secondary basal rods merge at the place of contact of these plates. Two large plates develop at the base of the larval body, bearing numerous spines on the lower margin and several small fenestrations. Thus, the "basket" in *S. mirabilis* comprises two containing parts. The height of the "basket" base is three-fourths its width. At this stage, the length of the larva is 200–400 μm (Figure 138).

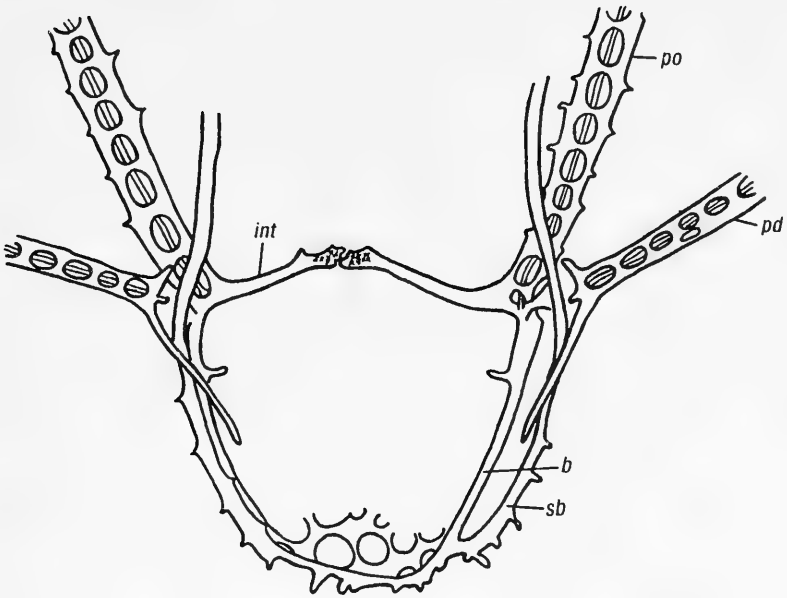


Figure 136: *Echinarachnius parma*.
Pluteus II stage. Structure of the larval skeleton.
Legend same as in Figure 107.

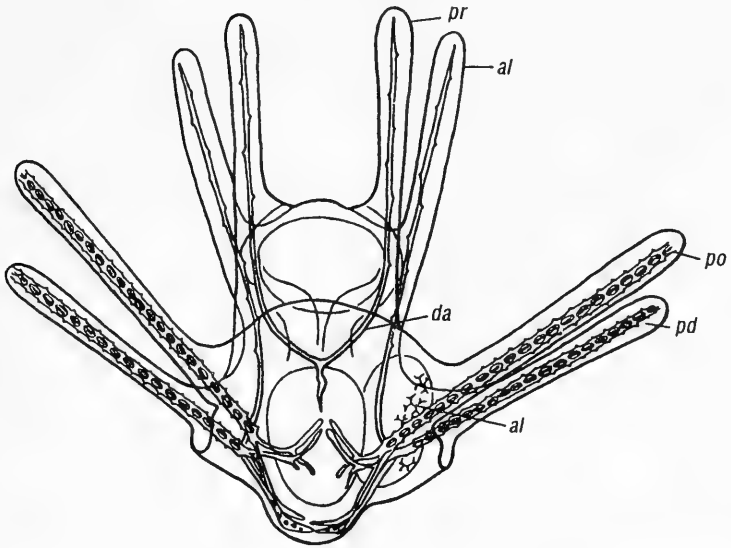


Figure 137: *Echinarachnius parma*.
Pluteus III stage.
da — dorsal arch. Remaining legend same as in Figure 109.

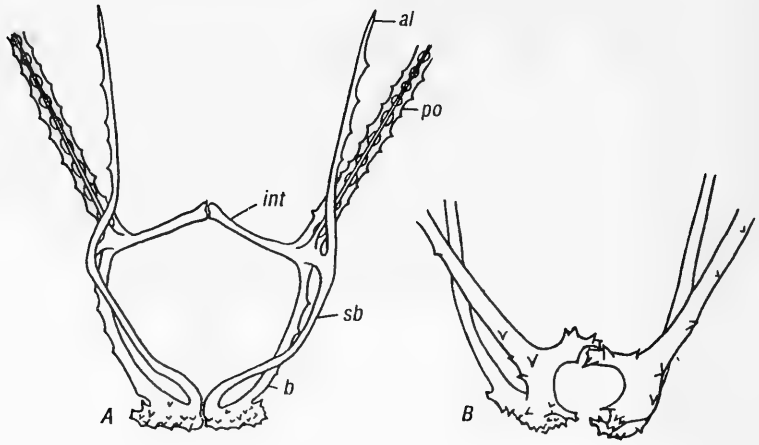


Figure 138: *Scaphechinus mirabilis*. Pluteus I stage.
A — structure of the larval skeleton; B — connection of the basal and secondary basal rods. Remaining legend same as in Figure 103.

Pluteus II Stage

The third pair of arms, the posterodorsal, appears in this stage. The rods of these arms are complexly fenestrated. The rudiment of the dorsal arch becomes discernible; it is considerably broader than in *Echinarachnius parma*, about 180°. In a live larva the accumulation of red pigment at the tips of the arms is visible under a microscope. When the larva reaches a length of 500–600 μm, the transverse rods differentiate and extend from the posterodorsal rods medially within the larva (Figure 139).

Pluteus III Stage

The preoral arms develop early in this stage; their supporting rods are simple. As in *Echinarachnius parma* larvae, there are no ciliated epaulettes and pedicellariae, but epidermal vibratile lobes are present. A gradual reduction of the plates forming the "basket" bottom takes place in the pluteus III stage. Soon after their disintegration, resorption of the inner transverse rods occurs. The amniotic sac becomes visible, arising, usually, on the 6th–7th day of development. The larva by this time has reached a length of 800–900 μm (Figure 140).

Ecology

Larvae of *S. mirabilis* appear in the plankton of Vostok Bay in late July when the water temperature in the surface layer is 18°C. Maximum density is observed in mid-August.

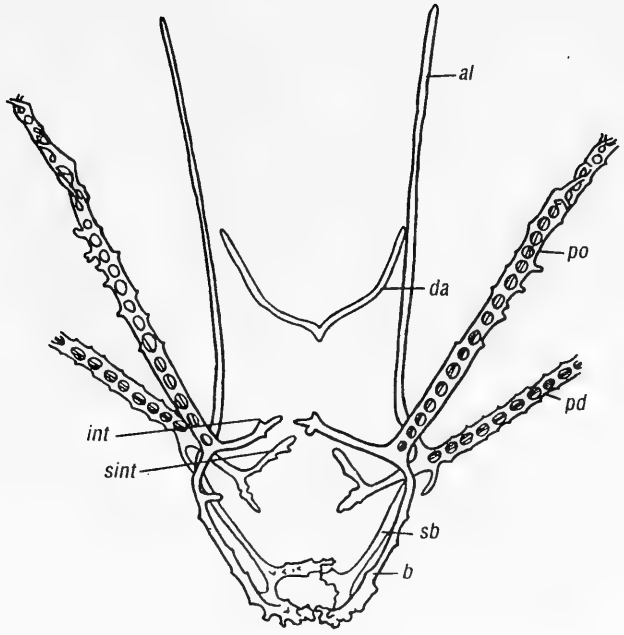


Figure 139: *Scaphechinus mirabilis*.
Pluteus II stage. Structure of the larval skeleton.
sint — secondary inner transverse rod; da — dorsal arch.
Remaining legend same as in Figure 107.

SCAPHECHINUS GRISEUS (MORTENSEN)

(Dendrasteridae)

The development of this and the preceding species has not yet been described by other authors. Sometimes the older individuals of *S. griseus* are easily confused with the juveniles of *Echinarachnius parma* because their size and color are almost identical. The only distinguishing feature in such cases is the position of the anal opening, which in *S. griseus* lies on the aboral side of the test.

Mature eggs in *S. griseus* are 90–100 μm in diameter but unlike in *S. mirabilis* and *E. parma*, the secondary egg membrane is not visible. At a temperature of 20–21°C, development proceeds at the same rate as in *E. parma*. Thus, the blastula appears 16 hrs and the gastrula 24 hrs after fertilization. The early pluteus develops 36 hrs after penetration of the egg by the spermatozoa.

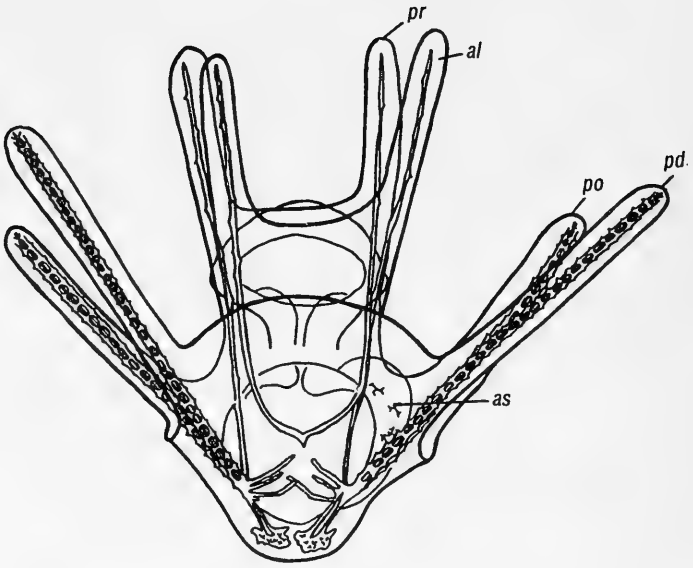


Figure 140: *Scaphechinus mirabilis*. Pluteus III Stage.
as — amniotic sac; Remaining legend same as in Figure 109.

Pluteus I Stage

The structure is identical in *S. griseus* to that of the pluteus of *E. parma*. The basic difference in the pattern of the connection of the basal and secondary basal rods. In *S. griseus* these are not fused and the true "basket," characteristic of the larvae of sand dollars, is not formed. The ends of basal rods have a similar thickening from which fairly long spines arise. These spines are somewhat smaller in secondary basal rods. The rods interlock through spines which fit into depressions formed by them on the opposite pair. True fusion does not occur. The structure resulting from such an arrangement may, at best, be termed a "pseudobasket". The width of the "pseudobasket" base is three-fourths of its height. The length of pluteus I does not exceed 400 μm (Figure 141).

Pluteus II Stage

The third pair of arms, the posterodorsal, appears in this stage. Like the postoral, they have complex fenestrated rods. Simultaneous with them, the dorsal arch develops which, as in *Echinarachnius parma*, is about 120°. The larval body remains transparent, devoid of pigment granules. By the end of stage II, the larva has increased in length up to 400 μm (Figure 142).

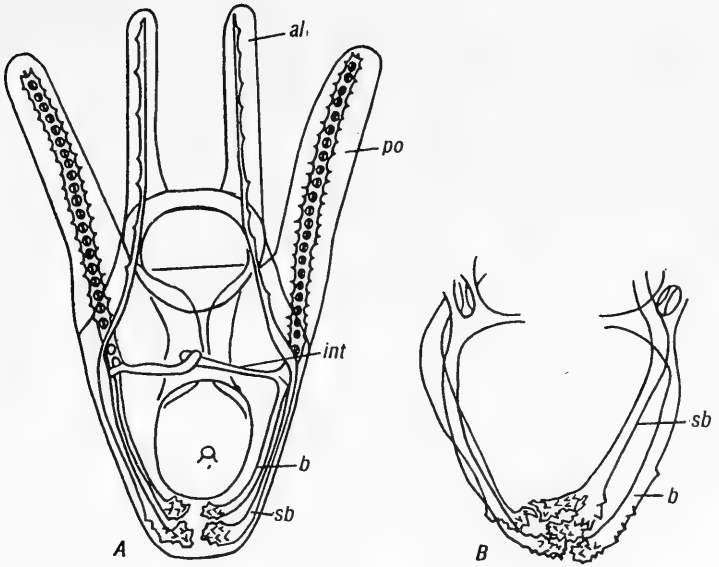


Figure 141: *Scaphechinus griseus*. Pluteus I stage.
A — general view of the larva; B — connection between the basal and secondary basal rods.
Remaining legend same as in Figure 103.

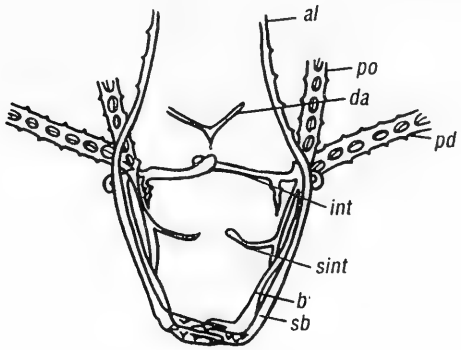


Figure 142: *Scaphechinus griseus*.
Pluteus II stage. Structure of the larval skeleton.
Legend same as in Figures 107 and 139.

Pluteus III Stage

The formation of the skeleton is completed and the fourth pair of arms, the preoral, develops in this stage. Supporting rods inside these arms form from elongated processes of the dorsal arch. As in the preceding species, there

are no ciliated epaulettes and pedicellariae in *S. griseus*, but the epidermal vibratile lobes are far less developed. With the appearance of the amniotic sac by the 5th–6th day of development, the basal and secondary basal rods elongate distally and intertwine. Both pairs of inner transverse rods begin to reduce. Few granules of red pigment appear at the arm tips. The larva reaches a length of 900–1000 μm. Like the larvae of *E. parma*, the pluteus III stage acquires a light green color when placed in 70° alcohol (Figure 143).

Ecology

Larvae of *S. griseus* begin to appear in the plankton of Vostok Bay in September when the water temperature in the surface layer is 17°C. The first settling urchins were obtained in the laboratory by mid-September.

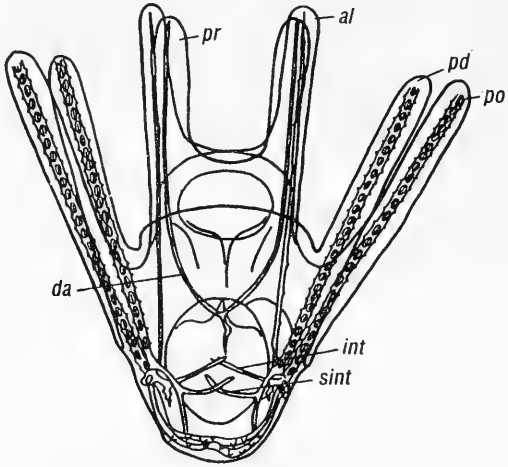


Figure 143: *Scaphechinus griseus*. Pluteus III stage.
Legend same as in Figures 109 and 139.

ECHINOCARDIUM CORDATUM (PENNANT)

(Loveniidae)

Mature eggs vary in diameter from 90 to 100 μm. The eggs are not pigmented. The blastula develops 28 hrs after fertilization and the gastrula after 42 hrs at a temperature of 20–21°C. The early pluteus, formed on the 3rd day of culturing, exhibited a large number of granules of red pigment. The bright color of the larvae of this heart urchin distinctly distinguishes them from the larvae of other urchins that may occur concurrently in the plankton.

Pluteus I stage

In the early pluteus the postoral arms, which are complexly perforated, are twice as long as the anterolateral arms represented by simple rods. The aboral rod is present as a transverse rod with a pair of processes. Short basal rods cross at the lower part of the larva. In shape, the larva initially resembles a triangle but later, after the upper transverse rods appear, does not. These rods fuse with each other and with the distal ends of the postoral rods. The secondary basal rods diverge below from the base of the anterolateral rods. These are likewise connected with each other by a short transverse rod formed through the fusion of the lower transverse rods. These processes arise in the secondary basal rods slightly above their distal ends. The secondary basal rods are almost half as long as the basal and hence the basal part of the larval body tapers slightly. Between each pair of these rods lies a transverse septum, which forms above the lower inner transverse rods. The aboral rod basally reaches the place of connection of the basal and secondary basal rods. On the 3rd–4th day of development, the aboral rod is equal in size to the anterolateral arms. The length of pluteus I is twice that of the larvae of other sea urchins, reaching 500–600 μm (Figure 144).

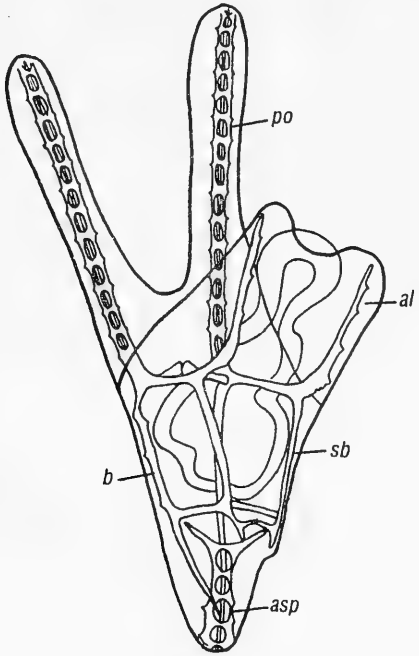


Figure 144: *Echinocardium cordatum.* Pluteus I stage.
asp — aboral spicule.
Remaining legend same as in Figure 103.

Pluteus II stage

Five days after fertilization the third pair of arms, the posterodorsal, appears. The rods supporting this pair of arms are complexly perforated. Before the rudiments of the posterodorsal rods emerge, the connection between the basal and secondary basal rods disintegrates and the secondary basal rods are reduced; however, the lower transverse septum is retained. The developing posterodorsal rods bear two basal processes, the larger of which fuses with the secondary basal rod while the smaller, hook-shaped, attaches itself to the aterolateral rod. After emergence of the lower inner transverse rods, diverging from the base of the secondary basal rods, the connection between the basal and secondary basal rods totally disappears. By the time of resorption of this connection, the smaller process of the posterodorsal rod has straightened somewhat and runs parallel to the anterolateral rod. On the side opposite to it, a new process begins to grow, which is directed below. The dorsal arch appears at this time.

As soon as the posterodorsal arms attain the size of the postoral arms, the ends of the dorsal arch begin to rapidly extend upward, giving rise to rods for a new pair of arms, the preoral. Simultaneous with their development, the lateral processes at the base of the aboral rod enlarge. The length of the pluteus II stage is 900–1,000 μm (Figure 145).

Pluteus III stage

On the 7th–8th day of development, when the basal ends of the aboral rod reach the base of the posterodorsal rods, a fifth pair of arms, the posterolateral, appear. The calcification centers of this pair appear from the outer side somewhat below the lower inner transverse rods. The simple rods growing from these centers fuse with the basal ends of the aboral rod. The posterolateral arms situated perpendicular to the anterolateral arms, together with the aboral rod constitute a single structural unit which serves as a support for the entire larval body. On the right, the arced rod connects the basal end of the aboral rod with the posterodorsal rod. Probably the aboral rod develops as a result of the enlargement of the lower lateral process of the posterodorsal rod. A small perforated plate develops on the outer side of the postoral rod. On the left side, likewise, a perforated plate appears on the postoral rod but there is no connection with the aboral and posterodorsal rods. At this time, on the lower side of the dorsal arch, a pair of processes appears on each side of the esophagus. The upper processes remain short while the lower ones grow rapidly. By the 10th–11th day, this lower pair has modified into rods of the anterodorsal arms. The short processes of the basal arch serve as an additional support for them from below. With the appearance of the sixth pair of arms, formation of the larval skeleton is complete. The larvae of *E.*

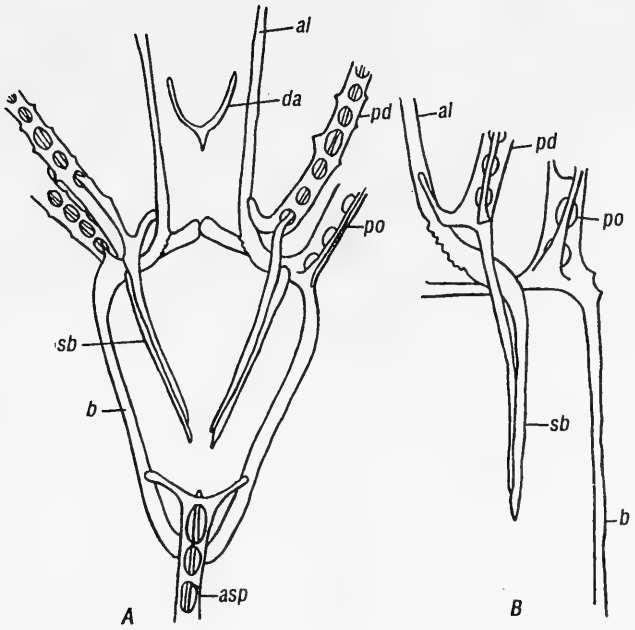


Figure 145: *Echinocardium cordatum*. Pluteus II stage.
A - structure of the larval skeleton; B — connection of the anterolateral, posterodorsal and postoral rods.
da — dorsal arch; asp — aboral spicule
Remaining legend same as in Figure 107.

cordatum have neither epaulettes, nor vibratile lobes, nor pedicellariae. The bright red color of the larva is retained in all the stages of development. The arms of a fully formed larva are very long and slender and the body is short. The length of the pluteus III stage is 2 mm (Figure 146).

Ecology

Early larvae of *E. cordatum* usually appear in Vostok Bay in the last 10 days of June when the water temperature in the surface layer is 16.5°C. They are found in maximum numbers in the last ten days of July, completely disappearing from the plankton by July end. In favorable years, larvae of *E. cordatum* are seen again in the middle ten days of September when the water temperature in the surface layer drops to 17°C and stays at this level for two-three weeks. Such a situation was observed, for instance, in 1970–1971.

According to the literature, reproduction of *E. cordatum* is observed off the coast of Scotland from the end of May to mid-September (McBride, 1914), on the Isle of Man in the Irish Sea from June to early November

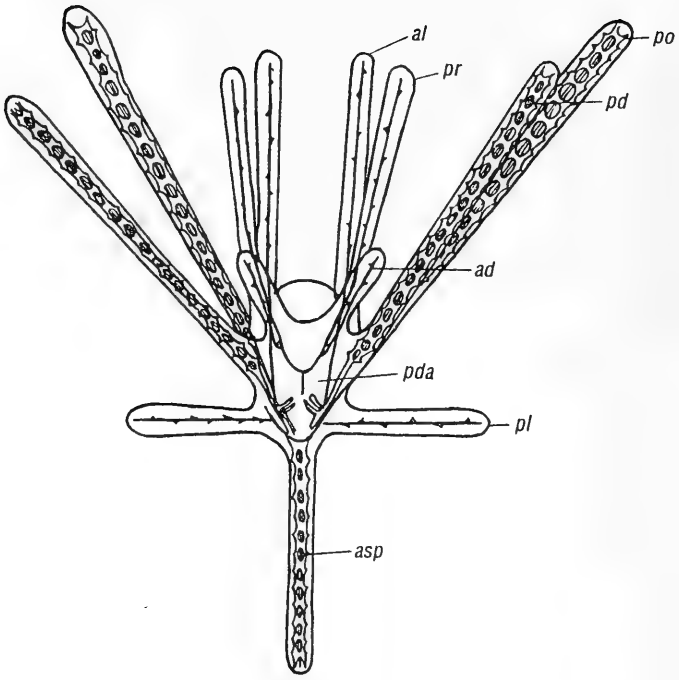


Figure 146: *Echinocardium cordatum*. Pluteus III stage.
asp — aboral spicule ; pda — process of the dorsal arch.
Remaining legend same as in Figure 109.

(Moore, 1936), in La Manche from mid-April to mid-August (Moore, 1936), in Öresund (The Sound) from mid-July to early November (Thorson, 1946), off the Swedish coast from mid-July to the end of October (Moore, 1966), and in the Mediterranean Sea from mid-September to the end of December (Moore, 1966).

CHAPTER IV

LARVAE OF BRITTLE STARS (MORPHOLOGY, PHYSIOLOGY, AND BEHAVIOR)

EARLY DEVELOPMENT

Information is available in the literature on the development of about 4% of the known species of brittle stars. Of the approximately 2,000 species, 55 are described as viviparous and nearly 30 as species with larval development; 48 species of larvae have been reported whose taxonomic position remains unclear. In brittle stars, three types of development are known: direct (viviparity including brood care); development with planktotrophic larva; and development with lecithotrophic larva.

Egg

According to Hendler (1975), there is no strict relationship between egg size and type of development. Thus, in species with direct development the egg diameter may range from 0.1 to 1.0 mm; a lecithotrophic larva develops from an egg of 0.13–0.35 mm in diameter, and a planktotrophic larva from an egg of 0.07–0.9 mm in diameter. There is, however, a relationship between the disk diameter of brittle stars, type of development, and number of eggs produced by a single family. species with planktotrophic larvae produce the largest number of eggs. For example, *Ophiocoma echinata*, in which the disk diameter is roughly 25 mm, spawn up to 1,000,000 eggs, while in *Ophionotus hexactis*, with a large diameter of nearly 40 mm, only 100 eggs mature by the spawning period. *Ophiocoma echinata* develops with planktotrophic larvae while in *Ophionotus hexactis* development is direct (Hendler, 1975). The eggs of brittle stars are often reddish, yellowish, or yellowish-brown (Mortensen, 1937; Olsen, 1942).

Egg membrane : Oocytes are surrounded by a thick jellylike membrane, which becomes loose (or disintegrates) after the oocytes are released into the water (Lonning, 1976). As early as 1916, Kirk described a larva grown from an egg with a dense chitinoid capsule. Unfortunately, the species affinity of this larva was not determined since he had removed the eggs from the plankton. In 1937, Mortensen described the secondary capsule, provided with spines, for three species of the genus *Ophiocoma: O. echinata, O. erinaceus,* and *O. scolopendrina*; he also noticed that the capsule obstructs emergence of the embryo during hatching. In structure these capsules resemble the gemmules of sponges or the chorion of eggs of some chitons.

Fertilization : The eggs in species with planktotrophic or lecithotrophic larvae are shed in water through a slitlike opening in the bursa, where fertilization occurs. One of the consequences of fertilization is the completion of maturation division of the egg. Olson (1942) found two polar bodies in *Ophiopholis aculeata*, which lie above the blastomeres after the first division. Hendler (1977), investigating the development of *Amphioplus abditus*, described the formation of polar bodies that remained quite distinct during the first three-four divisions.

During fertilization, the contents of the cortical granules of the eggs are released into the space between the plasma membrane of the egg and its yolk membrane, which transforms into a fertilization membrane and separates from the surface of the egg. At this time, a hyaline layer appears that lines the plasmatic membrane of the egg (Holland, 1979). This has been reported for *Ophiocoma nigra* (Narasimhamurti, 1933), *Gorgonocephalus caryi* (Patent, 1970a), and *Amphioplus abditus* (Hendler, 1977).

Cleavage : Completely radial cleavage is observed in brittle stars. The first two divisions occur in the meridional plane and the third in the equatorial (Figure 147). The blastomeres in the animal hemisphere in *Ophiocoma nigra* are somewhat smaller than those in the vegetal hemisphere (Narasimhamurti, 1933). Sometimes the blastomeres do not differ in size; the next division gives rise to the blastula.

Blastula

Early development from fertilization to the blastula takes 24 hrs in *Ophiothrix fragilis* (McBride, 1907), 21 hrs in *Ophiopholis aculeata* (Olsen, 1942), 6 hrs in *Ophimaza cacaotica* (Mortensen, 1937) and *Ophiura sarsi* and 2.5 hrs in *Ophiothrix oerstedi* (Mladenov, 1979). Mortensen (1937) noted that in *Ophiocoma lineolata* the embryo hatches from the envelopes at the morula stage. Formation of the blastocoel begins early in brittle stars. Narasimhamurti (1933) noted that indications of the blastocoel appear in *Ophiocoma nigra* at the 16-cell stage. In *Ophiura sarsi* an extensive primary cavity was noticed

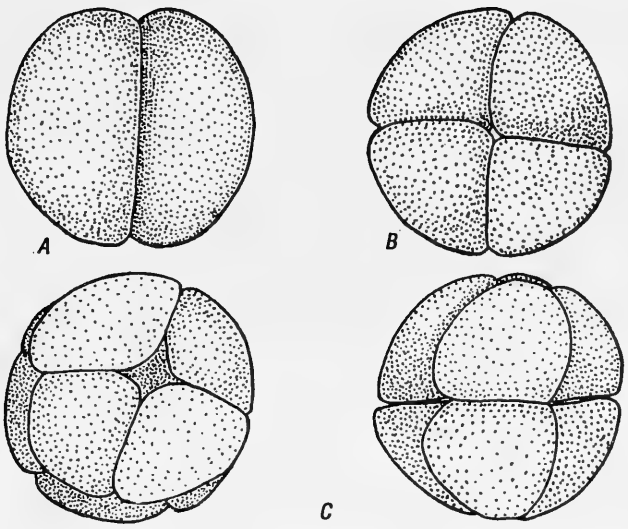


Figure 147: *Ophiura sarsi*. Cleavage.
A — two blastomeres; B — four blastomeres; C — eight blastomeres.
View from the vegetal pole and laterally.

at the 32-blastomere stage. On the other hand, in *Ophiocoma echinata* (Grave, 1898) and *Gorgonocephalus caryi* (Patent, 1970a) blastomeres of small size have been reported. The blastula does not emerge from the envelope with the appearance of cilia, sometimes it remains immobile inside it for two hours. Then the cilia begin to beat, initially slowly, but soon more and more rapidly. The blastula turns around on its axis, the speed of rotation increases, the envelope is ruptured, and the blastula begins to swim (Figure 148). Sometimes hatching does not occur. Patent (1970a) noted that in *Gorgonocephalus caryi* the blastula does not leave the envelope and that it is devoid of cilia. Cilia also do not develop in *Amphioplus abditus* (Hendler, 1977). In *Ophiura*

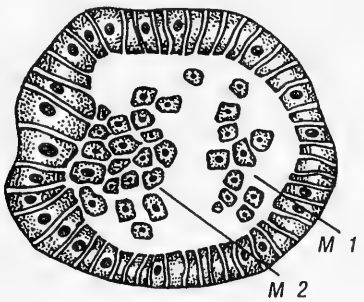


Figure 148: *Ophiothrix fragilis* (McBride, 1907).
Blastula.
M 1 — primary mesenchyme; M 2 — secondary mesenchyme.

sarsi the cilia are well developed but the fertilization membrane is not shed even though the cilia emerges from it.

Gastrula

Formation of the gastrula takes from 9–12 hrs in *Amphioplus abditus* (Hendler, 1977) and *Ophiothrix oerstedi* (Mladenov, 1979) to 40–48 hrs in *Ophiocoma nigra* (Narasimhamurti, 1933). In *Ophiura sarsi* the gastrula develops in one day.

In *Ophiopholis aculeata* (Olsen, 1942) and *Ophiura sarsi* the blastula elongates before gastrulation along the animal-vegetal axis.

As soon as the vegetal pole of the blastula flattens, emigration of the primary mesenchymal cells begins here (Figure 148). Then an invagination appears, which forms the archenteron. Simulataneously, tapering of the animal pole region occurs where the so-called crest is formed; the latter consists of vacuolated cells. Meanwhile the vegetal pole remains flat. At the same time, the secondary mesenchymal cells begin to accumulate at the base of the archenteron. Soon a bilobate coelomic sac develops from the archenteron, which later divides into the right and left coeloms. The archenteron bends in a ventral direction and touches the ectoderm to form an invagination in this site. A rudiment of the esophagus is formed. After the ectoderm and the bottom of the archenteron rupture, a gut is formed. The blastopore has now become the anal opening.

Until the formation of the oral opening, a dense ridge formed from the ciliated ectodermal cells is situated slightly above the blastopore. This ridge girdles the entire gastrula. It delineates the future preoral field of the larva (Figures 149, 150). Soon after the formation of the ciliated ridge, the crest, in species where it is present, reduces. Under the ridge, along the edges of the archenteron, in the accumulation of mesenchymal cells, spicules become differentiated, from which the basal rods of the larval skeleton will develop later. The embryo gradually acquires a triangular shape and changes over to the prism stage.

Prism Stage

This stage is reached by the embryo after 16 hrs of development in *Amphioplus abditus* (Hendler, 1977), after 48 hrs in *Ophiopholis aculeata* (Olsen, 1942), and after 2 days in *Ophiothrix fragilis* (McBride, 1907). The prism forms on the 4th day of development in *Ophiocoma nigra* (Narasimhamurti, 1933) and in *Ophiura sarsi*.

At this stage, the embryo gradually acquires the shape typical of the ophiopluteus. By this time, the blastopore has already shifted to the ventral side, although division of the gut into sections has yet to occur. The larva is

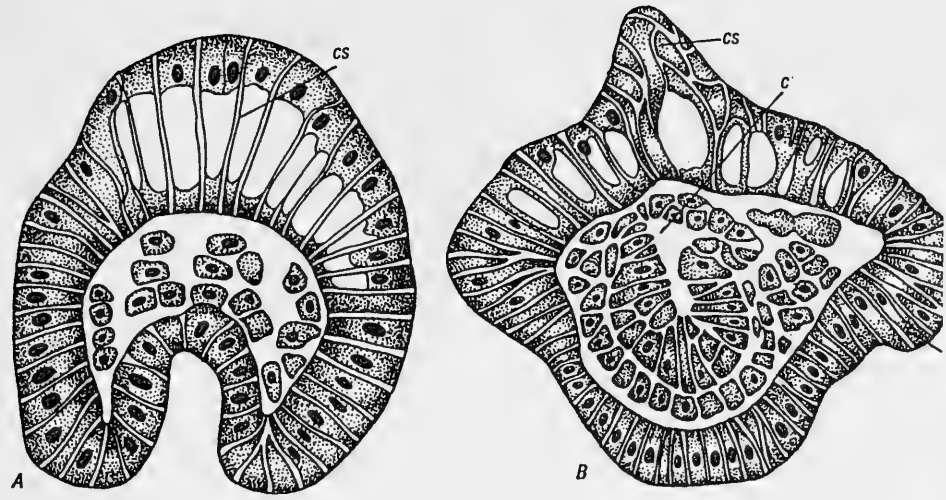


Figure 149: *Ophiothrix fragilis* (McBride, 1907).
Gastrula.
A — commencement of gastrulation; B — formation of coelomic sacs
c — coelom; cr — ciliated ridge; cs — crest.

flattened dorsoventrally. The lateral margins of the ridge are stretched and slightly upcurved. The ridge itself transforms into a ciliated band. Spicules, already formed in the gastrula, are now modified into skeletal rods. Both McBride (1907) in *Ophiothrix fragilis* and Olsen (1942) in *Ophiopholis aculeata* have demonstrated the initiation of triradiate spicules in the gastrula stage, which now give rise to three pairs of rods diverging from a common center. A study of the development in *Ophiura sarsi* established the presence of tetraradiate spicules. At the prism stage, only the upper and lower rays extend into rods (Figure 151).

Hendler's (1978) studies on the development of *Amphioplus abditus* showed that after 24 hrs of development triradiate spicules formed in the embryo, which after 5 hrs became tetraradiate. Examination of the structure of these spicules under polarized light revealed differences in the crystal lattice of individual spicular ends. Based on these results, Hendler concluded that the first spicules do not have a single center of crystallization but are a complex compound of different rods originating from different centers of crystallization. Such a state is possibly associated with the peculiarities of disposition of the spiculogenic cells.

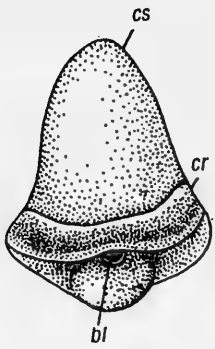


Figure 150: *Ophiopholis aculeata*. (Fewkes, 1893). Gastrula. General view. bl — blastopore; cr — ciliated ridge; cs — crest.

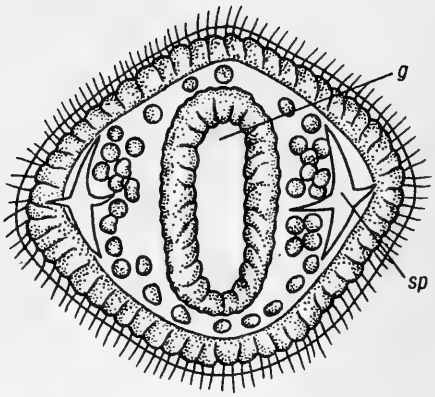


Figure 151: *Ophiura sarsi*. Prism stage. Optical section. g — gut; sp — tetraradiate spicule.

Pluteus I stage

Skeleton : In view of the fact that already at the prism stage there are in some species rudiments of two pairs of arms, as in *Ophiothrix fragilis* (McBride, 1907), or three pairs of arms in others, as in *Ophiura sarsi*, and Olsen (1942) describes a triradiate spicule in the prism stage and a tetraradiate spicule in the early pluteus in *Ophiopholis aculeata*, the division of the developing larvae into stages based on morphological characters is somewhat difficult. A comparison of the morphological features of plutei of various species of brittle stars based on the data of many authors (Fewkes, 1893; McBride, 1907; Mortensen, 1921, 1931, 1937, 1938; Narasimhamurti, 1933; Olsen, 1942) revealed that the first to develop are the basal and wideset, long posterolateral rods. The remaining arms, that is, the anterolateral and postoral, develop somewhat later, despite the fact that their rudiments are already present (Figure 152). The time interval between the growth of processes giving rise to the anterolateral and postoral rods may be quite substantial, from a few days to a few weeks. Thus, *Ophiura sarsi* needs one week to develop from the prism stage to the complete formation of the postoral rods, *Ophiothrix fragilis* requires three days (McBride, 1907), and *Ophiopholis aculeata* 10 days (Olsen, 1942). Since already in the early pluteus there are rudiments of the three

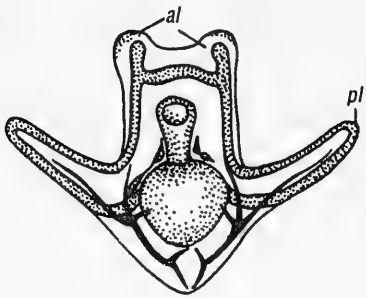


Figure 152: *Ophiopholis aculeata* (Fewkes, 1893). Early pluteus. General view. al — anterolateral arms; pl — posterolateral arms.

principal pairs of arms — posterolateral, anterolateral, and postoral (Figure 153) — the time of development of the postoral rods may be taken as the termination of the formation of pluteus I stage.

Feeding : At this stage, until the complete development of the anterolateral and posterolateral arms, the ciliated band passes along the margin of the preoral depression. The ciliated band is involved in obtaining food for the developing larvae only in species with planktotrophic larvae. According to Strathmann (1971), a part of the ciliated band between the anterolateral arms makes a loop above the preoral field towards the transverse section of the band of postoral arms after their development. Beating of the cilia produces a water current over the mouth opening and extends beyond the limits of the preoral field. Beating of the cilia of the posterolateral arms intensifies this current. As in the larvae of sea stars and sea urchins, the ciliated band in the ophiopluteus functions as a sieve which filters the food particles from the plankton (Figure 154). The lateral bands are made up of a single layer of cells. Studies conducted by Strathmann (1971) showed that in brittle stars each cell of the ciliated band bears one cilium. The ciliated bands on the arms are three to five cells wide; at some places the number of cells increases and, as a result, the band becomes broader. The preoral and aboral fields bear few cilia. Secretory cells have been detected in the tips of the arms of ophioplutei but, as in echinoplutei, these cells are few in number. Very likely, the

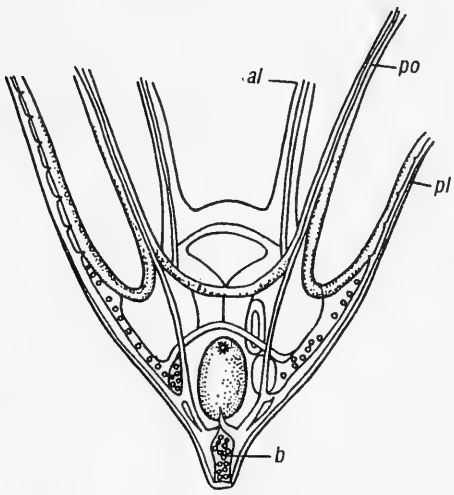


Figure 153: *Pluteus bimaculeatus* (Metchnikoff, 1869).
Pluteus I stage. General view.
al — anterolateral arms; b — basal rods; pl — posterolateral arms; po — postoral arms.

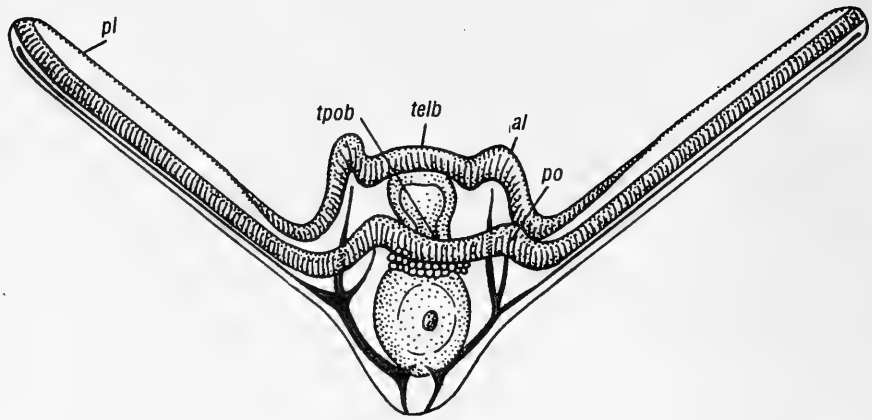


Figure 154: *Ophiothrix fragilis* (McBride, 1907).
General view of pluteus I stage.
al — anterolateral arms; pl — posterolateral arms; po — postoral arms; talb — transverse anterolateral band; tpob — transverse postoral band.

secretion produced by them helps to trap and to move food particles along the band. The food which reaches the oral opening is transported to the esophagus by means of the cilia in the oral cavity. All sections of the gut are provided with cilia. When the food enters the esophagus, it is transported up to the cardiac sphincter. As the latter opens, which is accompanied by a contraction of the esophageal muscles, the food clump passes into the stomach. Here the food is sorted. Strathmann (1971) demonstrated that when ophioplutei were fed a mixture of algae and carmine particles, the latter were soon discarded by the larvae, while the algae remained in the stomach for a long time. The rate of passage of food particles through the gut may be regulated by the speed with which the particles circulate in the upper part of the stomach and gather near the pyloric sphincter, from where they enter the small intestine and, upon contraction of the gastric muscles, are egested.

Brittle star larvae filter from the plankton microalgae that do not exceed 65 μm in diameter and 150 μm in length. These algae comprise various species of *Amphidinium, Cricosphaera, Phaeodactylum, Dunaliella* and others. The rate of filtration of food particles from the plankton varies from 1.8 to 3.0 ml/min.

In addition to sorting food in the stomach, brittle star larvae, like other echinoderms, can eject too large algae from the oral cavity or esophagus. For expulsion of such objects from the esophagus, the oral opening is enlarged, the direction of beating of the adoral band cilia changes, and the esophageal muscles contract. Enlargement of the oral opening by raising the preoral band

takes place through contraction of the muscles — dilatators — of the mouth, which extend from the ends of the preoral transverse band to the anterolateral arms. These muscles are able to contract together or individually. Expulsion of algae from the oral cavity is effected only by raising the preoral band through contraction of these muscles as well as contraction of the muscles of the dorsal wall of the oral cavity, without involvement of the esophageal muscles (Strathmann, 1971).

Respiration, transport of metabolites, and excretion: In brittle star larvae there are no special organs of respiration and excretion. The hemal system is also absent. Transport of nutrients is, possibly, done by the fluid of the primary and secondary body cavities.

At this stage, the coelomic sac is still not connected with the surrounding medium. The primary coelom is elongated and the two parts connected by a narrow canal are readily discernible. The left coelomic sac is divided into two: the upper — axocoel and hydrocoel, and the lower — somatocoel (Figure 155). Such a division was observed by McBride (1907) in *Ophiothrix fragilis* and by Grave (1898) in *Ophiocoma echinata*. Olsen (1942) found that in *Ophiopholis aculeata* the axocoel is the first to separate from the primary coelom.

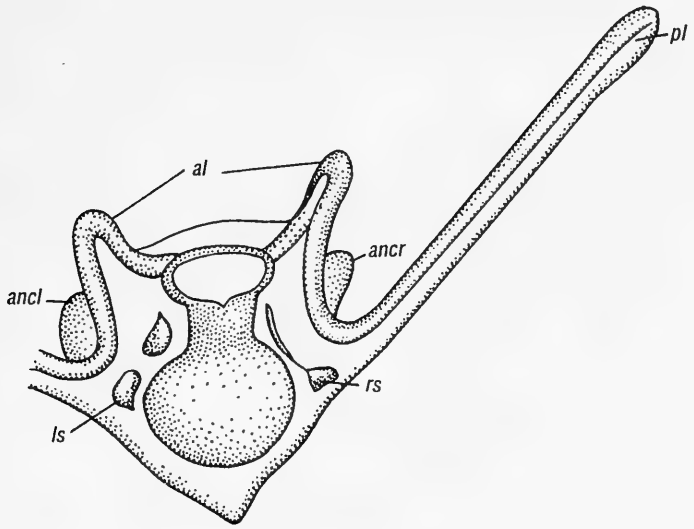


Figure 155: *Ophiothrix fragilis* (McBride, 1907).
Separation of the somatocoel from the anterior section of the coelom.
ancl — left anterior coelom; ancr — right anterior coelom; ls — left somatocoel; rs — right somatocoel.
Remaining legend same as in Figure 154.

Locomotion : The locomotory function, as in the larvae of other echinoderms, is performed by the ciliated band. The posterolateral arms attain maximum development in all planktotrophic larvae. During larval movement, the wave created by beating of the cilia passes along the band (Strathmann *et al.*, 1972).

Water currents along the outer edge of the arms are directed toward the narrowed basal part of the larva, pushing it forward. The brittle star larva does not have great maneuverability since the bands of the anterolateral and postoral arms participate basically in feeding. Moreover, in many brittle stars these are much shorter than the posterolateral ones. Nevertheless, by changing direction of beating of the cilia, the brittle star larva is capable of halting and turning. A change in the direction of beating of the cilia along the greater part of the ciliated band can produce a reverse movement of the larva. Swimming on the bottom of the dish in which they were reared, the larvae were capable of performing jerky movements with their oral opening down; the arms of brittle star larvae are rigidly fixed.

Nervous system and sensory organs : Mortensen (1937), describing the various larval stages of *Ophiocoma lineolata*, mentioned that nervous elements are present in different parts of the larval body. Unfortunately, he provided no description of these structures. Other information on the larval nervous system in brittle stars is lacking in the literature.

Pluteus II stage

Skeleton : Fully developed larvae of brittle stars have four pairs of arms. The last pair, the posterodorsal, appears after the anterolateral arms on the ventral side. The rays supporting them are processes of the anterolateral rods. The basal rods distally bear one or two pairs of transverse processes of varying lengths. In larvae of the genus *Ophiocoma*, these transverse processes are absent and the basal rods interlock (Figures 156, 157).

Feeding : McBride (1907) noted in the larva of this stage that the oral opening is bordered by the adoral ciliated band (Figure 158), in addition to the preoral band and lateral band, connecting the transverse areas of the anterolateral and postoral bands.

Respiration, transport of metabolites, and excretion : At this stage, the coelomic structures are more complex. The left anterior coelom is connected through the pore canal with the external environment and possibly participates in the excretion of products of metabolism. Studies on the development of *Ophiothrix fragilis* (McBride, 1907) and *Ophiocoma nigra* (Narasimhamurti, 1933) showed that soon after the formation of the pore canal, separation of

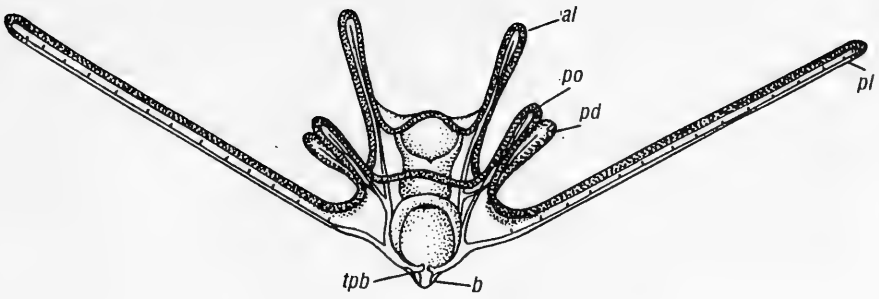


Figure 156: *Ophiothrix savignyi* (Mortensen, 1938).
General view of the larva.
b — basal rods; pd — posterodorsal arms; tpb — transverse processes of the basal rods.
Remaining legend same as in Figure 154.

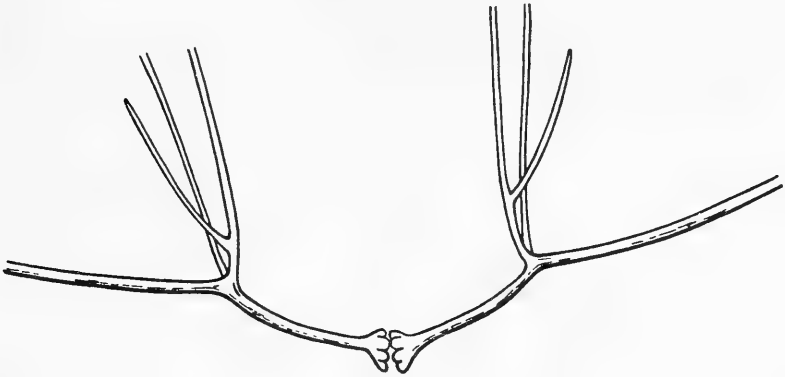


Figure 157: *Ophiocoma scolopendrina* (Mortensen, 1937).
General view of the skeleton. Note the absence of processes on the basal rods.

the hydrocoels begins. The left as well as the right hydrocoel remain connected with the axocoel through small canals (Figure 159). The canal on the left side of the larva later transforms into the stone canal.

Locomotion : With the appearance of the fourth pair of arms, the ciliated band enlarges but the pattern of larval movements does not change. Strathmann (1971) determined that the speed of horizontal movement of the larvae is roughly 0.5 mm/sec and the length of the cilia in the band 25–30 µm. At this stage, in some species vibratile lobes bordered with cilia develop between the posterolateral, postoral, and posterodorsal arms (Figure 160). Their

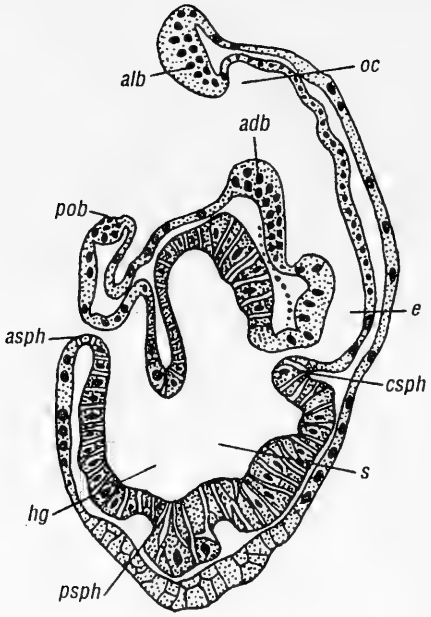


Figure 158: *Ophiothrix fragilis* (McBride, 1907).
Longitudinal section of the pluteus II stage.
adb — adoral band; alb — anterolateral band; asph — anal sphincter; csph — cardiac sphincter; e — esophagus; hg — hind gut; oc — oral cavity; pob — postoral band; psph — pyloric sphincter; s — stomach.

appearance is associated with the commencement of metamorphosis, when growth of the juvenile begins, and the larva becomes heavier.

Nervous system and sense organs: In larvae of many species of brittle stars an accumulation of pigment granules is seen at the tips of the arms and in the body alongside the stomach. The pigmentation may be reddish, yellowish, or greenish. It may be suggested that the cells containing the pigment granules perform the function of photoreceptors, analogous to what has been described by Ryberg and Lundgren (1979) in sea urchins.

Among the *rudiments of the definitive organs* in the ophiopluteus II stage, we can mention the processes of the hydrocoel and the first spicules of the definitive skeleton.

METAMORPHOSIS

In brittle stars metamorphosis occurs in free-swimming plutei. The definitive brittle star develops on the ventral side of the larva and the fully

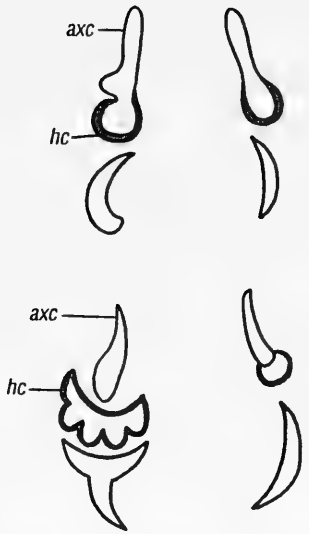


Figure 159: *Ophiothrix fragilis* (McBride, 1907).
Separation of hydro- and axocoel. Formation of primary evaginations of hydrocoel.
axc — axocoel; hc — hydrocoel.

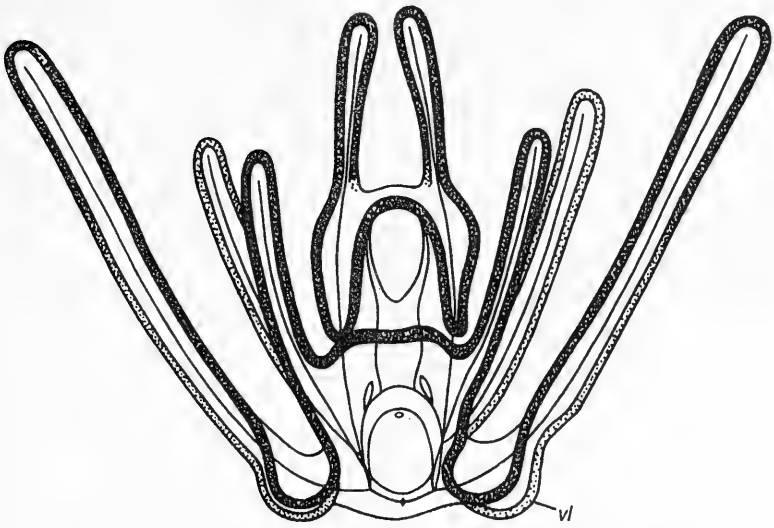


Figure 160: *Ophiocoma scolopendrina* (Mortensen, 1937).
Formation of vibratile lobes.
vl — vibratile lobes.

formed individual settles on the bottom. As in the sea stars and sea urchins, metamorphosis in the brittle stars is catastrophic. The larval organs and tissues degenerate and are reorganized. The posterolateral arms supporting the juvenile in the plankton remain longer than the other arms. In some species, after the brittle star settles on the bottom, these arms with their fringe of ciliated band swim independently in water for some time, similar to the preoral lobe of bipinnariae of astropectinids and luidiids after the conclusion of metamorphosis.

Skeleton : No amniotic sac forms in brittle stars and the commencement of metamorphosis can be considered coincident with the appearance of processes in the hydrocoel. However, the first spicules, from which the elements of the definitive skeleton will develop, appear somewhat earlier than the hydrocoelic processes. They are situated on either side of the stomach, with five spicules on each side (Figure 161). With further development, they give rise to five radial and five terminal plates. The central plate of the aboral side appears somewhat later. Next come the rudiments of the proximal oral plates

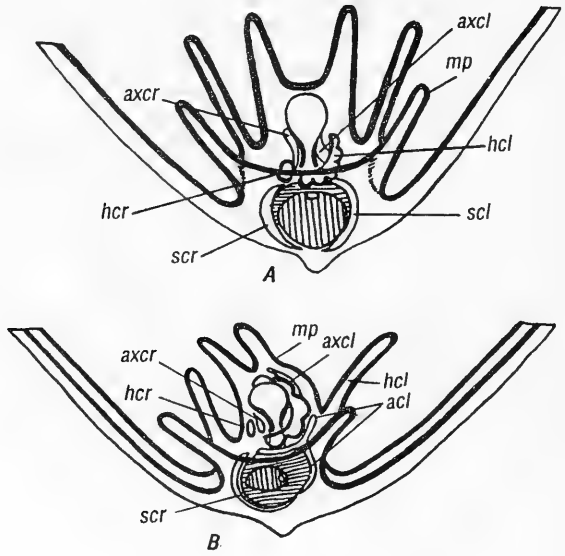


Figure 161: *Ophiothrix fragilis* (McBride, 1907).
Arrangement of different parts of the coelom at commencement of metamorphosis in brittle stars.

A — before turning and reduction; B — after turning and reduction of larval arms; axcl — left axocoel; axcr — right axocoel; hcl — left hydrocoel; hcr — right hydrocoel; mp — madreporic pore; scl — left somatocoel; scr — right somatocoel.

or ambulacralia. After this the paired distal oral plates develop (Figures 162, 163, 164). Soon after settling, rudiments of the dental plates appear between the proximal oral plates. Development of the definitive skeleton of brittle stars was studied by Fewkes (1887), Mortensen (1921, 1937, 1938), and Hendler (1978).

Simultaneous with the development of the juvenile organism, reduction of the larval arms starts with disappearance of the anterolateral and posterodorsal arms. The posterolateral arms are retained the longest. None of the fragments of the larval skeleton take part in the formation of the elements of the definitive skeleton.

Digestive system : Like other areas of the larval epithelium, the ciliated band is dedifferentiated and partially resorbed. The definitive epithelium is formed from the larval epithelium (Chia and Burke, 1978).

Brittle star larvae do not feed during metamorphosis since the small intestine of the larva is destroyed and resorbed; the esophagus and stomach

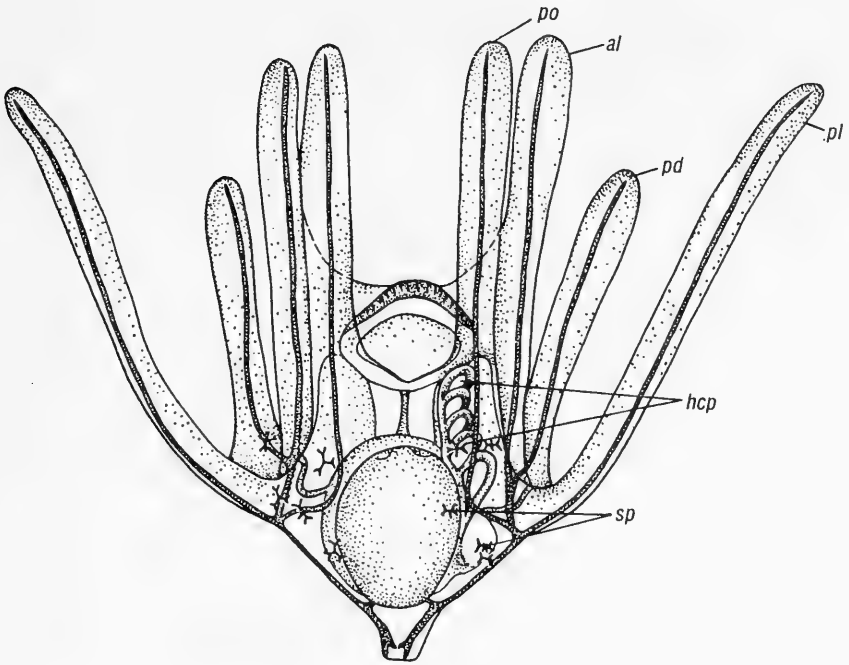


Figure 162: *Ophiura sarsi*.
General view of the larva during metamorphosis.
al — anterolateral arms; hcp — hydrocoel process; pd — posterodorsal arms; pl — posterolateral arms; po — postoral arms; sp — spicules, forerunners of the definitive skeleton.

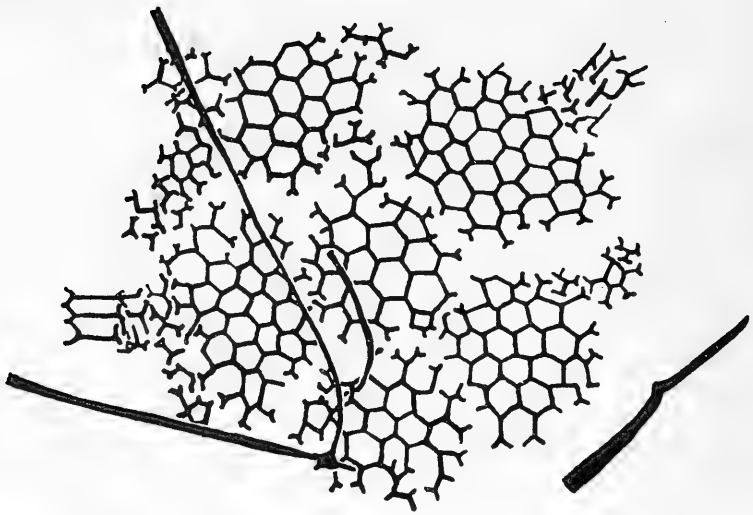


Figure 163: *Ophiura sarsi*.
Arrangement of plates on the aboral side of the juvenile.

Figure 164: *Ophiura sarsi*.
Arrangement of plates on the oral side of the juvenile.

are reorganized, acquiring the shape of a homogeneous cellular mass in which, at a later stage, lumens appear and the epithelial structure is restored. At this time, formation of the oral disk proceeds on the ventral side concomitant with ectodermal thickening. The oral opening lies in the center of this disk and is covered by the peristomial membrane. The peristomial membrane delimits the peristomial cavity in which the dental apparatus develops after the larva has settled. Brittle stars lack an anal opening (McBride, 1907; Narasimhamurti, 1933; Olsen, 1942).

Respiration : The respiratory functions are passed on from the larval epithelium to the definitive epithelium, including the epithelium covering the ambulacral podia. The transport functions are transferred to the hemal and perihemal systems and the visceral coelom. Spheroid bodies with phagocytes and, possibly the axial organ, take part in excretion processes. Considerable modifications of the coeloms lead to the formation of an ambulacral system, hemal and perihemal systems, and perivisceral coelom of the definitive individual.

Locomotion : During metamorphosis, the locomotor functions are passed on from the ciliated band to the first terminal and first ambulacral podia; in lecithotrophic larvae of *Ophiura brevispina* and *Ophiolepis elegans* the two locomotor systems function simulataneously (Strathmann, 1978). Later, the ambulacral system loses its leading role in locomotion in brittle stars and the mobile arms of the definitive brittle stars act as the principal locomotor organs.

Nervous system : The epineural radial and ring canals form under the lateral processes of the hydrocoel and ring canal of the ambulacral system. The ectoneural system passes in the canals of the epineural system. The hyponeural system develops in the walls of the perihemal canals (McBride, 1907; Olsen, 1942).

Reproductive system : The primary gonads appear in the walls of the left somatocoel adjacent to the stone canal and begin to form the gonadial strand after the juvenile individual settles (Figure 165).

Settling : Development of the juvenile individual proceeds during the planktonic larval period. Completely formed individuals settle on the substrate. No attachment organs are present in brittle stars. There is no reliable information on ability to search the substrate before settling (Strathmann, 1978). The juvenile brittle stars, on settling, attach themselves to the substrate by primary ambulacral podia. Usually, by this time, nearly all the larval arms are fully resorbed. However, McBride (1907) noted that in *Ophiothrix fragilis* the posterolateral arms are shed after the juveniles settle on the bottom. Thus,

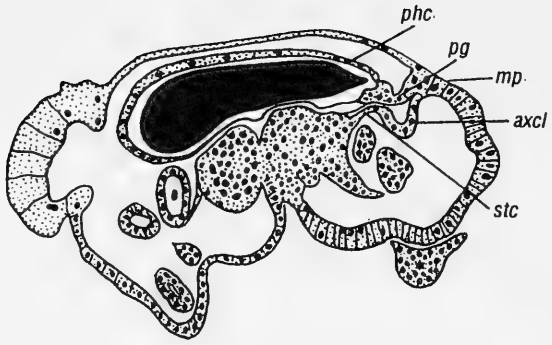


Figure 165: *Ophiothrix fragilis* (McBride, 1907).
Transverse section. Appearance of primary gonads.
axcl — left axocoel; mp — madreporic pore; pg — primary gonads; phc — perihemal canal; stc — stone canal.

young brittle stars are capable not only of creeping on the substrate, but also swimming over the bottom as well, for which they use the remains of the ciliated band.

LECITHOTROPHIC LARVAE

Some brittle star species have lecithotrophic larvae, which are similar to planktotrophic larvae; these are, for example, *Amphiura filiformis* (Mortensen, 1931), *Amphiura chiajei* (Fenaux, 1963), and *Ophiothrix oerstedi* (Mladenov, 1979). Other species have larvae of the doliolaria type; these are *Ophioderma brevispine* (Grave, 1916), *Ophiolepis cincta* (Mortensen, 1938), *Ophioderma longicauda* (Fenaux, 1969), and *Ophiolepis elegans* (Stancyk, 1973). Development of the third group of species is close to direct; these include *Gorgonocephalus caryi* (Patent, 1970a) and *Amphioplus abditus* (Hendler, 1977). The development of the latter group of species is interesting in that the egg membrane persists until the young brittle star hatches, although until the prism stage it does not differ in development from planktotrophic larvae, and rudiments of the larval skeleton remain up to much later stages (Figure 166). Thus, this type of development resembles the development of gastropods in clutches or capsules.

Generally, in any type of development with a lecithotrophic larva, cleavage and formation of the blastula proceed in the same manner as in the case of a planktotrophic larva. If in the process of development the larval skeleton is formed, then it, too, develops as in a planktotrophic larva (Figure 167). *Amphiura chiajei* (Fenaux, 1963) and *Ophiothrix oerstedi* (Mladenov, 1979) develop only the posterolateral arms.

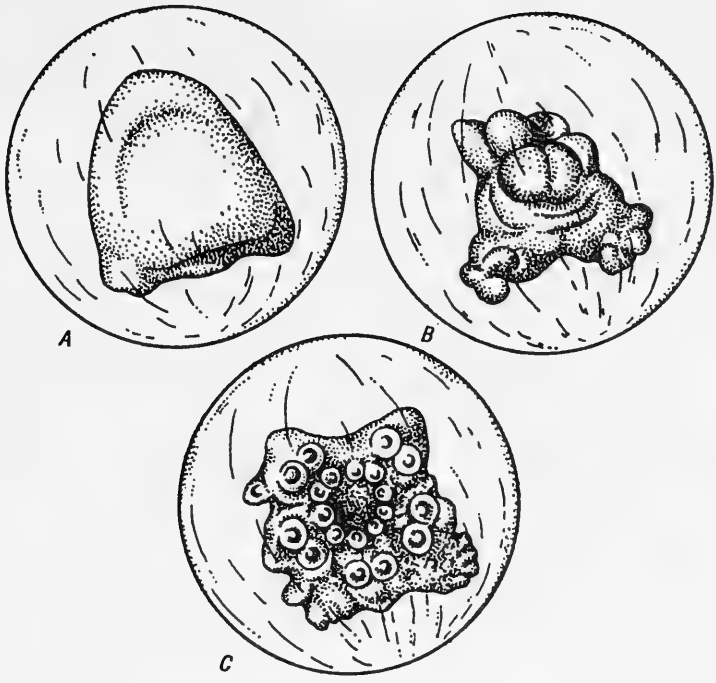


Figure 166: *Amphioplus abditus* (Hendler, 1977).
Three stages of development of brittle stars within the envelope.
A — prism stage; B — first separation of the rudiments of the juvenile; C — formation of rudiments of the ambulacral podia and mouth.

In the case of a larva of the doliolaria type development up to the gastrula does not differ from development of a planktotrophic larva. The blastopore closes early in the gastrula. The preoral lobe develops at the anterior end and the oral opening itself is shifted to the posterior end.

Separation of the left hydrocoel, forming five rudiments of the various canals of the ambulacral system (Figure 168), begins before the formation of ciliated bands. Then, in the place of a uniform ciliary cover, four transverse ciliated bands are formed, as in doliolariae of sea cucumbers. One of the bands passes at the level of the oral opening, near which it becomes discontinuous (Figure 169). At this stage, in some brittle stars, rudiments of the larval skeleton become visible (in *Ophiolepis cincta* — Mortensen, 1938). Then the posterior part of the larva gradually acquires a pentagonal shape and the larva descends to the bottom where metamorphosis is completed (Figure 170).

With reference to the settling of doliolaria-type larvae, Stancyk (1973)

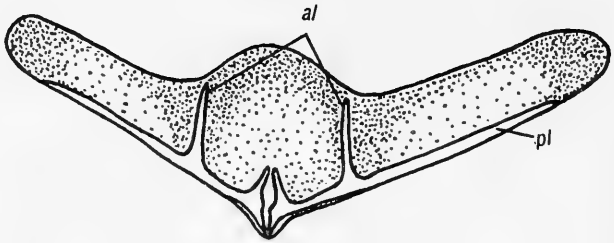


Figure 167: *Ophiothrix oerstedi* (Mladenov, 1977*).
Formation of the larval skeleton in the lecithotrophic larva.
al — anterolateral arms; pl — posterolateral arms.

noted that larvae of *Ophiolepis elegans* were able to swim as well as creep for some time before they actually settled down.

In addition to development with planktotrophic and lecithotrophic larvae, viviparity has been confirmed for many species of brittle stars. A majority of these species live in polar regions or at great depths. Among them, some species occur only in specific regions, for example, *Stegophiura vivipara* (Matsumoto, 1915) off the coast of Japan. On the other hand, there are cosmopolitan species, such as *Amphipholis squamata*, found almost universally in temperate latitudes. Wide distribution has also been reported for some deepwater species, such as *Ophiomusium lymani* (Tyler, 1980) reported for the Atlantic as well as the Pacific Ocean.

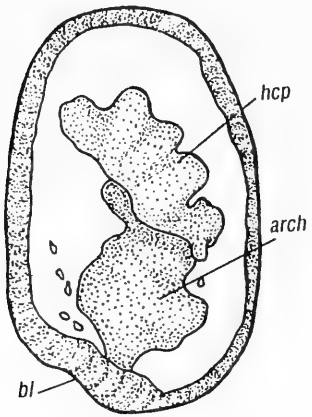


Figure 168: *Ophioderma longicauda* (Fenaux, 1969).
Formation of hydrocoel processes.
arch — archenteron; bl — blastopore; hcp — hydrocoel processes.

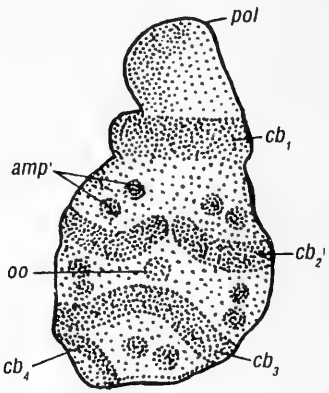


Figure 169: *Ophiolepis elegans* (Stancyk, 1973).
Formation of the transverse ciliated bands in the doliolaria-type larva.
amp — rudiment of ambulacral podia; cb (1, 2, 3, 4) — transverse ciliated bands; oo — oral opening; pol — preoral lobe.

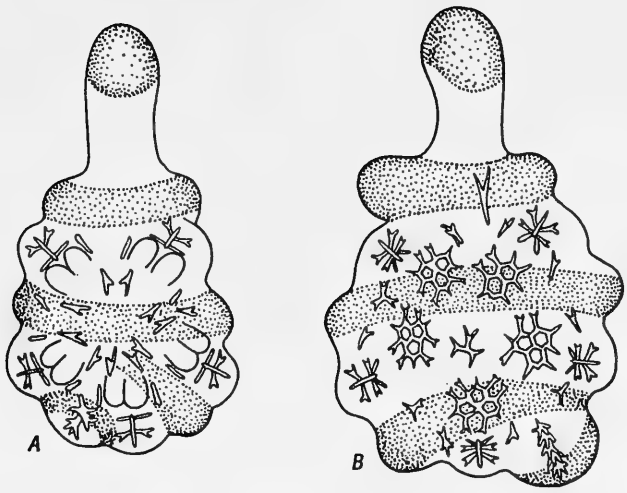


Figure 170: *Ophiolepis cincta* (Mortensen, 1938).
Arrangement of primary plates of the definitive skeleton.
A — oral side of the juvenile; B — aboral side of the juvenile.

Ophiuroidea is the only class of echinoderms in which dwarf males are found. It is not clear if all brittle stars with dwarf males (four species are known to date) have brood care as in bivalves (see Chapter 1); however, in *Astrochlamys bruneus*, in which dwarf males perch on the aboral surface of the females, viviparity has been observed.

In viviparous brittle stars the development of the young occurs in the female bursae. The number of embryos is small, usually one or two. However, the number of developing embryos is sometimes fairly large. Murakami (1941) — cited after Hendler, 1975 — found up to 70 individuals in *Stegophiura sculpta* and Mortensen (1936) up to 200 individuals in *Astrochlamys bruneus* in each bursa.

Does viviparity actually occur in brittle stars? Or do we observe only brood care in brood chambers, as in sea urchins and sea cucumbers? For many species, this problem has yet to be solved. Only one comprehensive work is available on the development of *Amphipholis squamata* (Fell, 1946), in which viviparity has been confirmed. Fell demonstrated that the developing embryos were attached to the horn of the bursa and not to the ovary. After differentiation of layers in the embryo, the latter was surrounded by the wall of the horn. At the site of attachment of the embryo to the horn of the bursa, the parental and embryonal tissues fused. Later, the stalk on which the developing embryos are suspended in the bursal cavity appeared at this site. In his earlier works, Fell proposed that feeding of the embryos is accomplished through this stalk. In a later work, (Fell, 1946), he suggested that this stalk is used only for attachment.

Experiments on embryos reared *in vitro* showed that for their normal development additional substances are required. Observing the morphological changes in the bursal wall in the last stages of development of embryos, Fell concluded that nutrients are produced by the wall itself and feeding of the embryo occurs by absorption through the entire surface of the embryo.

Another case of true viviparity has been described by Mortensen (1921) in the Antarctic brittle star *Ophionotus hexactis*. In this species only one egg matures in the ovary; development of the juvenile is also introovarian, evidently due to feeding nutritive and visceral fluid (Turner and Dearborn, 1979). After emergence of the young brittle star, a new ovary develops.

Hyman (1955), based on data on the reproduction of brittle stars, concluded that in the viviparous species the spawning period is more protracted than in the species with lecithotrophic and planktotrophic development. A list of species and their mode of development is given in Table 6.

IDENTIFICATION OF PELAGIC LARVAE OF BRITTLE STARS (Terminology and Diagnostic Characters)

Brittle star larvae have an endoskeleton composed of rods that support the arms and basal part of the body, which is flattened dorsoventrally. The arms are listed in the order of their appearance. In the early stages of plutei the posterolateral and anterolateral arms develop on the ventral side and later the postoral arms develop on the dorsal side. Generally, the rods supporting the arms are simple, but in some species the rods of the posterolateral arms may be fenestrated. The basal rods passing in the body of the larva may be distally bifurcate and sometimes the ends are interlocked. In many species one or two pairs of transverse processes develop in the lower third of the basal rods. Another pair of arms, the posterodorsal, appears at a later stage; these arms develop behind the anterolateral arms on the ventral side. Their supporting rods appear as processes of the anterolateral rods. Between the basic arms, except the anterolateral, vibratile lobes may develop. Pigment granules appear under the ciliated band at the tips of the arms and in the region of the stomach. Pigmentation varies in different species.

The following diagnostic characters are useful for identification of brittle star larvae.

1. Number of arms. Three pairs in the first stage and four pairs in the second stage.
2. Structure of rods of the larval skeleton. In larvae of the family amphiuridae all skeletal rods are simple.

Table 6: Types of development in brittle stars

Species	Type of development	Author
	Order Ophiurida	
Ophiomyxa serpentaria	Lecithotrophic larva	Tyler, 1980
Ophiomyxa brevirima	Viviparity	Hendler, 1975
Ophiomyxa vivipara	Same	Same
Ophioscolex nutrix	Same	Same
Ophiacantha normani	Same	Tyler, 1980
Ophiacantha anomala	Same	Same
Ophiacantha bidentata	Same	Same
Ophiacantha dansispina	Same	Hendler, 1975
Ophiacantha vivipara	Same	Same
Ophiomitrella clavigera	Same	Same
Ophiomitrella ingrata	Same	Same
Ophiolebella biscutifera	Same	Same
Amphiura chiajei	Planktotrophic larva	Fenaux, 1963
Amphiura filiformis	Same	Mortensen, 1920
Amphiura annulifera	Viviparity	Mortensen, 1931
Amphiura stepanovii	Same	Same
Amphiura belgicae	Same	Hendler, 1975
Amphiura monorima	Same	Same
Amphiura stimpsoni	Same	Same
Amphiura capensis	Same	Same
Amphiura magellanica	Same	Same
Amphiura microplax	Same	Same
Amphioplus abditus	Lecithotrophic larva	Hendler, 1977
Amphipholis squamata	Viviparity	Russo, 1891; Fell, 1946; Hendler, 1975
Amphipholis torelli	Same	Hendler, 1975
Axiognathus japonica	Same	Same
Ophiopholis aculeata	Planktotrophic larva	Olsen, 1942
Ophiactis balli	Same	Mortensen, 1913
Ophiactis savignyi	Planktotrophic larva	Mortensen, 1931
Amphilepis ingolfiana	Lecithotrophic larva	Tyler, 1980
Ophiothrix angulata	Planktotrophic larva	Mortensen, 1921
Ophiothrix fragilis	Same	McBride, 1907
Ophiothrix quinquemaculata	Same	Hendler, 1975
Ophiothrix savignyi	Same	Mortensen, 1938
Ophiothrix triloba	Same	Mortensen, 1937

(*Contd.*)

(*Table 6 contd.*)

Species	Type of development	Author
Ophiomaza cacaotica	Same	Mortensen, 1937
Ophionereis squamulosa	Lecithotrophic larva	Mortensen, 1921
Ophionereis vivipara	Viviparity	Hendler, 1975
Ophiocoma echinata	Planktotrophic larva	Grave, 1898
Ophiocoma erinaceus	Same	Mortensen, 1937
Ophiocoma pica	Same	Same
Ophiocoma pumila	Planktotrophic larva	Hendler, 1975
Ophiocoma scolopendrina	Same	Mortensen, 1937
Ophiocomina nigra	Same	Narasimhamurti, 1933
Ophioderma brevispina	Lecithotrophic larva	Hendler, 1975
Ophioderma longicaudum	Same	Fenaux, 1969
Ophioconis vivipara	Viviparity	Mortensen, 1931
Pectinura cylindrica	Same	Same
Pectinura gracilis	Same	Same
Ophiura ljungmani	Planktotrophic larva	Same
Ophiura texturata	Same	Same
Ophiura sarsi	Same	Our data
Ophiura albida	Same	Mortensen, 1931
Ophiura robusta	Same	Thorson, 1946
Ophiura affinis	Lecithotrophic larva	Hendler, 1975
Ophiura meridionalis	Viviparity	Hendler, 1975
Ophiura ronchi	Same	Same
Ophiura loveni	Same	Tyler, 1980
Homalophiura tesselata	Lecithotrophic larva	Same
Stegophiura vivipara	Viviparity	Matsumoto, 1915
Stegophiura sculpta	Same	Hendler, 1975
Amphiophiura rowetti	Same	Same
Amphiophiura pachylax	Same	Tyler, 1980
Amphiophiura bullata	Same	Same
Ophiolepis cincta	Lecithotrophic larva	Mortensen, 1938
Ophiolepis elegans	Same	Stancyk, 1973
Ophiocten sericeum	Planktotrophic larva	Tyler, 1980
Ophiomusium lymani	Lecithotrophic larva	Same
Ophyophycis gracilis	Viviparity	Hendler, 1975
Ophiozonella falklandica	Same	Same

(*Contd.*)

(*Table 6 contd.*)

Species	Type of development	Author
Ophionotus hexactis	Viviparity	Hendler, 1975
Ophiopyren striatum	Lecithotrophic larva	Tyler, 1980
Ophiopleura borealis	Planktotrophic larva	Same
Ophioceres incipiens	Viviparity	Hendler, 1975
Ophiophrixus spinosus	Same	Tyler, 1980
Ophioplocus esmarki	Same	Hyman, 1955
Ophiotjalfa vivipara	Same	Hendler, 1975
Ophiurolepis gelida	Same	Same
Ophiurolepis martensi	Same	Same
Cryptopelta granulifera	Same	Mortensen, 1933
Order Phrynophiurida		
Astrotoma waitei	Viviparity	Hendler, 1975
Astrochlamys bruneus	Same	Same
Gorgonocephalus caryi	Lecithotrophic larva	Patent, 1970a
Gorgonocephalus arcticus	Same	Mortensen, 1931
Gorgonocephalus euchemis	Same	Same

3. Joining of the basal rods of the skeleton.
4. Presence and number of transverse rods issuing from the basal rods.
5. Presence of vibratile lobes in the second stage larvae.
6. Presence and color of the pigment.
7. Length of the larva from body base to tips of arms, perpendicular.
8. Distance between tips of the posterolateral arms in the second-stage larva.

Key to Species Based on Larvae at the Pluteus Stage

1 (2). Larva with one pair of arms.
2 (5). Larva with two–three pairs of arms.
3 (4). Basal rays smooth. . . . . **Amphipholis kochii,** Stage I
4 (3). Basal rays with spines. . . . . **Ophiura sarsi,** Stage I
5 (2). Larva with two pairs of arms.
6 (9). Larva with three pairs of arms.
7 (8). Basal rays with three short terminal processes. . . . . **Amphipholis kochii,** Stage II
8 (7). Basal rays without terminal processes. . . . . **Ophiura sarsi,** Stage II

9 (6). Larva with four pairs of arms.
10(11). All terminal processes on basal rays with many short spines. . . . . .**Amphipholis kochii,** Stage II
11(10). Only two terminal processes of basal rays with spines. . . . . **Ophiura sarsi,** Stage II

FAMILY CHARACTERS OF LARVAL BRITTLE STARS

Ophiuridae

It is not possible to identify only one type of development as typical for the brittle stars of this family. Planktotrophic and lecithotrophic larvae as well as brood care have been observed here. In the planktotrophic type, larval development is marked by very slender, elongate posterolateral arms; the rays supporting them may be fenestrated in some species. A fully developed larva has four pairs of arms. At later stages a bright green stomach becomes very distinct. The pigment in the arms and body of the larva varies in color in different species. Unlike larval sea urchins, there are no vibratile plates, pedicellariae and ciliated epaulettes.

Ophiura sarsi Lütken and *Ophiura sarsi vadicola* Djakonov are found in the Sea of Japan. The larvae have been described by Kryuchkova (1988).

Amphiuridae

Viviparity is characteristic of most of the studied species of this family. During planktotrophic development of the larva the typical pluteus with four pairs of arms develops. The transition to a larva with one pair of arms occurred in the course of evolution of viviparity. The skeletal rods are simple in all larvae. In larvae with four pairs of arms the body is compact and opaque in the early stages; at later stages the body becomes almost transparent. In larvae with a reduced number of arms the body continues to remain opaque at all stages of development. At later stages, in species with a fully developed larva an orange or red pigment appears along the rods supporting the arms and at the end of the arms.

One species, *Amphipholis kochii* Lütken, is found in Peter the Great Bay. The larva of this species has been described by Yamashita (1985) and Kryuchkova (1988).

OPHIURA SARSI LÜTKEN

(Ophiuridae)

Mature eggs are reddish, nontransparent, 100 μm in diameter. Under laboratory conditions the 8-cell stage is formed 1 hr after fertilization at a temperature of 16°C. After 6 hrs, the blastula can be seen; 2 hrs later the blastula begins to swim but hatching from the membrane does not occur. Cilia pass through the membrane adjoining the outer wall of the blastula. At this stage, the blastula is spherical. After 21 hrs, the blastula changes, elongating along the animal-vegetal axis; the animal pole is slightly tapered and the vegetal pole flattened. The gastrula with a well-developed archenteron is formed after 45 hours. An accumulation of primary mesenchymal cells is observed around the base of the archenteron. In shape the gastrula resembles an isosceles triangle whose base is situated at the vegetal pole. The next day, tetraradiate calcite spicules — rudiments of the larval skeleton — are discernible among the cells of the primary mesenchyme. The length of the embryo at this stage is 150 μm. Along the perioral depression a ciliated band is formed; all other cilia, except in the basal part of the body, disappear. Pluteus I stage is fully formed on the 6th day.

Pluteus I Stage

At the point of divergence of the basal rods, the larval body has a distinct girdle. All the skeletal rods are simple and provided with fine spinules. The posterolateral arms are the first to differentiate, followed by the anterolateral arms. The preoral arms remain for some time in a rudimentary state. As the pluteus grows, the structure of the basal rods becomes more and more complex. Large spines, two on each rod, arise on their distal ends, they contact to form a ring. The ends of the basal rods, initially pointed, now become thickened and flattened. The yolk membrane, yolk granules, and cilia disappear at the basal end of the pluteus. By the time rudiments of the fourth pair of arms appear, the pluteus has reached 450 μm in length; 550 μm between tips of the posterolateral arms (Figure 171).

Pluteus II Stage

Plutei of this stage are distinguished by the yellow color of the stomach. The fourth pair of rods, the posterodorsal, forms as processes of the anterolateral rods, which are found in their lower third (Figure 171). On full development, these rods are slightly shorter than the postoral. As soon as the larva reaches a length of 750 μm and 1,250 μm between the tips of the posterolateral arms, the skeletal rods become yellowish-brown and the stomach becomes green. The basal rods are distally form thick processes, by means of which the rods

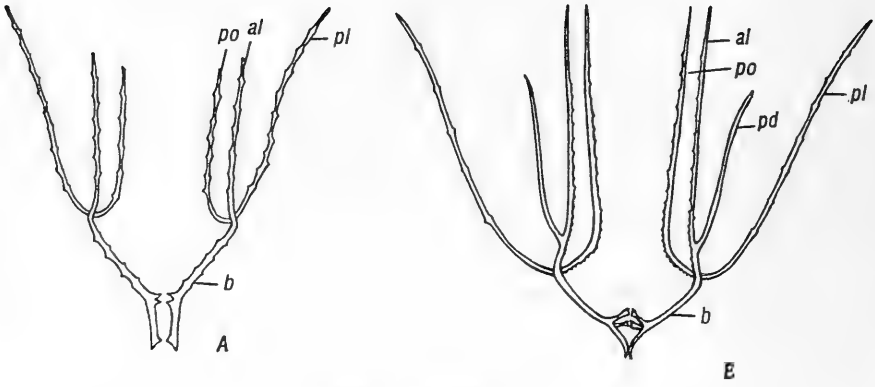


Figure 171: *Ophiura sarsi*.
A — Pluteus I stage; general view of the larval skeleton; B — Pluteus II stage; beginning of formation of the posterodorsal rods.
Legend same as in Figure 162.

are interconnected. At this stage, it is possible to distinguish spicules in the larvae, which give rise to the first plates of the definitive skeleton (see Figure 182).

Ecology

Brittle stars of this species are ready for spawning in Vostok Bay in late April when the water temperature is 4.9°C. Larvae of this species were found in the plankton only one month later, in May, when the water temperature was 11°C. Larvae completing metamorphosis were found in early July when the water temperature was 15°C.

Mortensen (1898, 1931) described the larva of "*Ophiopluteus compressus*" with characteristic perforated rods and purplish-black granules of the posterolateral and posterodorsal arms and proposed that it might belong to *Ophiura sarsi* on the basis that the adult animals of this species are fairly numerous in Danish waters and their reproduction period coincides with the appearance of the larvae in the plankton. Thorson (1946), based on Mortensen's data, also proposed that *Ophiopluteus compressus* might possibly be the larva of *O. sarsi*. These larvae are found in Öresund Strait (The Sound) in April at a water temperature of 5.8°C. However, Thorson does not describe the larvae obtained by him while rearing *O. sarsi*.

AMPHIPHOLIS KOCHII LÜTKEN

Spawned eggs of *A. kochii* are 100 μm in diameter, opaque and slightly brownish. After 6.5 hrs of development, the early blastula appears, which is spherical and covered with a transparent, hyaline membrane through which cilia protrude. Soon the shape of the blastula changes; it becomes oval and elongates along the animal-vegetal axis. The gastrula forms after 20 hrs of development. It is somewhat flattened laterally, retains the hyaline membrane, and its surface is uniformly covered with cilia. After 25 hrs of development, the gastrula forms a crest and then acquires a triangular shape. After some time, it is possible to distinguish four axial spicules, rudiments of the larval skeleton.

Pluteus I Stage

After 42 hrs of development, the early pluteus is formed. All the skeletal rods in it are simple. At this stage, cilia are still retained over the entire body of the larva but their length varies; the longest occur in the ciliated band and at the basal end of the body. The crest is also retained. The entire larva is opaque and reddish-brown. The hyaline membrane persists but its thickness reduces considerably. In live specimens the skeletal rods are poorly visible. at the 49th hr of development, the posterolateral arms increase somewhat in length and their ends become transparent. The basal rods of the larval skeleton distally bear three prominent, short processes forming an analogue of a lock. Cilia in the basal part of the body and the hyaline membrane are still retained. The entire larva, except for the ends of its posterolateral arms and the loop of the ciliated band of the oral region, is reddish-brown (Figure 172).

When the pluteus dimensions reach 350 μm × 165 μm, the skeletal rods begin to show minute spines. The lower process of the basal rod elongates, its length reaching 25 μm. At the tip it becomes bifurcate. The larval body in the region of the processes is drawn towards the ventral side. The reddish-brown color disappears but the hyaline membrane is still intact at places. Cilia of the basal part of the larva disappear. When the larva dimensions reach 400 μm × 200 μm, the rudiments of the posterolateral arms become visible. The rods of these arms, as also the entire skeleton, are simple. At dimensions of 450 μm × 250 μm, the lateral processes of the basal rods of the skeleton elongate and form a rhombic structure, but do not fuse into a single complex. At this stage, the hyaline membrane still persists at some places, although its thickness reduced very significantly.

At dimensions of 500 μm × 300 μm, the posterolateral arms in the pluteus become especially elongate and orange pigment granules begin to appear along their spines. The hyaline membrane disappears completely.

Later, the posterolateral arms form and the overall body size of the larva increases (Figure 172).

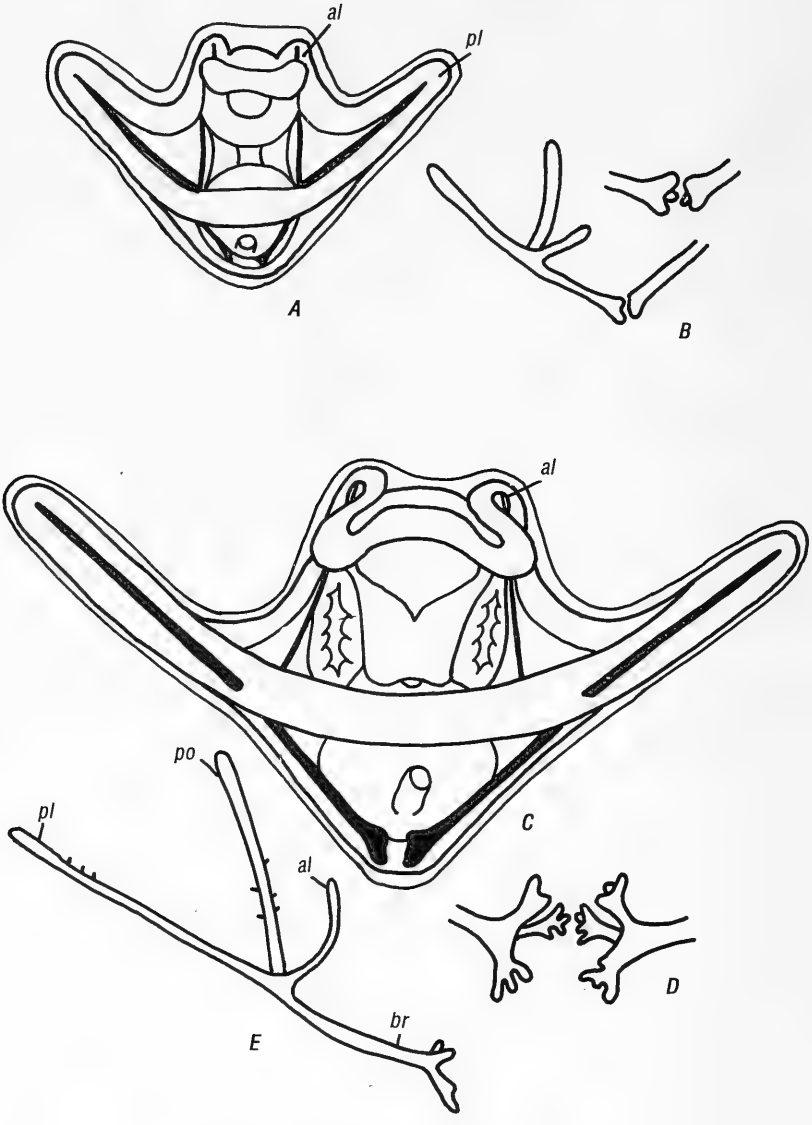


Figure 172: *Amphipholis kochii*.

A — early pluteus I stage; B — joining of rods of the larval skeleton in pluteus I stage; C — pluteus I stage; D — joining of rods of the left half of the skeleton; E — joining of basal rods of the skeleton.

al — anterolateral arms; br — basal rod; pl — posterolateral arm; po — postoral arm.

CHAPTER V

LARVAE OF SEA CUCUMBERS (MORPHOLOGY, PHYSIOLOGY, AND BEHAVIOR)

EARLY DEVELOPMENT

Egg

Among holothurians, Mortensen (1937) identified two species — *Synaptula vittata* and *Synaptula reciprocans* — in which the egg diameter is 50 μm. For most species, eggs with a diameter of 100–200 μm are characteristic. These are *Ophiodesoma grisea, Holothuria papillifera, H. difficilis* (Mortensen, 1938), *Leptosynapta inhaerens* (Runnström, 1927), and *Stichopus japonicus.* Among holothurians of the genus *Cucumaria,* the egg diameter varies from 300 μm in *C. echinata* to 1.5 mm in *C. laevigata* (Ohshima, 1921). The maximum egg diameter has been observed in deepwater holothurians. According to Ohshima (1921), *Benthodytes gotoi* and *Euphronides depressa* have eggs with a diameter of about 2.5 mm and *Enypniastes eximia* of 3.5 mm.

Mortensen (1938) noted that in *Ophiodesoma grisea* the eggs are transparent. Generally, the eggs of holothurians are opaque because of their large yolk content, which is often red or yellowish-brown. In holothurians of the genus *Cucumaria,* the eggs are yellowish-red at the animal pole and green at the vegetal.

Smaller eggs are spherical. Large eggs are oval and often flattened at the animal pole. This peculiar feature was noticed in *Cucumaria echinata* (Ohshima, 1921), *Thyone briareus* (Ohshima, 1925), *Cucumaria elongata* (Chia and Buchanan, 1969), and *Caudina chilensis* (Inaba, 1930). In *Psolua phantapus* (Runnström and Runnström, 1919) the eggs are oval.

The eggs are covered with vitelline and jellylike envelopes. The jellylike envelope in some species is considerably thick. For example, in *Cucumaria echinata* it is 50–70 μm (Ohshima, 1921) and in *C. elongata* 40–60 μm

(Chia and Buchanan, 1969). The presence of a micropyle process has been reported at the animal pole of the oocyte, which is connected with the follicular cells.

Fertilization: In holothurians extrusion of gametes in water as well as their release in the coelomic sac has been observed, for example in *Chiridota rotifera* (Clark, 1910). The spermatozoa penetrate not the mature egg but the oocyte. When a micropyle is present, the sperm reaches the oocyte through it. Ohshima (1925) observed in *Thyone briareus* sperm penetration at the equator from the side of the vegetal hemisphere. During fertilization an acrosomal reaction of the sperm occurs and a distinct fertilization cone is formed (the primary eminence) in the eggs of *Holothuria atra* and *Thyone briareus* (Colwin and Colwin, 1957).

After sperm penetration, meiotic division of the oocyte is completed with the formation of polar bodies. Inaba (1930) observed in *Caudina chilensis,* in the second meiotic division, the formation of three polar bodies which were retained at the animal pole at the beginning of cleavage.

Cleavage: In holothurians, except for *Cucumaria glacialis*, independent of the quantity of yolk in the egg, a complete uniform cleavage of the radial type is observed. The first two divisions are meridional and the third equatorial. Thereafter, meridional and equatorial divisions alternate (Figure173). As the number of blastomeres increases, they shift to the animal and vegetal poles, but the blastocoel remains open for some time in the polar region (Chia and Buchnan, 1969). After formation of the 32-cell stage, the time of division for different blastomeres differs and their radial disposition is disturbed (Kume and Dan, 1968). In *Thyone briareus* (Ohshima, 1925), *Cucumaria echinata* (Ohshima, 1921), and *Caudina chilensis* (Inaba, 1930), features appear during division which are characteristic of spiral division. A unique division is observed in *Cucumaria glacialis* in which the eggs are large and rich in yolk. As reported by Ohshima, (1931), citing Mortensen, in the holothurian initially only the nucleus divides and the newly formed nuclei are situated along the periphery of the egg; thereafter division of the cytoplasm occurs with the formation of blastomeres.

Blastula

According to Mortensen (1938), in *Ophiodesoma grisea* the blastula is formed 4 hrs after fertilization. It takes 12–14 hrs before the blastula is fully formed. In most species the blastula is spherical and the large blastocoel has a cover of cilia (Figure 174). For several species (*Synaptula vittata, Ophiodesoma grisea, Holothuria spinifera,* and *H. papillifera*) Mortensen (1937,1938) reported that despite the presence of cilia, the blastula remains inside the envelope. Usually, hatching takes place at this stage.

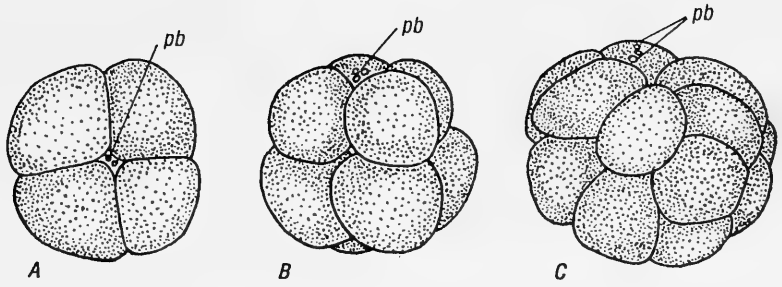


Figure 173. *Caudina chilensis* (Inaba, 1930).
Early stages of division.
A — 4 blastomeres; B — 8 blastomeres; C — 16 blastomeres; pb — polar bodies.

In *Caudina chilensis*, as in some sea stars, several invaginations enter the blastula cavity, depressions marking them on the surface (Inaba, 1930) (Figure 175). Folos remain up to the beginning of gastrulation when they begin to gradually smoothen. A wrinkled blastula has also been reported in *Cucumaria normani* and *C. saxicora* (Kume and Dan, 1968).

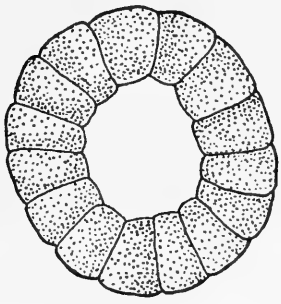


Figure 174. *Cucumaria frondosa* (=*Psolinus brevis*).
(Kowalewsky, 1867).
Blastula. Blastocoel is well developed.

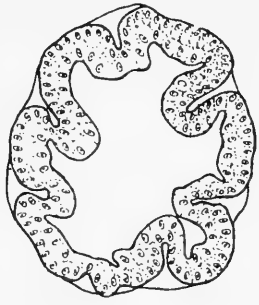


Figure 175. *Caudina chilensis* (Inaba, 1930).
Wrinkled blastula. General view.

In species in which development occurs in the body of the adult individual, the blastula remains immobile. Such a blastula is found in *Holothuria floridana* (Edwards, 1909), *Synapta vivipara* (Clark, 1898, 1910), *Chiridota rotifera* (Clark, 1910), and *Thyone briareus* (Ohshima, 1925).

Gastrula

In *Ophiodesoma grisea* and *Holothuria difficilis* the gastrula is formed 10 hrs after fertilization (Mortensen, 1938). Development of the gastrula takes 18 –20 hrs in *Synaptula reciprocans, Holothuria impatien, H. pardalis,*

H. papillifera, and *H. spinifera* (Mortensen, 1937, 1938). In *Caudina chilensis* the gastrula develops during 33 hrs (Inaba, 1930). According to Mortensen (1937, 1938), in *Ophiodesoma grisea, Synaptula vittata, Holothuria spinifera,* and H. *papillifera*, embryos hatch at this stage.

In holothurians, gastrulation proceeds through invagination. Before that, the blastula slightly stretches along the animal-vegetal axis and its vegetal pole flattens. Ohshima (1921) in *Cucumaria echinata* and Inaba (1930) in *Caudina chilensis* have reported immigration of a large number of mesenchymal cells before the initiation of gastrulation. In other species immigration of the mesenchymal cells generally occurs from the tip of the archenteron, after it reaches the middle of the gastrula (Figure 176). Later, the archenteron bends to the future ventral side. Then the mouth opens, a through gut appears, and the blastopore becomes the anus. Division of the gut into sections is not yet discernible. In species in which development occurs through the planktotrophic auricularia stage, a dipleurula is formed.

Dipleurula

Formation of the dipleurula begins when the gastrula changes shape. It bends on the dorsal side and a large preoral depression forms on the ventral side. The larva acquires a beanlike shape. The formed preoral lobe slightly overhangs the oral depression. Formation of the anal lobe involves displacement of the anus and turning of the lower end of the intestine. The anus is now situated on the ventral side in the middle of the anal lobe. Cilia covering the gastrula disappear altogether, except on the edge of the preoral depression and lobes. A single ciliated band is formed.

Soon the gut divides into sections; esophagus, stomach and hind gut (Figure 177). The epithelium of the gut is provided with cilia. At this stage, no lateral body processes arise. Rudiments of the coelom are present in the form of clusters of mesenchymal cells.

Auricularia

In most species the early auricularia develops in two days. Such are the auriculariae of *Ophiodesoma grisea, Holothuria scabra, H. spinifera, H. impatiens,* and *H. pardalis* (Mortensen, 1937, 1938). Lateral processes form at this stage. In the late auricularia the lateral processes, up to six pairs, are well developed but not equal in length. Sometimes one or two pairs are especially prominent in their size (Figure 178). In the larvae of holothurians these processes are designated as follows: the anterodorsal and mediodorsal lie above the mouth opening, while the preoral processes lie at the level of the mouth opening. In the lower part of the larvae there are postoral, posterodorsal and posterolateral processes.

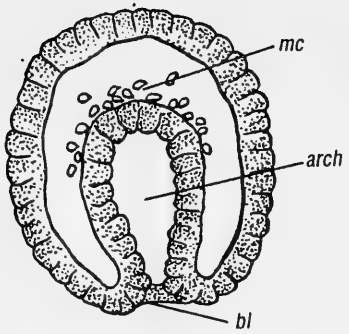


Figure 176. *Cucumaria frondosa* (=*Psolinus brevis*) (Kowalewsky, 1867). Immigration of mesenchyma after gastrulation.
arch — archenteron; bl — blastopore; mc — mesenchymal cells.

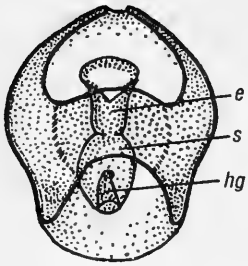


Figure 177: *Holothuria nobilis* (Mortensen, 1938).
Late dipleurula. Division of the tubular gut into sections.
e — esophagus; hg — hind gut; s — stomach.

Skeleton : a well-developed larval skeleton is not found in the larvae of holothurians; the skeletal elements are represented by rods of different shapes and small wheels, which are retained in the later stages. These structures are especially characteristic of holothurian auriculariae of the genera *Holothuria* and *Stichopus* (Mortensen, 1921, 1937, 1938).

Feeding : The mechanism of feeding in the holothurian larvae is similar to that in the larvae of other echinoderms. In the early auricularia the preoral lobe above the oral depression has a notch, while the tip of the anal lobe is drawn out somewhat. Between these lobes lies the arched preoral depression (Figure 178).

The perioral field in holothurian larvae lacks a ciliary cover. The food particles are held in the perioral field by the water currents produced by beating of the cilia in the lateral areas of the band. As in all echinoderms, each cell of the ciliated band bears one cilium. Three to seven cells make up the width of the ciliated band (Strathmann, 1971). On both sides of the ciliated band, numerous secondary cells are present in the auricularia of *Parastichopus.*

As the size of the ciliated band bordering the lateral processes increases, the feeding mechanism in the larvae, exhibiting no change whatsoever, becomes more effective. Besides the single ciliated band, another, the adoral ciliated band, appears around the oral cavity. Cilia are not present in the oral cavity itself and, evidently, because of this, the auricularia has well-developed esophageal muscles and the muscles situated in the dorsal wall of the oral cavity. From the perioral field the food is directed to the esophagus.

Here, upon contraction of the muscles surrounding the esophagus after opening of the cardiac sphincter, the food particles are pushed into the stomach. Here the food is sorted and food particles suitable for feeding are retained for some time in the anterior part of the stomach, while unsuitable particles accumulate near the pyloric sphincter separating the stomach from the hind gut. When the pyloric sphincter opens, the stomach contents pass into the hind gut and then, after the anal sphincter opens, are egested.

As was demonstrated by Strathmann (1971), the primary sorting may occur in the oral cavity. Rejection of food from the oral cavity or esophagus, or unsuitable food, is done by contracting the muscles of the esophagus and oral cavity, accompanied by a change in direction of beating of the cilia of the aboral band.

Holothurian larvae can feed on microalgae of no more than 70 μm in diameter and no more than 150 μm long. Different species of the genera *Phaeodactylum, Dunaliella, Amphidinium*, and some others can also be food objects of holothurians. The rate of filtration of algae from the water in *Parastichopus californicus* is about 3 ml/m (Strathmann, 1971).

Respiration, transport of metabolites, and excretion: Holothurian larvae lack organs for respiration and excretion. The provisional hemal system is also not formed. Transport of food substances and excretion of metabolic products is effected by the fluids of the primary and secondary body cavities.

In the early auricularia, the secondary body cavity or coelom is represented by the unpaired coelomic sac with the pore canal. The coelomic sac soon divides into three sections; the hydrocoel and the left and right somatocoels (Figure 179) (Kume and Dan, 1968).

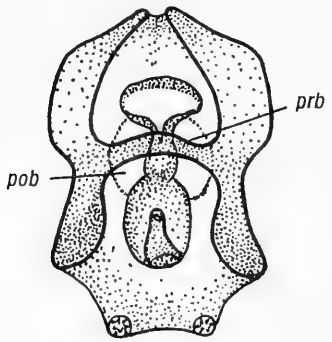


Figure 178: *Holothuria impatiens* (Mortensen, 1938).
Arrangement of ciliated bands in the perioral field.
pob — postoral band; prb — preoral band.

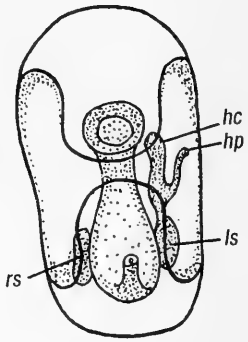


Figure 179: Arrangement of coelomic sacs in the auricularia (Kume and Dan, 1968).
hc — hydrocoel; hp — hydropore; ls — left somatocoel; rs — right somatocoel.

In the late auricularia, the hydrocoel has six diverticulae, lying initially on the left side. These diverticulae later produce the primary tentacles and the polian vesicle (Figure 180). The change in shape and size of diverticulae in *Stichopus japonicus* is accompained by pulsation of the walls (Figures 181, 182).

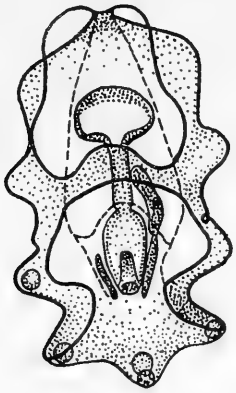


Figure 180: *Holothuria impatiens* (Mortensen, 1938).
General view of the late auricularia.

Locomotion : The locomotor function, as in all echinoderms, is performed by the ciliated band. The larva is capable of moving horizontally, turning in various directions, and remaining stationary. All of these complex movements are accompanied by a change in direction of beating of the ciliated band. Strathmann's (1971) observations have shown that beating of the cilia is not synchronous throughout the entire length of the band; there is a strict alternation of sections in which beating occurs in opposite directions. Due to such alternation of direction of beating of the cilia, a running wave is created, which involves the water layer surrounding the larva. The resultant water currents produce a movement of the larva with its preoral lobe directed forward and performance of other locomotory maneuverings.

Nervous system and sensory organs : Metschnikoff (1869) detected a larval nervous system in the auricularia of *Labidoplax digitata*. In the ectoderm of the perioral field there are two bands of cilia situated in an arch. These bands comprise two rows of cells, under which lie the bi- and tripolar neurons. Mortensen (1937, 1938) also mentioned that nervous elements are situated in the perioral field of auriculariae of various species of sea cucumbers. Unfortunately, no detailed information is available in the literature on the structure of the larval nervous system.

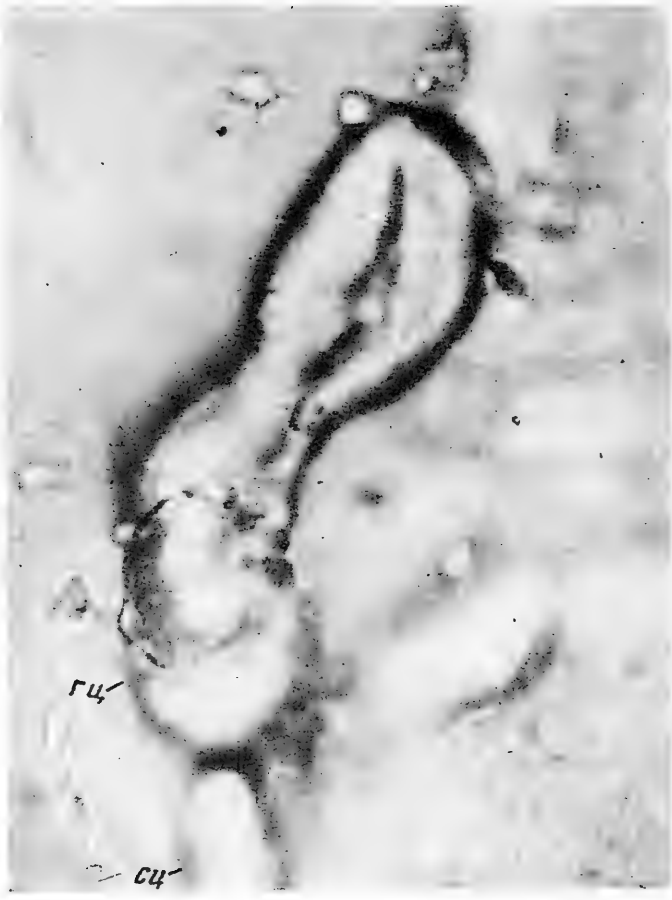


Figure 181: *Stichopus japonicus*.
Formation of coelomic diverticula — rudiments of primary tentacles.
hc — hydrocoel; sc — somatocoel.

The bands of cells in the perioral field are sensory. According to Semon (1888), these cells are provided with cilia. Sensory cilia are also situated on the anterior end of the larval body, where the aboral organ is located.

The diverticula of the hydrocoel may be considered rudiments of the *definitive organs* in the auricularia. The elastic spheres situated at the ends of the lateral processes of the auricularia can be considered rudiments of the provisional formation of the next larval state, the doliolaria.

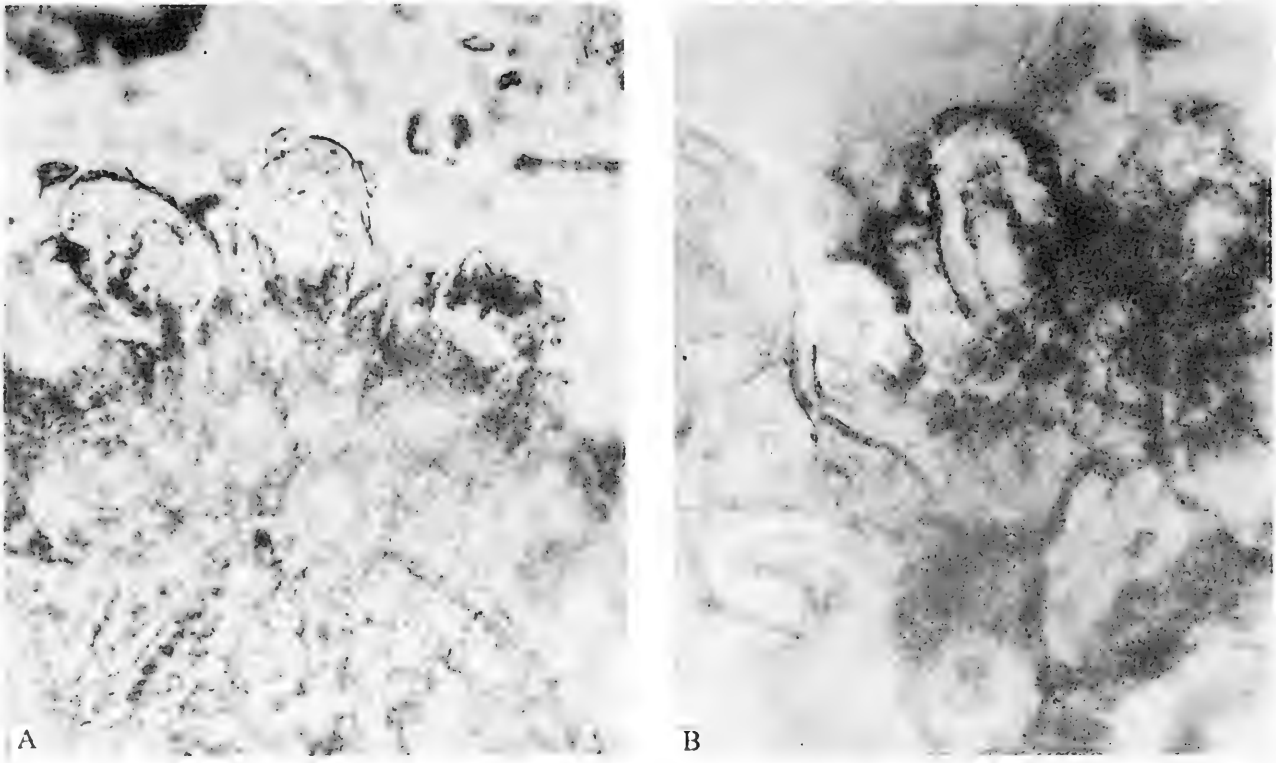


Figure 182: *Stichopus japonicus*.
Change of shape and size of the coelomic diverticula in the auricularia.
A — short and roundish diverticula; B — diverticula becoming cylindrical.

METAMORPHOSIS

Unlike the classes of echinoderms described above, metamorphosis in sea cucumbers is evolutive; the processes of histolysis and resorption during metamorphosis of sea cucumbers are expressed less markedly than in other echinoderms. During this period several larval stages pass in which the external shape changes and internal readjustment of larval systems occurs and definitive structures are formed. The planktotrophic, bilaterally symmetric auricularia changes into a nonfeeding planktonic, radially symmetric doliolaria; while living in the plankton, the doliolaria transforms into a pentactula, which is morphologically the closest to the definitive juvenile sea cucumber. The concluding stage of metamorphosis — transition from the pentactula to the definitive individual — occurs after settling on the substrate. The axis of symmetry of the larva and the definitive organism coincides in holothurians (Smiley, 1986).

Transition of auricularia into doliolaria : In the developed auricularia of *Holothuria* and *Stichopus*, before its change into a doliolaria, the so-called elastic spheres are situated under the ciliated band at the ends of the lateral processes (Mortensen, 1937, 1938). Their disposition and number are variable in different species. The function of these structures is not altogether clear. Possibly, their appearance is associated with the transformation of the ciliated band since they are found in the places where the ciliated band formed in the doliolaria. It may also be assumed that these spheres are particular depots of reserve substances as they disappear earlier than the ciliated bands (Figure 183).

Studies on the development of *Stichopus japonicus* have revealed that soon after the appearance of elastic spheres, resorption of the lateral body processes begins. In the posterior part of the larva the posterolateral processes come closer while the posterodorsal ones completely disappear. The ciliated band between them reduces and only small areas remain near the elastic spheres. The anal lobe also reduces. The ciliated band disappears completely. The anal opening closes and the intestine shortens. Simultaneous with the changes occurring in the posterior half of the larva, its anterior end is also transformed. The mediodorsal and anterolateral processes disappear. The body becomes flat in the region of the anterodorsal processes. Remains of the ciliated band, as in the posterior part of the larva, are retained only near the elastic spheres. The preoral lobe disappears completely. The preoral processes only shorten. The larva acquires the shape of a barrel with five transverse ciliated bands. These run in the areas of the elastic spheres (Figure 184). In other species of sea cucumbers fragments of the ciliated band of the auricularia play a great part in the formation of the ciliated bands of the doliolaria. Thus,

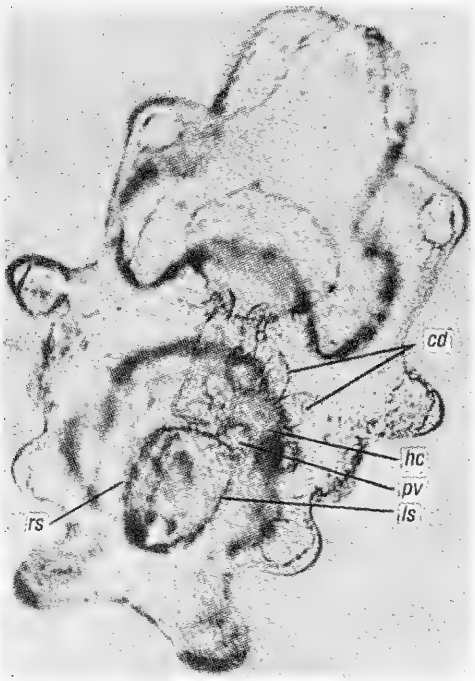


Figure 183: *Stichopus japonicus*.
Arrangement of coelomic sacs and diverticulae in the auricularia before metamorphosis.
cd — coelomic diverticula; hc — hydrocoel; ls — left somatocoel; pv — polian vesicle; rs — right somatocoel.

the lowermost band is formed through the fusion of the remains of the band of the posterolateral processes. The band lying above them is formed from the two fragments of the band of the posterodorsal processes and the two fragments of the band of the anal lobe. The medial band is formed from areas of the band of the mediodorsal processes; the band lying above them is formed from two parts of the band of the anterodorsal processes and one part of the band right of the preoral lobe. The uppermost band is formed from the parts of the band of the oral zone of the larva and the left side of the preoral lobe (Kume and Dan, 1968).

Formation of the cilliated bands of the doliolaria proceeds fairly rapidly; in *Stichopus japonicus* it takes 30–36 hrs. Formation of the doliolaria is the turning point in the life of a sea cucumber larva since metamorphosis begins from this stage.

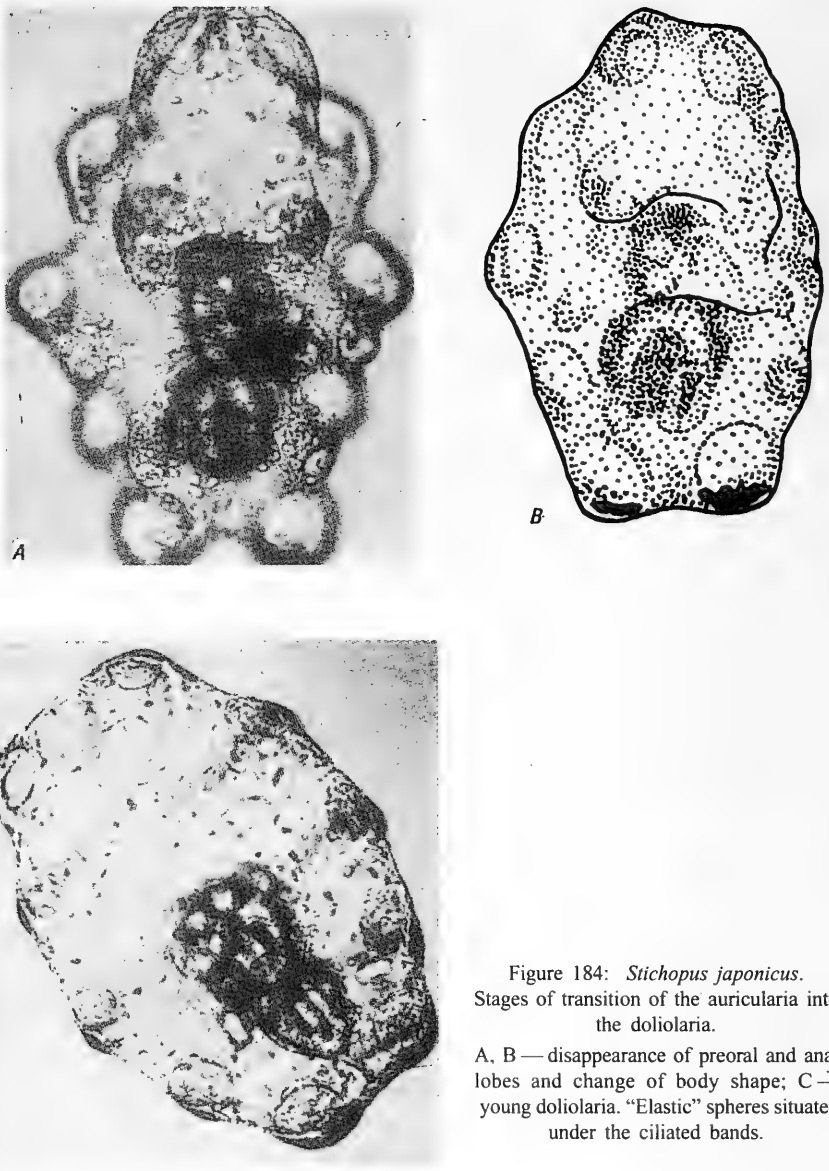


Figure 184: *Stichopus japonicus*. Stages of transition of the auricularia into the doliolaria.

A, B — disappearance of preoral and anal lobes and change of body shape; C — young doliolaria. "Elastic" spheres situated under the ciliated bands.

Doliolaria

The larval body is barrel-shaped with four–five transverse ciliated bands. All of the skeletal elements present in the auricularia are retained here (Figure 185). The doliolaria is smaller than the auricularia; its length sometimes

constitutes one-half to three-fourths the length of the auricularia (Kume and Dan, 1968). Retaining contact with the external environment, the oral cavity transforms into a vestibule (vestibulum), homologous with the amniotic sac of the late pluteus of sea urchins. In the vestibule the integument of the former oral cavity surrounds the coelomic diverticulae that shifted here. In the late doliolaria the vestibule is shifted to the anterior end of the larva and formation of the primary tentacles commences in it.

The hydropore closes and the pore canal turns to the ventral side and transforms into the stone canal, at the end of which the madreporite forms. In *Stichopus japonicus* the madreporite has already developed in the auricularia stage (Kume and Dan, 1968). In this sea cucumber, at the place of appearance of the future medioventral radial ambulacral canal, a small protrusion appears on the ring canal, which initiates the first unpaired ambulacral podium. This podium remains inside the body for some time. In other sea cucumbers the medioventral radial canal elongates and passes along the stomach to the posterior end of the body. Here it bifurcates and a pair of coelomic rudiments of the ambulacral podia forms on its ends (Kume and Dan, 1968).

In some sea cucumber species it is possible to identify one more stage, the prepentactula, distinguished by a wide opening of the vestibule from which primary tentacles may protrude. The ciliated bands are retained. In *Stichopus japonicus* at this time, the ambulacral podium shifts to the outside of the body and the larva uses it for attachment to the substrate. The elastic spheres disappear completely. Radial and interradial spicules arise from the perioral calcareous ring.

Pentactula

At this stage, the larva has five well-developed primary tentacles; it retains the ciliated bands and skeletal elements formed earlier. Some species have a pentactula stage and, in addition, one or several ambulacral podia (Figure 186). It is in this stage that the definitive organ systems develop.

Skeleton : Besides the skeletal rods already formed in the auricularia and the perioral calcareous ring, new spicules appear. These are situated along the interradii and constitute the rudiments of intradermal plates and rods. The newly formed spicules are diverse in shape. In some sea cucumber species the skeleton of the pentactula is better developed than that of the definitive individual.

Digestive system : The oral opening, surrounded by primary tentacles, opens and leads into the esophagus. Primary, and then secondary, tentacles serve as the trapping apparatus substituting for the trapping function of the ciliated band of the auricularia, which is basically resorbed. A large part of

Figure 185: *Holothuria impatiens* (Mortensen, 1938).
Arrangement of ciliated bands in the doliolaria.

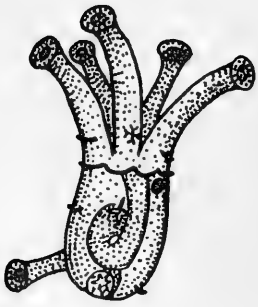


Figure 186: *Holothuria impatiens* (Mortensen, 1938).
Pentactula before settling. Part of the ciliated bands of the doliolaria is retained.

the larval integumental ephithelium transforms into the definitive. The anterior section of the gut is modified into the larval esophagus and stomach while the middle and posterior sections give rise to the small intestine. The anal opening appears again (Ivanov-Kazas, 1978), as in *Stichopus californicus* (Smiley, 1986), or the primary one is retained (Chia and Burke, 1978).

During metamorphosis the *respiratory* functions are passed on from the larval epithelium to the definitive ephithelium and then to the special respiratory organs, the respiratory tree. These organs together with the so-called brown bodies take upon themselves the function of *excretion*. As is common for echinoderms, the *transport of metabolites* after completion of metamorphosis, is done by the hemal and perihemal systems and coelomic body cavities.

Locomotion : During metamorphosis of sea cucumbers, the locomotory function is performed successively by the single ciliated band of the auricularia, the ringed ciliated band of the doliolaria, the primary tentacles and sometimes the first ambulacral podia of the pentactula, and finally, by the ambulacral podia and (or) muscles of the body wall of the definitive animal.

In the pentactula, the ambulacral system consists of the perioral ambulacral ring canal, from which issue the five primary tentacles and the polian vesicle. Moreover, rudiments of all the radial canals are present which, starting from the ring canal, descend along the stomach to the posterior end of the larva. Ambulacral podia, except for those already present, do not form in some species.

Nervous system : The pentactula has a definitive nervous system consisting of the nerve ring surrounding the esophagus at the base of the primary

tentacles and five radial nerves extending along the radial ambulacral canals. The ring canal develops from the thickening of the vestibular bottom (Kume and Dan, 1968). According to Ivanova-Kazas (1978), the presence of a connection between the larval and definitive nervous system is assumed. This assumption is based on the data of Metchnikoff, who observed that before metamorphosis the nerve elements present in the auricularia in the preoral field shift to the oral opening and become a part of the vestibular bottom of the doliolaria. Semon (1888) was also of this view.

Statocysts lie at the base of the radial nerves of the pentactula; possibly they are involved in larval settling.

Settling : After the appearance of spicules, the pentactula loses its ciliated bands and finally settles down. Now the formation of secondary tentacles and ambulacral podia commences. In the literature there is no information about the mechanism of settling of sea cucumber larvae. Nothing specific is known about their ability to recognize a suitable substrate for settling. Chia and Spaulding (1972) mentioned that the polychaete tubes of *Phyllochaetopterus* induce settling in *Cucumaris miniata* and *Psolus chitinoides*. Slime stimulates metamorphosis in *Molpadia intermedia* (McEuen and Chia, 1985).

The pentactulae of all sea cucumbers have primary tentacles. In addition to them, the species with ambulacral podia, develop one or two podia by the time of settling. Strathmann (1978a) reported that various synaptids which lack ambulacral podia in the adult stage, use their primary tentacles for digging into the ground or creeping.

In the pentactula stage, *Stichopus japonicus* is capable of attaching to the substrate by means of a single ambulacral podium which, by this time, has appeared at the posterior body end. The larva, on attachment with this podium, remains sessile for some time, then retracts the podium within its body and resumes swimming. It repeats such maneuvers until the primary tentacles are finally formed and the vestibule is reduced. After this, the podium is no longer retractable, but the larva continues for some time to alternate swimming over the substrate with creeping on it. While swimming, it touches the substrate from time to time.

Based on the information available on the structure of the terminal podia of sea urchins (Burke, 1980) (see Figure 127), it may be assumed that the ambulacral podia in sea cucumbers have an analogous structure. If the ambulacral podia of sea cucumbers have sensory cells, they ought to play an important role in the selection of the substrate and settling. Judged from the observations of various researchers, the primary tentacles are capable of discharging the same role.

LECITHOTROPHIC LARVAE

Species of sea cucumbers with lecithotrophic larvae have large eggs rich in yolk. Their early development differs little from various species with planktotrophic larvae. Differences are observed only from the gastrula stage. A larva entirely covered with cilia and having a coelom and gut divided into sections develops later (Kowalewsky, 1867; Ohshima, 1921; Inaba, 1930). The anal end becomes slightly flattened and the oral opening forms from the ventral side. The ciliary cover changes. Cilia persist at the preoral end and near the anus; between these fields two-five ciliated bands form (Figure 187). Thus, the doliolaria is formed, avoiding the stages of dipleurula and auricularia. Oil drops are present in the preoral part of the doliolaria, which enable the larva to maintain a vertical position in water. The doliolaria swims by rotating around the animal-vegetal axis. In lecithotrophic larvae the digestive system is not fully formed and the principal formative processes are associated with the development of the coelom (Figure 188).

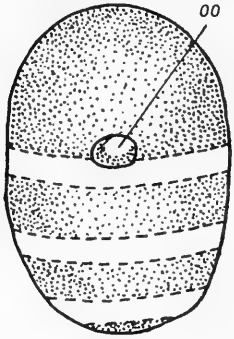


Figure 187: *Caudina chilensis* (Inaba, 1930).
Doliolaria of lecithotrophic type of development. Ciliary cover is retained on the preoral lobe. oo — oral opening.

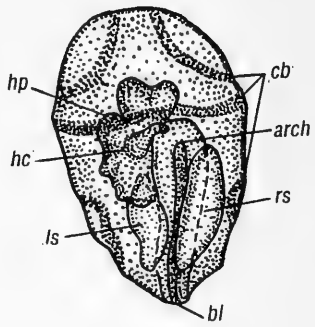


Figure 188: *Chiridota rotifera* (Clark, 1910). Differentiation of coelom into sections.
arch — archenteron; bl — blastopore; cb — ciliated band; hc — hydrocoel; hp — hydropore; ls — left somatocoel; rs — right somatocoel.

The structure of the pentactula in sea cucumbers with planktotrophic larvae shows no substantial difference. The ciliated bands are retained and the larva can swim as well as creep. In apodous pentaculae the ambulacral podia do not develop, while in cucumariids one or two podia appear at this stage (Figure 189). Their development, as in the species with planktotrophic larvae, is associated with the medioventral ambulacral canal.

It is necessary to note that in some species development with lecithotrophic

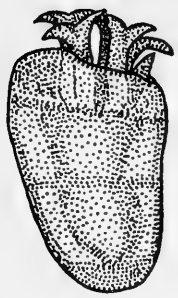


Figure 189: *Caudina chilensis* (Inaba, 1930).
Pentactula before settling. Preoral lobe has disappeared. Primary tentacles protrude from the oral cavity. Ciliated bands are still retained.

larvae is quite close to direct development. In *Cucumaria frondosa* (Edwards, 1909), for example, the pentactula hatches from the envelope with five tentacles and one ambulacral podium.

A review of the literature shows that development with lecithotrophic larvae is often found in species of the order Dendrochirotido (see Table 7). Moreover, in this order as well as in Apodida, either brood care or direct development is characteristic of many species. At present, nearly 30 such species are known, among which almost half are inhabitants of polar and adjacent regions. Such, for example, are the Dendrochirotida species *Cucumaria laevigata* and *Psolus koehleri* and the Apoda species *Taeniogyrus controtus* from the Antarctica, and the Dendrochirotida species *Cucumaria glacialis* from the Arctic. Brood sacs also occur in one Sakhalin species, namely, *Thyone imbricata* (order Dendrochirota).

Brood care of the young in cold-water sea cucumbers takes place in various brood sacs or pockets, which are specific dermal processes. In several species (*Psolus antarcticus, Psolus granulosus, Psolus punctatus, Psolus figulus, Psolidium incubans, Cucumaria parva,* and *Cucumaria curata*) the young are carried on the smooth part of the creeping side (Hyman, 1955).

It is interesting to note that in tropical sea cucumbers the young develop inside the body coelom of the mother. Sometimes lecithotrophic larvae develop in such sea cucumbers. In Apodida the larva of *Chiridota rotifera* (Clark, 1910) retains the ciliary cover while *Synapta vivipara* (Clark, 1898, 1910) does not, even though the larva of this sea cucumber develops through the same stages as does *Chiridota rotifera*. One more type of brood care has also been identified, wherein development of the young takes place in the ovaries of the female. This type of development has been described in particular for the Antarctic Apodid, *Taeniogyrus contortus* (Hyman, 1955).

Besides brood care, instances of direct development are known in sea cucumbers. In this case the eggs are spawned in water and the juvenile develops avoiding both the auricularia and doliolaria stages. Development in *Thyone briareus* (Ohshima, 1925) and *Holothuria floridana* (Edwards, 1909) proceeds in this manner.

The feature common to species with brood care and species with direct development is the presence of large yolky eggs. A list of species of sea cucumbers and their type of development is given in Table 7.

Table 7: Types of development in sea cucumbers

Species	Type of development	Source
	Order Dendrochirotida	
	Family Cucumariidae	
Cucumaria laevigata	Brood care	Hyman, 1955
Cucumaria glacialis	Same	Mortensen, 1894
Cucumaria parva	Same	Hyman, 1955
Cucumaria curata	Same	Same
Cucumaria lateralis	Same	Same
Cucumaria crocea	Same	Same
Cucumaria joubini	Same	Same
Cucumaria ijimai	Same	Same
Cucumaria lamperti	Same	Same
Cucumaria planci	Lecithotrophic larva	Same
Cucumaria coatsi	Brood care	Same
Cucumaria vaneyi	Same	Same
Cucumaria echinata	Lecithotrophic larva	Ohshima, 1921
Cucumaria elongata	Lecithotrophic larva	Chia and Buchanan, 1969
Cucumaria saxicola	Same	Thorson, 1946
Cucumaria normani	Same	Same
Cucumaria frondosa	Same	Same
Pseudocucumis africanus	Brood care	Hyman, 1955
	Family Phyllophoridae	
Thyone rubra	Brood care	Same
	Family Sclerodactylidae	
Thyone briareus	Direct development	Ohshima, 1925
	Family Phyllophoridae	
Thyone imbricata	Brood care	Hyman, 1955
	Family Psolidae	
Psolus ephippifer	Same	Same
Psolus antarcticus	Same	Same
Psolus granulosus	Same	Same
Psolus koehleri	Same	Same
Psolus punctatus	Same	Same
Psolus figulus	Same	Same
Psolus phantapus	Lecithotrophic larva	Thorson, 1946
Thyonepsolus nutriens	Brood care	Hyman, 1955
Psolidium incubans	Same	Same
	Family Phyllophoridae	
Phyllophorus urna	Brood care	Hyman, 1955

Species	Type of development	Source
	Order Aspidochirotida	
	Family Holothuriidae	
Holothuria arenucola	Planktotrophic larva	Mortensen, 1937
Holothuria spinifera	Same	Same
Holothuria scabra	Same	Same
Holothuria impatiens	Same	Mortensen, 1938
Holothuria pardalis	Same	Same
Holothuria papillifera	Same	Same
Holothuria difficilis	Same	Same
Holothuria nobilis	Planktotrophic larva	Mortensen, 1938
Holothuria marmorata	Same	Mortensen, 1937
Holothuria floridana	Direct development	Edwards, 1909
Actinopyga mauritiana	Planktotrophic larva	Mortensen, 1937
Actinopyga serratidens	Same	Same
	Family Stichopodidae	
Stichopus variegatus	Planktotrophic larva	Mortensen, 1937
Stichopus japonicus	Same	Our data
	Family Synallactidae	
Bathyplotes natans	Brood care	Hyman, 1955
	Order Molpadiida	
Paracaudina chilensis	Lecithotrophic larva	Inaba, 1930
	Order Apodida	
	Family Synaptidae	
Synapta vivipara	Brood care	Clark, 1910
Synaptula hydriformis	Same	Hyman, 1955
Synaptula vittata	Planktotrophic larva	Mortensen, 1937, 1938
Synaptula reciprocans	Same	Mortensen, 1937
Ophiodesoma grisea	Same	Mortensen, 1938
Leptosynapta minuta	Brood care	Hyman, 1955
Leptosynapta inharens	Lecithotrophic larva	Thorson, 1946
Labidoplax digitata	Planktotrophic larva	Metschnikoff, 1869
	Family Chiridotidae	
Chiridota rotifera	Brood care	Clark, 1910; Engstrom, 1980
Taeniogyrus contortus	Same	Hyman, 1955
Trochodota dunedinensis	Same	Same

IDENTIFICATION OF PELAGIC LARVAE OF SEA CUCUMBERS (Terminology and Diagnostic Characters)

The absence of a developed endoskeleton is characteristic of holothurian larvae. The larvae develop through several stages differing in external morphological features, which are important for their identification.

Species with planktotrophic larvae pass through the stages of dipleurula, auricularia, doliolaria, and pentactula. Species with lecithotrophic larvae pass through the stages of doliolaria and pentactula. The species characters at the stage of dipleurula are very poorly developed and cannot be used for the identification of larvae. The latter becomes practically possible only from the stage of auricularia, when lateral processes appear. There are generally six pairs of processes differing in size but sometimes some of them do not develop at all. Their position in a fully formed larva is as follows: above the preoral lobe lie the anterodorsal processes, followed by the mediodorsal, and the preoral process behind them. Somewhat lower are the postoral processes, below them the posterodorsal, and at the base of the anal lobe the posterolateral processes. The auricularia has a single ciliated band. The lower end of its body may be triangular, as in the larvae of the genus *Holothuria*, or flat, as in the genus *Stichopus*. At this stage, the larvae of some sea cucumbers have various spicules in the form of simple calcite plates of different shapes or in the form of wheels and hooks. These skeletal elements are retained in the later stages of larval development. In some members of the genera *Holothuria* and *Stichopus* elastic spheres appear in the auricularia stage at the tips of the processes and sometimes at the base of the larval body (*Holothuria*). Their number and arrangement vary in different species. These spheres also persist in later stages of development.

The doliolaria is barrel-shaped with four–five transverse ciliated bands that are isolated from each other.

The lecithotrophic doliolaria differs in that the preoral and anal fields do not shed their ciliary cover. The larva has no skeletal elements and elastic spheres and the ciliated bands range from two to five.

The pentactula has well-developed primary tentacles, which may be distally bifurcate or bear numerous papillae of various shapes. Rods, the rudiments of definitive ossicles, appear at this stage. In larvae with a planktotrophic type of development the ossicles formed in the auricularia stage and the ciliated bands are retained.

For identification of planktotrophic larvae, of primary importance are the structure of the skeletal elements, the presence and number of elastic spheres and their arrangement, and the degree of development of the lateral processes in the auricularia.

For identification of lecithotrophic larvae, the significant characteristics are the number and arrangement of ciliated bands in the doliolaria, and the presence or absence of ambulacral podia and the shape of the tentacles in the pentactula.

The diagnostic features for the larvae of sea cucumbers are given below:

1. *In the auricularia stage*:
   a. presence or absence of lateral processes;
   b. shape of the lower end of the larva;
   c. presence, number, and shape of calcite ossicles;
   d. presence, number and arrangement of elastic spheres in the late auricularia;
   e. color of larva.
2. *In the doliolaria stage*:
   a. presence, number, and shape of ciliated bands;
   b. presence, number, and shape of calcite ossicles;
   c. color of larva.
3. *In the pentactula stage*:
   a. presence, number, and shape of calcite ossicles;
   b. presence or absence of first ambulacral podia;
   c. number of ambulacral podia;
   d. shape of primary tentacles.

Key to Families Based on Eggs

1 (2). Eggs large, oval, buoyant, reddish-green. . . . . **Cucumariidae**
2 (1). Eggs small, spherical, grayish. . . . . **Stichopodidae**

Key to Families Based on Larvae in the Doliolaria Stage

1 (2). Larva large, opaque and completely covered with short cilia. No calcite ossicles in the basal part . . . . . **Cucumariidae** sensu lato
2 (1). Larva small, transparent, with incomplete cover of short cilia and five transverse ciliated bands. Calcite ossicles present in the basal part. . . . . **Stichopodidae** (*Stichopus japonicus*)

Key to Families Based on Larvae in the Pentactula Stage

1 (2). Primary tentacles with five papillae. Ciliated bands absent . . . . . **Cucumariidae**
2 (1). Primary tentacles lack papillae. Ciliated bands present. . . . . **Stichopodidae** (*Stichopus japonicus*)

CHARACTERS OF LARVAE ACCORDING TO FAMILIES

Cucumariidae sensu lato

Development with lecithotrophic larva: The eggs are large, float on the surface layer, 300–450 μm in diameter. The animal pole may be tinted reddish-orange, but the rest of the larva is greenish. Either the larva is entirely and uniformly covered with short cilia or a few transverse ciliated bands occur in its lower half. The pentactula has five primary tentacles, which are distally bifurcate and provided with numerous papillae, as well as one or two ambulacral podia, located above the anal opening and connected with the medioventral ambulacral canal.

Two species of this family — *Cucumaria japonica* Samper and *Eupentacta* (= *Cucumaria*) *frudatrix* (Djakonov and Baranova) — are found in Peter the Great Bay.

Stichopodidae

Development with planktotrophic larva: The eggs are about 100 μm in diameter and spherical. The larva is transparent. The postoral processes are best developed in the auricularia (*Stichopus japonicus*). Calcite lumps of various shapes and sizes lie at the base of the anal lobe on both sides. The posterior end of the larva is flat. Five pairs of elastic spheres appear in the late auricularia. Five transverse ciliated bands are present in the doliolaria and the elastic spheres and calcite lumps persist. The pentactula has five primary tentacles and one ambulacral podium; elastic spheres are absent while calcite ossicles and ciliated bands persist.

The only member of this family found in Peter the Great Bay is *Stichopus japonicus* Selenka. The auricularia of this species has been described by Kume and Dan (1968). A more complete description of the development of *S. japonicus* is given below.

FAR EASTERN TREPANG *STICHOPUS JAPONICUS* SELENKA

Mature eggs in the trepang are nontransparent, about 150 μm in diameter. Artificial fertilization is not always successful. Thermostimulation is the reliable method for obtaining viable larvae, whereby the female releases mature eggs. The blastula forms 6–8 hrs after fertilization at a water temperature of 20–21°C. The blastula is spherical but gradually elongates in the animal-

vegetal axis. The gastrula forms by the end of the first day of development. It is highly transparent, slightly flattened at the vegetal pole, with short cilia completely covering its surface. At the end of the second day the gastrula transforms into a dipleurula. This stage may last as long as two days. Thereafter the next stage, the auricularia, sets in, which is the longest stage in the development of the trepang.

Auricularia

The larva is transparent. In each corner of the anal lobe an irregularly shaped calcite ossicle forms, which is much larger in the left corner. Under the ciliary band, at the ends of the lobes, there are five pairs of round cavities, the elastic spheres. Mortensen (1937) mentioned similar structures while describing the larvae of *Holothuria arenicola* and *H. scabra*. These cavities are possibly the organizing centers from which formation of the ciliated bands of the doliolaria originates. After their appearance, the oral and anal lobes reduce and the ciliated band on them disappears. In the late auricularia the lateral lobes are smooth. Before transition to the doliolaria, the length of the auricularia is about 400 μm (Figures 190, 191).

Doliolaria

This stage continues for two days. It is characterized by a barrel-shaped larva in either a ventral or dorsal view. In a lateral view it is clearly apparent that the depression in the region of the mouth persists. The fully developed doliolaria has five ciliated bands: anterolateral, preoral, oral, preanal, and postanal. The doliolaria is less transparent than the auricularia. The calcite ossicles are large and lie under the postanal band along the corners of the doliolaria. The anterior and under the anterolateral band thickens. The length of the larva at this stage is 400 μm (Figs. 192, 193).

Prepentactula I

The larva is elongate. The round cavities are almost indistinguishable but the ciliated bands are completely retained. The calcite granules underlying the postanal band gather at this stage in the middle of the posterior end of the larva. The five primary tentacles are distinctly visible through the integument; they are sometimes extruded and again retracted into the vestibular cavity. Further, the perioral calcite ring and the madreporite are distinguishable. Below the calcite ring the unpaired ambulacral podium lies along the stomach. The length of the larva at this stage is about 400 μm (Figure 194).

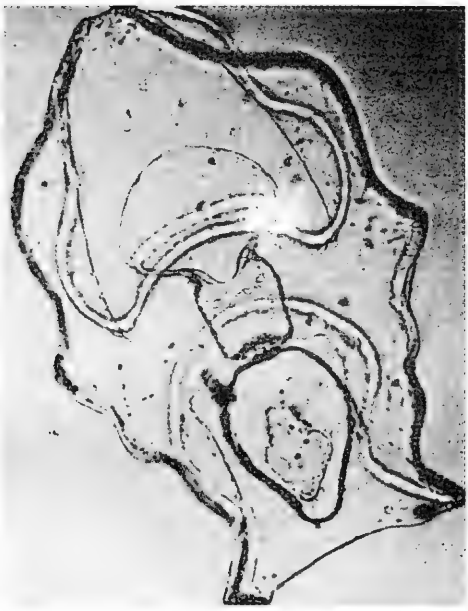


Figure 190: *Stichopus japonicus*.

Figure 191: *Stichopus japonicus*.
Auricularia in stage of disappearance of the oral and anal lobes. Large cavities visible under the ciliated bands.

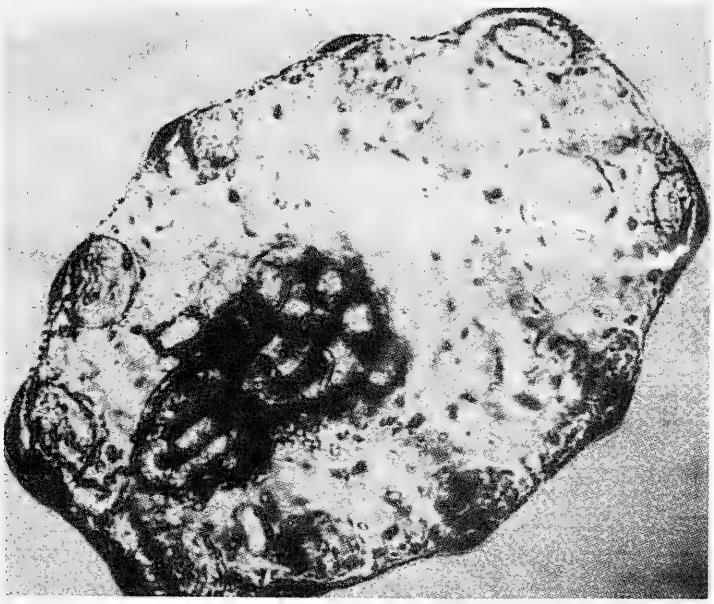


Figure 192: *Stichopus japonicus*.
Doliolaria. General view.

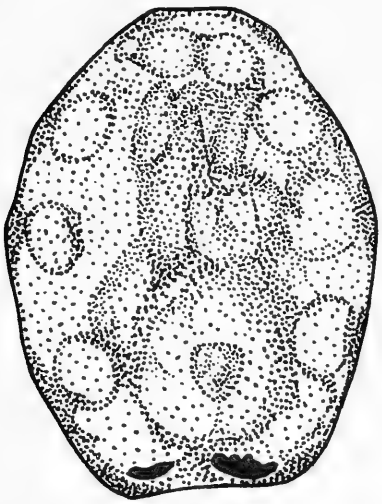


Figure 193: *Stichopus japonicus*.
Postdoliolaria. Large cavities persisting. Calcite ossicles visible at the bottom.

Prepentactula II

This stage is characterized by the anal ambulacral podium which can extrude by means of it the larva is capable of attachment to the substrate. All the five ciliary rings persist and continue to perform a locomotory function (Figure 195).

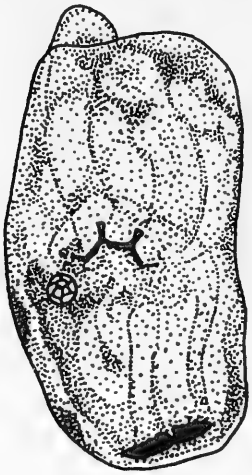


Figure 194: *Stichopus japonicus.* Prepentactula. Large cavities have disappeared. Primary tentacles are distinctly visible in the vestibular cavity.

Figure 195: *Stichopus japonicus.* Prepentactula. Anal ambulacral podium has emerged outside the body. One of the primary tentacles protrudes from the vestibular cavity.

Pentactula

At this stage, the primary tentacles of the larva are not retracted into the vestibular cavity, which now remains wide open. The larva is capable of moving by means of its tentacles and podia. At this stage, it is possible to distinguish skeletal rods of different shapes scattered throughout the body under the integument. The length of the larva is about 500 μm (Figure 196). In the trepang as well as in *Thyone briareus* (Ohshima, 1925) and *Cucumaria elongata* (Chia and Buchanan, 1969), the first tentacles begin to appear only in the juvenile.

Ecology

Larvae of the trepang begin to appear in Vostok Bay in July when the water temperature is 18°C. Spawning is observed until August. According to Mokretsova (1975), in Posjet Bay the average duration of development from

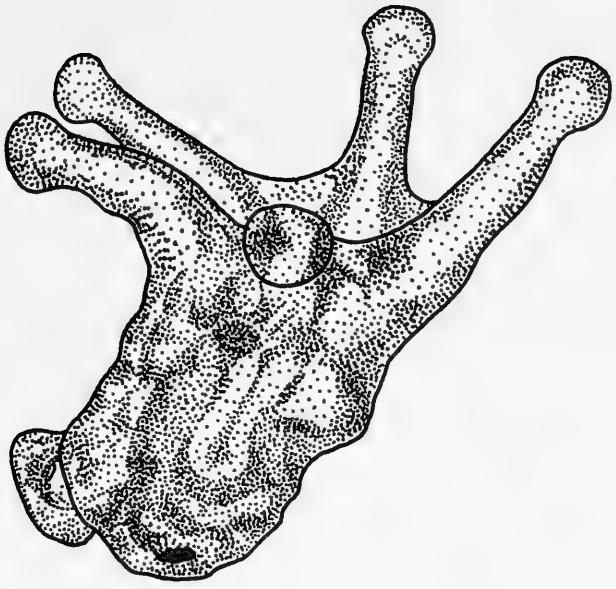


Figure 196: *Stichopus japonicus*.
Pentactula. General view of the larva.

fertilization to settling at a water temperature of 21°C is 16–20 days. Spawning, as in Vostok Bay, continues from June to August. Kinosita (1938) also reported these periods for Hokkaido, Tanaka (1958) reported for southern Hokkaido that spawning of the trepang begins at the end of June. In other parts of Japan the trepang may begin spawning in mid-May (Mitsukuri, 1903) and even in mid-March (Choe, 1962).

JAPANESE CUCUMARIA
CUCUMARIA JAPONICA SEMPER

Eggs large, dark green, rich in yolk, 450 μm in diameter. They are found in the plankton at a water temperature of 11°C. The blastula forms at the end of the first day of development and is oval in shape. The gastrula develops two days after fertilization. It is slightly flattened dorsoventrally. Like the blastula, the gastrula is also entirely covered with short cilia. Both the blastula and the gastrula swim in the surface water layer, rotating around their axis with the animal pole directed forward.

Doliolaria

Formed on the third day of development, the doliolaria is 650 μm long. Its entire body is covered with cilia and is tinted green. No ciliated bands were observed, which are typical of the larvae of other holothurians of this family. The oral opening is situated in the anterior third of the larva. A yolk accumulation at the animal pole in the preoral lobe tints this part of the larva dark green (Figure 197A).

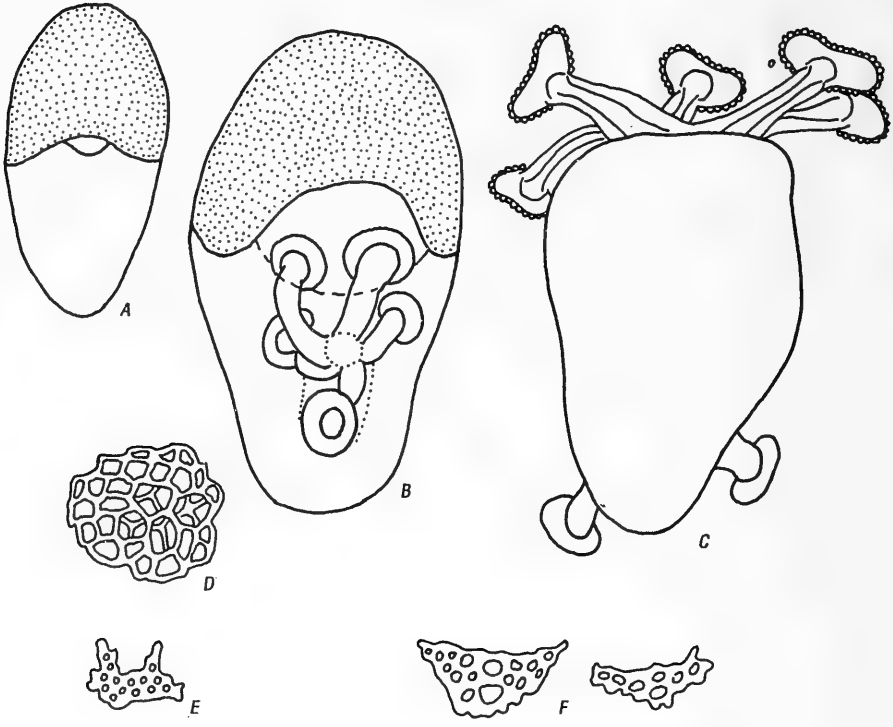


Figure 197. *Cucumaria japonica.*
A — doliolaria; B — early pentactula; C — pentactula; D — madreporite; E — plate of the perioral calcite ring; F — plates of the ambulacral podia.

Pentactula

The early pentactula may not differ in size from the doliolaria but the green tinge diappears except in the preoral lobe. In a dorsal view of the larva the primary tentacles and two ambulacral podia of the medioventral canal are visible. At this stage, these are still immobile. In the *late pentactula* stage the

podia begin to protrude from the vestibular cavity (oral opening) and small papillae appear on their suckers (Figure 197B). The pentactula may reach a length of 1 mm. The dermal plates and skeletal elements of the ambulacral podia begin to form while the pentactula is still in the plankton. Skeletal elements are absent in the primary tentacles. Plates are visible in a live larva at low microscopic magnification when the larva is slightly pressed (Figure 197D, E, F). On settling, the preoral lobe is reduced and the juvenile moves over the substrate using its primary tentacles and two ambulacral podia (Figure 197C). Sometimes juveniles are trapped in bottom catches of plankton.

FRAUDULENT EUPENTACTA *EUPENTACTA FRAUDATRIX* (DJAKONOV AND BARANOVA)

Eggs large, ellipsoidal, dark green, yolky, 400–420 μm in diameter. They are enveloped in a thick jellylike envelope. The blastula forms after 13–15 hrs of development at a water temperature of 20–21°C. It is greenish and slightly flattened dorsoventrally.

The gastrula has formed within 24 hrs upon fertilization. Like the blastula, it has a greenish tint too, is flattened and uniformly covered with short cilia. Both the blastula and the gastrula swim in the surface water layer, they rotate around their axis with the animal pole directed forward.

Doliolaria

This stage develops within two days. It is slightly flattened dorsoventrally. The oral opening is situated slightly above the equator. The entire doliolaria is uniformly covered with short cilia and tinted green. The preoral lobe forms now and contains the entire nutrient reserve, because of which it is darker than the rest of the larval body. The length of the larva at this stage is 400–450 μm (Figure 198A).

Pentactula

This stage is attained after 57 hrs of development. The body is also slightly flattened dorsoventrally and covered with short cilia. As in *C. japonica*, ciliated bands do not form in this species. In the broadened vestibular cavity the suckers of the five primary tentacles are discernible. At the lower end of the body above the anus lie the two ambulacral podia of the medioventral canal. The length of the larva at this stage is 500 μm (Figure 198B). In the late pentactula the madreporite and plates of the perioral calcite ring are clearly visible. In addition, spicules develop on the dermal plates and two plates of ambulacral podia, which lie in the suckers (Figure 198D, E, F). The skeletal elements can be seen in a live larva at low microscopic magnification and with slight pressing of the larva. On settling, the preoral lobe reduces and

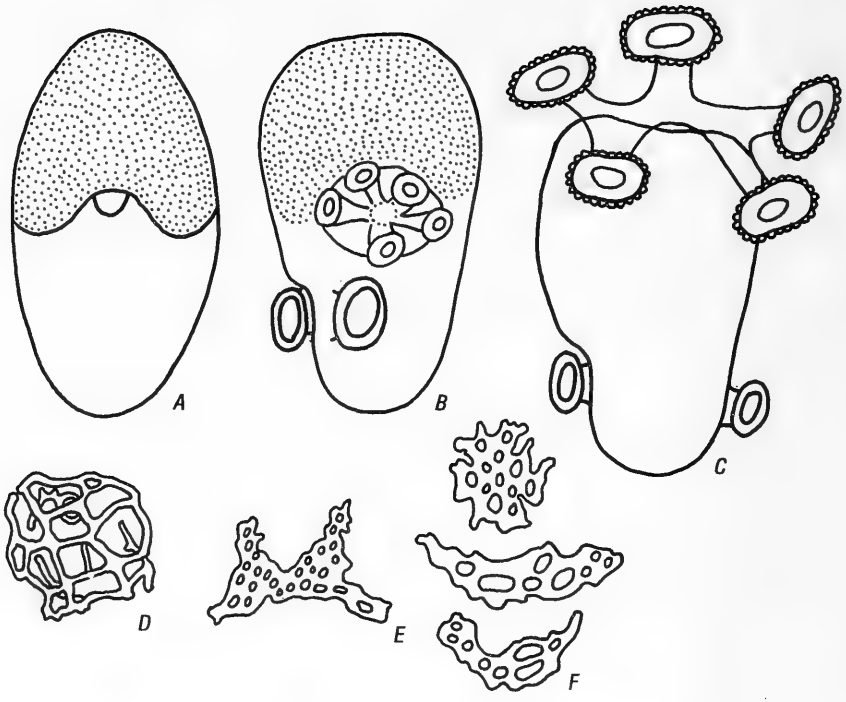


Figure 198: *Eupentacta fraudatrix*.
A — doliolaria; B — early pentactula; C — pentactula; D — madreporite; E — plate of the perioral calcite ring; F — plates of the ambulacral podia.

the juvenile individual moves over the substrate by means of the primary tentacles and two ambulacral podia. Sometimes juvenile individuals are trapped in bottom catches of plankton (Figure 198C).

CONCLUSION

The main purpose of this book has been to present the bulk of factual material which requires further observations and analysis. In concluding it, perhaps a brief comparison of the larvae of bivalves and echinoderms is warranted. To a significant extent independent of the phylogenetic affinity of the organisms and the similarity of the ecological niches occupied by them, the planktotrophic larvae of these animals are highly similar in morphology, physiology, and behavior. Such a similarity is the result of adaptation to a pelagic mode of life. In contrast to the diversity of ecological conditions in the benthic period of their life cycle, these organisms experience in the water column a more uniform habitat or environment. The most important adaptation of larvae to swimming and feeding in water was the appearance of the ciliated band — the principal multifunctional provisional organ, which is primarily a locomotory and trapping apparatus. The function of the ciliated band also facilitates the processes of respiration and excretion and its separate elements serve as sensory organs. The location of the ciliated bands on various processes of the larval body (arms, processes, velum) facilitates floatation of the larvae; these processes often function as stabilizers and rudders. The characteristic defensive feature of pelagic larvae, as also of other planktonic organisms, is their relative colorlessness and transparency. There are also some other characters ensuring for planktotrophic larvae life in the water column. Some of these features can be traced directly from the larvae of primitive multicellular creatures, while others arose secondarily during the evolution of various groups.

Comparing larval periods in the life cycles of bivalves and echinoderms, we note that the postembryonal larval period begins exceptionally early, from the stage of the late blastula or the early gastrula. Such an early transition to the postembryonal period is encountered in lower multicellular animals, for example hydroid polyps, but in most other animals it is delayed as a result

of embryonization of development (Ivanova-Kazas, 1975), which is not the case in the groups under discussion. Of course, the free-swimming blastula or early gastrula of echinoderms differs in many features from the similar stage of bivalves. The principal difference is the presence already at this stage in mollusks of the rudiment of a shell gland, which is a clear example of the tendency towards "adultation" of development in bivalves (Jagertsen, 1972). In echinoderms this tendency appears much weaker. As a result of "adultation" the transition of larvae to definitive organisms has the nature of "evolutive" metamorphosis in bivalves. For echinoderms, catastrophic metamorphism is characteristic, which has caused greater divergence in the structure of pelagic larvae and definitive organisms due to the changeover in the ancestral type to radial symmetry and a sessile mode of life in the adult animal.

Speaking of the parallel paths in the evolution of pelagic larvae of bivalves and echinoderms, mention must be made of lecithotrophic larvae, in which the ciliary cover serves mainly as a locomotory apparatus. The ciliary cover in the doliolaria of sea cucumbers is quite identical with the cover of the doliolaria of sea lilies and brittle stars; on the other hand, the ciliary cover of these echinoderm larvae is analogous with that of the lecithotrophic larvae of bivalves of the subclass Protobranchia.

In conclusion, we would like to say a few words on some, in our opinion, promising trends in investigation of the life cycles of bivalves and echinoderms. The results presented in the preceding chapters together with the material presented in our book "Razmnozhenie iglokozhikh i dvustvorchatykh mollyuskov" [Reproduction of Echinoderms and Bivalves] (1980) provide an overall picture of the life cycles of the investigated groups of animals in a morphological aspect. Some answers have been obtained to the first questions arising during studies on the life cycles of marine invertebrates with pelagic larvae: when do the animals spawn? what processes occur in their gonads throughout the year? which type of larva do they have? and, how to identify this larva? All of this information is necessary but still insufficient for understanding how the actual life cycles proceed and which mechanism ensures them.

Morphological approaches to investigation of the life cycles, based on a knowledge of the reproductive cycles occurring in the gonads on one hand, and descriptions of larval morphology, on the other, may at the cytological level explain the cytological peculiarities that ensure any variation of the life cycle. However, the considerable data on gametogenesis and cytology of larvae have not yet been examined from this viewpoint.

Our book does not consider the ecological aspects of larval life. Numerous investigations on the ecology of larvae in nature, conducted in the Sea of Japan and various regions of the World Ocean have been supplemented in the last decade with laboratory studies on the influence of ecological factors

on larvae. These data on the larvae of bivalves and echinoderms, diverse in methods, conditions, and accuracy of studies requires systematization. The next step to understanding the ecology of life cycles as a whole would be to present the entire descriptive and experimental material in the conceptual framework of any model of the life cycle —*r*, *K*-strategy — or other more adequate models of the strategy of the life cycle, providing a vivid picture of its "economy" in conditions of variable biotic factors. This step has been done. In 1989, we published a book entitled "Reproduktivnaya strategiya morskikh dvustvorchatykh mollyuskov i iglookozhikh" [Reproductive Strategy of Marine Bivalves and Echinoderms] (Kasyanov, 1989). We leave it to the reader to judge whether our step was in the right direction and whether it was successful.

REFERENCES

Abbott, R.T. 1954. *American Seashells*. Van Nostrand, New York, pp. 1–541.

Adrianov, V.B. and A.G. Vol'ter. 1947. Morskie drevotochtsy. Materialy po biologii drevotochtsev i sposoby zashchity dereva [Marine Wood-boring Mollusks. Data on the Biology of Wood-boring Mollusks and Methods of Wood Protection]. *Izv. TINRO*. no. 24, pp. 3–32.

Aiyar, R.G. 1936. Early development and metamorphosis of the tropical echinoid, *Salmacis bicolor* (Agassiz). *Proc. Ind. Acad. Sci.*, 1, 13, 714–728.

Alatalo, Ph., C.J. Berg and Ch. N.D. D'Asaro. 1984. Reproduction and development in the lucinid clam *Codakia orbicularis* (Linné, 1758). *Bull. Mar. Sci.,* 34, 3, 424–434.

Allen, J.A. 1961. The development of *Pandora inaequivalvis* (Linné). *J. Embryol. and Exp. Morphol.*, 9, 2, 252–268.

Allen, J.A. and R.S. Scheltema. 1972. The functional morphology and geographical distribution of *Planktomya henseni*, a supposed neotenous pelagic bivalve. *J. Mar. Biol. Assoc. U.K.*, vol. 52, pp. 19–31.

Amemiya, I. 1929. Another species of monoecious oyster, *Ostrea plicata* Chemnitz. *Nature*, 123, 3110, 874.

Amemiya, S. and T. Tsuchiya. 1979. Development of the echinothurid sea urchin *Astenosoma ijimai. Mar. Biol.*, vol. 52, pp. 93–96.

Bachman, S. and A. Goldschmid. 1978. Fine structure of the axial complex of *Sphaerechinus granularis* (Lam.) (Echinodermata: Echinoidea). *Cell and Tissue Res.*, 193, 1, 107–123.

Baranova, Z.I. 1968. Iglokozhie [Echinoderms]. In: *Zhizn' Zhivotnykh*. Prosveshchenie, Moscow, vol. 2, 276 pp.

Barker, M.F. 1977. Observations on the settlement of the brachiolaria larvae of *Stichaster australis* (Verrill) and *Coscinasterias calamaria* (Gray) (Echinodermata: Asteroidea) in the laboratory and on the shore. *J. Exp. Mar. Biol. and Ecol.*, 30, 1, 95–108.

Barker, M.F. 1978a. Descriptions of the larvae of *Stichaster australis* (Verrill) and *Coscinasterias calamaria* (Gray) (Echinodermata: Asteroidea) from New Zealand, obtained from laboratory culture. *Biol. Bull.*, vol. 154, pp. 32–46.

Barker, M.F. 1978b. Structure of the organs of attachment of brachiolaria larvae of *Stichaster australis* (Verrill) and *Cosciasterias calamaira* (Gray) (Echinodermata: Asteroidea). *J. Exp. Mar. Biol. and Ecol.*, vol. 33, pp. 1–36.

Bayne, B.L. 1964a. Primary and secondary settlement in *Mytilus edulis* L. (Mollusca). *J. Anim. Ecol.*, 33, 3, 513–523.

Bayne, B.L. 1964b. The responses of the larvae of *Mytilus edulis* L. to light and to gravity. *Oikos*, vol. 15, pp. 162–174.

Bayne, B.L. 1971. Some morphological changes that occur at the metamorphosis of the larvae of *Mytilus edulis*. In: *4th Europ. Mar. Biol. Symp., Cambridge,* pp. 259–280.

Bayne, B.L. 1976. The biology of mussel larvae. In: *Marine Mussels: Their Ecology and Physiology.* Cambridge Univ. Press, pp. 81–120.

Belogrudov, E.A. 1973. O kharaktera osedaniya i osobennostyakh rosta lichinok morskogo grebeshka na razlichnykh substratakh [On the nature of settling and peculiarities of growth of the larvae of marine scallops on different substrates]. In: *Issledovaniya po Biologii Ryb i Promyslovoi Okeanografii.* Vladivostok, pp. 87–90.

Belogrudov, E.A. 1974. O nekotorykh osobennostyakh osedaniya lichinok na kollektory i rosta molodi grebeshka *Mizuhopecten yessoensis* Jay i drugikh zhivotnykh v zalive Pos'eta (Yaponskoe more) [On some peculiarities of settling of larvae on collectors and growth of young ones of the scallop *Mizuhopecten yessoensis* Jay and other animals in Posjet Bay (Sea of Japan)]. In: *Biologiya Morskikh Mollyuskov i Iglokozhikh.* Vladivostok, pp. 7–8.

Bernard, F. 1897. Études comparatives sur la coquille des lamellibranches. 2. Les genre *Philobrya* et *Hochsteteria. J. Conchol.*, vol. 45, pp. 1–46.

Bernard, F. 1898. Recherches ontogeniques et morphologiques sur la coquille de lamellibranches. *Ann. Sci. Natur. Zool. et Biol. Anim.,* sér. 8, vol. 8, pp. 1–208.

Berner, L. 1935. La reproduction des moules comestibles (*M. edulis* L. et *M. galloprov.* Lmck.) et leur répartition géographique. *Bull. Inst. Oceanogr. (Monaco),* no. 680, pp. 1–8.

Birkeland, C., F. -Sh. Chia, and R. Strathmann. 1971. Development, substratum selection, delay of metamorphosis and growth in the sea star, *Mediaster aequalis* Stimpson. *Biol. Bull.,* vol. 141, pp. 99–108.

Bisgrove, B.W. and R.D. Burke. 1987. Development of the nervous system of the pluteus larva of *Strongylocentrotus droebachiensis. Cell Tissue Res.,* vol. 248, pp. 335–343.

Blacknell, W.M. and A.D. Ansell. 1974. The direct development of the bivalve *Thyasira gouldi* (Philippi). *Thalassia Jugosl.*, 10, 1/2, 23–44.

Bohle, B. 1971. Settlement of mussel larvae *Mytilus edulis* on suspended collectors in Norwegian waters. In: *4th Europ. Mar. Biol. Symp., Cambridge,* pp. 63–69.

Boidron-Metairon, I.F. 1988. Morphological plasticity in laboratory-reared echinoplutei of *Dendraster excentricus* (Eachsholtz) and *Lytechinus variegatus* (Lamarck) in response to food conditions. *J. Exp. Mar. Biol. Ecol.*, 119, 1, 31–41.

Booth, J.D. 1979a. Common bivalve larvae from New Zealand: Pteriacea, Anomiacea, Ostreacea. *N.Z. Journal Mar. and Freshwater Res.,* 13, 1, 131–139.

Booth, J.D. 1979b. Common bivalve larvae from New Zealand: Leptonacea. *N.Z. Journal Mar. and Freshwater Res.,* 13, 2, 241–254.

Bosch, I., K.A. Beauchamp, M.E. Steele and J.S. Pearse. 1987. Development, metamorphosis and seasonal abundance of embryos and larvae of the Antarctic sea urchin *Sterechinus neumayeri. Biol. Bull.,* 173, 1, 126–135.

Boveri, T. 1901. Die Polarität der Oocyte, Ei und Larvae der *Strongylocentrotus lividus. Zool. Jb. (Anat.),* vol. 14, pp. 630–651.

Boyle, P.J. and R.D. Turner. 1976. The larval development of the wood-boring piddock, *Martesia striata* (L.) (Mollusca: Bivalvia; Pholadidae). *J. Exp. Mar. Biol. and Ecol.,* vol. 22, pp. 55–68.

Brooks, W.K. and C. Grave. 1899. *Ophiura brevispina. Mem. Nat. Acad. Sci. Wash.*, vol. 8, pp. 79–100.

Broom, M.J. 1985. The biology and culture of marine bivalve molluscs of the genus *Anadara. ICLARM Stud. Rev.*, no. 12, pp. 1–37.

Brun, S. 1978. Ecology and taxonomic position of *Henricia oculata* Pennant. *Thal. Jugosl.*, 12, 1, 51–66.

Burke, R.D. 1978. The structure of the nervous system of the pluteus larva of *Strongylocentrotus purpuratus. Cell Tissue Res.*, 191, 2, 233–249.

Burke, R.D. 1980a. Podial sensory receptors and the induction of metamorphosis in echinoids. *J. Exp. Mar. Biol. and Ecol.*, vol. 47, pp. 223–234.

Burke, R.D. 1980b. Morphogenesis of the digestive tract of the pluteus larva of *Strongylocentrotus purpuratus*: shearing and bending. *Intern. J. Invertebr. Reprod.*, vol. 2, pp. 13–21.

Burke, R.D. 1980c. Development of pedicellariae in the pluteus larva of *Lytechinus pictus* (Echinodermata; Echinoidea). *Can. J. Zool.*, vol. 58, pp. 1674–1682.

Burke, R.D. 1981. Structure of the digestive tract of the pluteus larva of *Dendraster excentricus* (Echinodermata: Echinoidea). *Zoomorpholegie*, 98, 3, 209–235.

Burke, R.D. 1983a. Development of the larval nervous system of the sand dollar, *Dendraster excentricus. Cell Tissue Res.*, vol. 229, pp. 145–154.

Burke, R.D. 1983b. The structure of the larval nervous system of *Pisaster ochraceus* (Echinodermata: Asteroidea). *J. Morphol.*, vol. 178, pp. 23–35.

Burke, R.D. 1984. Pheromonal control of metamorphosis in the Pacific sand dollar, *Dendraster excentricus. Science,* vol. 225, pp. 442–443.

Burke, R.D. 1986. Pheromonas and the gregarious settlement of marine invertebrate larvae. *Bull. Mar. Sci.*, 39, 2, 323–331.

Burke, R.D. and F. -Sh. Chia. 1980. Morphogenesis of the digestive tract of the pluteus larva of *Strongylocentrotus purpuratus*: sphincter formation. *Intern. J. Invertebr. Reprod.*, vol. 2, pp. 1–12.

Burne, R.H. 1910. Mollusca. Anatomy of Pelecypoda. *Nat. Hist. Report. British Antarctic (Terra Nova) Expedition. Brit. Mus. London,* vol. 2, pt. 4, pp. 233–256.

Bury, H. 1895. Metamorphosis of Echinoderms. *Quart. J. Micr. Sci.*, vol. 38, pp. 45–137.

Buyanovskii, A.I. 1987. O vozmozhnosti kul'tivirovaniya midii obyknovennoi *(Mytilus edulis)* na vostochnom poberezh'e Kamchatki [On the prospects of culturing edible mussel *(Mytilus edulis)* on the eastern coast of Kamchatka]. In: *Mollyuski. Rezul'taty i Perspektivy ikh Issledovanii.* Leningrad, pp. 433–434.

Buznikov, G.A. and V.K. Podmarev. 1975. Morskie ezhi *Strongylocentrotus dröbachiensis, S. nudus, S. intermedius* [Sea urchins *Strongylocentrotus dröbachiensis, S. nudus,* and *S. intermedius*]. In: *Ob"ekty Biologii Razvitiya.* Nauka, Moscow, pp. 178–216.

Cahn, A.R. 1950. Oyster culture in Japan. *US fish and Wildlife Serv. Fish. Leaft.*, vol. 383, pp. 1–80.

Cameron, J.L., F.S. McEuen and C.M. Young. 1987. Floating lecithotrophic eggs from the bathyl echinothurids *Phormosoma placenta* and *Araeosoma fenestratum. Abstr. 6th Internat. Echinoderm Confer. Victoria.* Univ. Victoria Press.

Cameron, R.A. and R.T. Hinegardner. 1974. Initiation of metamorphosis in laboratory-cultured sea urchins. *Biol. Bull.*, vol. 146, pp. 335–342.

Cameron, R.A. and R.T. Hinegardner. 1978. Early events of metamorphosis in sea urchins, description and analysis. *J. Morphol.*, vol. 157, pp. 21–32.

Campos, B. and L.M. Ramorino. 1980. Larval and early benthic stages of *Brachiodontes glomerata* (Bivalvia: Mytilidae). *Veliger,* 22, 3, 277–281.

Carriker, M.R. 1961. Interrelation of functional morphology, behaviour, and autoecology in early stages of the bivalve *Mercenaria mercenaria. J. Elisha Mitchel Sci., Sec.*, 77, 2, 168–241.

Chanley, P.E. 1965a. Larval development of the large blood clam *Noetia ponderosa* (Say). *Proc. Nat. Shellfish Assoc.*, vol. 56, pp. 53–58.

Chanley, P.E. 1965b. Larval development in the brackish-water mactrid clam *Rangla cuneata. Chesapeake Sci.*, 6, 4, 209–213.

Chanley, P.E. 1968. Larval development in the class Bivalvia. In *Marine Biological Association of India. Symp. on Mollusca*, pp. 475–481.

Chanley, P.E. and J.J. Andrews. 1971. Aids for identification of bivalve larvae of Virginia. *Malacologia*, 11, 1, 45–119.

Chanley, P. E. and M. Castanga. 1966. Larval development of the pelecypod *Lyonsia hyalina. Nautilus*, vol. 79, pp. 123–128.

Chanley, P.E. and M. Castanga. 1971. Larval development of the stout razor clam, *Tagelus plebeius solander* (Solecurtidae: Bivalvia). *Chesapeake Sci.*, 12, 3, 167–172.

Chanley, P.E. and M.H. Chanley. 1970. Larval development of the commensal clam *Montacuta percompressa* Dall. *Proc. Malacol. Soc.* London, vol. 39, pp. 59–67.

Chanley, P. and P. Dinamani. 1980. Comparative descriptions of some oyster larvae from New Zealand and Chile, and a description of a new genus of oyster, Trostrea. *N.Z. Journal Mar. and Freshwater Res.*, 14, 2, 103–120.

Chia, F.-S. 1966. Brooding behaviour of a six-rayed starfish, *Leptasterias hexactis. Biol. Bull.*, vol. 130, pp. 304–315.

Chia, F.-S. 1968. The embryology of a brooding starfish, *Leptasterias hexactis. Acta Zool.*, vol. 49. pp 321–364.

Chia, F.-S. 1977. Scanning electron microscopic observations of the mesenchyme cells in the larvae of the starfish, *Pisaster ochraceus. Acta Zool.*, vol. 58, 45–51.

Chia, F.-S. and J.R. Buchmann, 1969. Larval development of *Cucumaria elongata. J. Mar. Biol. assoc. U.K.*, vol. 49, pp. 151–159.

Chia, F.-S. and J.G. Spaulding. 1972. Development and juvenile growth of the sea anemona, *Tealia crassicornis. Biol. Bull.*, vol. 142, pp. 206–218.

Chia, F.- S. and R. Burke. 1978. Echinoderm metamorphosis; fate of larval structures. In: *Settlement and Metamorphosis of Marine Invertebrate Larvae.* Elsevier, N.Y., pp. 219–234.

Chia, F.-S. and D.G. Atwood. 1982. Pigment cells in the jelly of sand dollar eggs. *Echinoderms. Proc. Internat. Conf. Tampa.* Balkema, Rotterdam, pp. 481–484.

Chia, F.-S., C.M. Young and F.S. McEuen. 1984. The role of larval settlement behaviour in controlling patterns of abundance in echinoderms. *Adv. Invertebrate Reproduction*, vol. 3. pp. 409-424.

Chipperfield, P.N.Y. 1953. Observations on the breeding and settlement of *Mytilus edulis* (L.) in British waters. *J. Mar. Biol. Assoc. U.K.*, 32, 2, 449–476.

Choe, S. 1962. Biology of Japanese sea cucumber *Stichopus japonicus* Selenka. *Pusan: Fish.* College Pusan Nat. Univ., 226 pp.

Clark, H.L. 1898. *Synapta vivipara* a contribution to the morphology of echinoderms. *Mem. Boston Soc. Natur. Hist.*, vol. 5, pp. 53–88.

Clark, H.L. 1910. The development of an apodous holothurian (*Chiridota rotifera*). *J. Exp. Zool.*, vol. 6, pp. 497–516.

Clark, H.L. 1923. The echinoderm fauna of South Africa. *Ann. S. Afr. Mus.*, vol. 13, pp. 221–426.

Coe, W.R. 1941. Sexual phases in wood-boring mollusks. *Biol. Bull.* vol. 81, pp. 168–176.

Coe, W.R. and H.J. Turner. 1938. Development of the gonads and gametes in the softshell clam (*Mya arenaria*). *J. Morphol.*, vol. 62, pp. 91–111.

Colwin, A.L. and L.H. Colwin. 1957. Morphology of fertilization: acrosome filament formation and sperm entry. In: *The Beginnings of Embryonic Development.* Wash., pp. 135–168.

Coon, S. and D.B. Boner. 1985. Induction of settlement and metamorphosis of the Pacific oyster, *Crassostrea gigas* (Thunberg), by L-DOPA and catecholamines. *J. Exp. Mar. Biol. Ecol.*, vol. 94, pp. 211–221.

Costello, D.P., M.E. Davidson, A. Egger *et al.* 1957. *Methods for Obtaining and Handling of Marine Eggs and Embryos*. Mar. Biol. Lab. Woods Hole (Mass.), 245 pp.

Cragg, S.M. 1980. Swimming behaviour of the larvae of *Pectan maximus* (L.) (Bivalvia). *J. Mar. Biol. Assoc. U.K.*, vol. 60, pp. 551–564.

Cragg, S.M. 1985. The abductor and retractor muscles of the veliger of *Pecten maximus* (L.). *J. Mollusc. Stud.*, 51, 3, 276–283.

Cragg, S.M. and L.D. Gruffydd. 1975. The swimming behaviour and the pressure responses of the veliconcha larvae of *Ostrea edulis* L. In: *Proc. 9th Europ. Mar. Biol. Symp.* pp. 43–47.

Cranfield, H.J. 1973a. A study of the morphology, ultrastructure and histochemistry of the foot of the pediveliger of *Ostrea edulis. Mar. Biol.*, 22, 3, 187–202.

Cranfield, H.J. 1973b. Observations on the behaviour of the pediveliger of *Ostrea edulis* during attachment and cementing. *Mar. Biol.*, 22, 3, 203–209.

Cranfield, H.J. 1973c. Observations on the function of the glands of the foot of the pediveliger of *Ostrea edulis* during settlement. *Mar. Biol.*, 22, 3, 211–223.

Creek, G.A. 1960. The development of the lamellibranch *Cardium edule* L. *Proc. Zool. Soc. London*, 135, 2, 243–260.

Culliney, J.L. 1974. Larval development of the giant scallop, *Placopectan magellanicus* (Gmelin). *Biol. Bull.*, 147, 2, 321–332.

Culliney, J.L. and R.D. Turner. 1976. Larval development of the deep-water wood-boring bivalve, *Xylophaga atlantica* Richards (Mollusca, Bivalvia, Pholadidae). *Ophelia*, 15, 2, 149–161.

Culliney, J.L., R.D. Turner and P.J. Boyle. 1975. Comparative larval development of the shipworms *Bankia gouldi* and *Teredo navalis. Mar. Biol.*, no. 29, 245–251.

Dall, W.H. 1903. Synopsis of the Carditacea. *Proc. Acad. Natur. Sci. Philadelphia,* vol. 54, 696–716.

Dan, J.C. 1970. The acrosomal process membrane. In: *Comparative Spermatology*. Acad. Press, N.Y., pp. 487–497.

Dan, K. 1968. Asteroidea. In: *Invertibrate Embryology*. Nolit, Belgrade, pp. 303–308.

Dan-Sohkawa, M. 1976. A 'normal' development of denuded eggs of the starfish, *Asterina pectinifera. Develop., Growth and Differ.*, vol. 18, 439–445.

Dan-Sohkawa, M. 1977. Formation of joined larvae in the starfish, *Asterina pectinifera. Develop., Growth and Differ.*, 19, 3, 233–239.

Dan-Sohkawa, M. and N. Satoh. 1978. Studies on dwarf larvae developed from isolated blastomeres of the starfish, *Asterina pectinifera. J. Embryol. and Exp, Morphol.*, vol. 46, 171–185.

Dan-Sohkawa, M. and H. Fujisawa. 1980. Cell dynamics of the blastulation process in the starfish, *Asterina pectinifera. Develop. Biol.*, 77, 2, 328–339.

Dan-Sohkawa, M., G. Tamura and H. Mitsui. 1980. Mesenchyme cells in starfish development; effect of tunicamycin on their differentiation, migration and function. *Develop., Growth and Differ.*, 22, 3, 495–502.

D'Asaro, C.N. 1967. The morphology of larval and postlarval *Chione cencellate* Linné (Eulamellibranchia; Veneridae) reared in the laboratory. *Bull. Mar. Sci.*, 17, 4, 949–972.

Dautov, S. Sh. 1979. Izmenenie povedencheskikh reaktaii v protsesse ontogeneze u lichinok morakikh zvezd semeistva Asteriidae [Change in behavioral reactions during ontogenesis in the larvae of sea stars of the family asteriidae]. In: *Materialy IV Vses. Kollokv. po Iglokozhim.* Izd-vo Tbil. Un-ta, Tbilisi, pp. 69–73.

Dautov, S. Sh. and V.L. Kasyanov. 1981. Ranee razvitie nekotorykh vidov morskikh zvezd Yaponskogo morya [Early development of some species of sea stars of the Sea of Japan]. In: *VI Vses. Soveshch. Embryology/Tez. Dokl.* Nauka, Moscow, p. 49.

Davis, H.C. and P.E. Chanley. 1956. Effects of some dissolved substances on bivalve larvae. *Proc. Nat. Shellfish Assoc.* no., 46, 59–74.

Dell, R.K. 1972. Antarctic benthos. *Adv. Mar. Biol.*, vol. 10, 216 pp.

Deroux, G. 1960. Formation réguliere de males murs, de tsille et d'organization larvaire chez un Eulamellibranche commensal (*Montacute phascolionis* Dautry). *C.R. Acad. Sci.*, vol. 250, 2264–2266.

Dinamani, P. 1973. Embryonic and larval development in the New Zealand rock oyster, *Crassostrea glomerata* (Gould.). *Veliger*, 15, 4, 295–299.

Drew, G.A. 1897. Notes on the embryology, anatomy and habits of *Yoldia limatula* Say. *Johns Hopkins Univ. Circ.*, vol. 17, 11–14.

Drew, G.A. 1899a. Some observations on the habits, anatomy and embryology, of members of the Protobranchia. *Anat. Anz.,* vol. 15, 493–519.

Drew, G.A. 1899b. The anatomy, habits and embryology of *Yoldia limatula. Mem. Biol. Lab. Johns Hopkins Univ. Circ.*, 4, 3, 1–37.

Drew, G.A. 1901. The life history of *Nucule dephinodonata. Quart. J. Microsc. Soc.,* vol. 44, 313–391.

Drozdov, A.L. and V.A. Kulikova. 1979. Razvitie krenomidii *Crenomytilus grayanus* Dunker. Prizhiznennye nablyudeniya [Development of crenomytilid *Crenomytilus grayanus* Dunker: *In vivo* observations]. In: *Promyslovye Dvustvorchatye Mollyuski-midii i Ikh RoI' V Ekosistemakh.* Izd-vo Zool. In-ta AN SSSR, Leningrad, pp. 54–56.

Drozdov, A.L. and V.L. Kasyanov. 1985a. Razmery i formy gamet u iglokozhikh [Shape and sizes of gametes in echinoderms]. *Ontogenez.*, 16, 1, 49–59.

Drozdov, A.L. and V.L. Kasyanov. 1985b. Razmery i forma gamet u morskikh dvustvorchatykh mollyuskov [Shape and size of gametes of marine bivalves]. *Biol. Morya,* no. 4, 33–40.

D'yakonov, A.M. 1950. Morskie zvezdy morei SSSR [Sea stars of the seas of the USSR]. In : *Opredelitel' po Fauna SSSR.* Izd-vo AN SSSR, Leningard, vol. 34, 1–202.

Dzyuba, S.M. 1972. Morfologicheskaya i taitokhimicheskaya kharakteritika ovogeneza i polovykh tsiklov u primorskogo grebeshka i dal'nevostochnoi gigantskoi midii [Morphological and cytochemical description of ovogenesis and reproductive cycles in the Primorsk scallop and the far-eastern giant mussel]. Avtoref. Diss. Kand. Biol. Nauk. Vladivost. Med. Inst., Vladivostok, 24 pp.

Edwards, C.L. 1909. The development of *Holothuria floridana* Pourtales with special reference to the ambulacral appendages. *J. Morphol.*, vol. 20, 211–230.

Elston, R. 1980. Functional morphology of the coelomocytes of the larval oysters (*Crassostrea virginica* and *Crassostrea gigas*), *J. Mar. Biol. Assoc. U.K.*, 60, 4, 947–957.

Emlet, R.B. 1988. Larval form and metamorphosis of a "primitive" sea urchin *Eucidaris thouarsi* (Echinodermata: Echinoidea: Cidaroida) with implications for developmental and phylogenetic studies. *Biol. Bull.*, 174, 1, 4–19.

Engle, J.B. and V.L. Loosanoff. 1944. On season of attachment of larvae of *Mytilus edulis* L. *Ecology*, 25, 4, 433–440.

Engstrom, N.A. 1980. Development, natural history and interstitial habits of the apodous holothurian *Chiridota rotifera* (Pourtales, 1851) (Echinodermata; Holothuroidea). Brenesia, vol. 17, 85–96.

Falk-Petersen, I.-B. and J.R. Sargent. 1962. Reproduction of asteroids from Balsfierden, Northern Norway, Analysis of lipids in the gonads of *Ctenodiscus crispatus, Asterias lincki* and *Pteraster militaris. Mar. Biol.*, 69, 3, 291–298.

Fell, H.B. 1941. Probable direct development of some New Zealand ophiuroids.*Trans. Roy. Soc. N. Z.*, vol. 71, 25–26.

Fell, H.B. 1945. A revision of the current theory of echinoderm embryology. *Trans. Roy. Soc. N. Z.*, vol. 75, pt. 2, 73–101.

Fell, H.B. 1946. The embryology of the viviparous ophiuroid *Amphipholis squamata. Trans. Roy. Soc. N.Z.*, vol. 75, pt. 4, 419–464.

Fenaux, L. 1961. Une large de Spatangide *Echinopluteus solidus* (Mortensen) du plancton de Villefranche-sur-Mar. *Cah. Biol. Mar.*, 2, 20, 209–221.

Fenaux, L. 1963. Note préliminaire sur développement larvaire de *Amphiura chiajei* (Forbes). *Vie et Milieu* 14, 1, 91–96.

Fenaux, L. 1969. Le développement larvaire chez *Ophioderma longicauda* (Retzius). *Cah. Biol. Mar.*, 10, 1, 59–62.

Fenaux L. and R. Fenaux, 1974. Premier stade larvaire de l'oursin régulier *Tripnustes gratilla* (Linné). Nouvelles données sur la formation du squelette somatique. *Isr. J. Zool.*, 23, 3/4, 119–124.

Fewkes, W. 1887. On the development of the calcareous plates of *Amphiura squamata. Bull. Mus. Comp. Zool. Harvard Coll.* vol. 13, 107–150.

Fewkes, W. 1893. Preliminary observations on the development of *Ophiopholis* and *Echinarachnius. Bull. Mus. Comp. Zool. Harvard Coll.*, 24, 4, 106–152.

Field, G.V. 1892. The larva of *Asterias vulgaris. Quart. J. Microsc, Sci.* vol. 34, 105–128.

Field, G.V. 1922. Biology and economic value of the sea mussel *Mytilus edulis. Bull. US Bur. Fish.*, no. 38, 127–259.

Fioroni, P. 1971. Die Entwicklungstypen der Mollusken. *Ztschr. Wiss. Zool.*, vol. 182, 263–394.

Fuji, A. 1960a. Studies on the biology of the sea urchin. I. Superficial and histological changes in gametogenic process of two sea urchins, *Strongylocentrotus nudus* and *Strongylocentrotus intermedius*. *Bull. Fac. Fish. Hokkaido Univ.*, vol. 2, 1–14.

Fuji, A. 1960b. Studies on the biology of the sea urchin. III. Reproductive cycle of two sea urchin *Strongylocentrotus nudus* and *S. intermedius*. in southern Hokkaido. *Bull. Fac. Fish. Hokkaido Univ.*, 11, 2, 49–57.

Fujita, T. 1929. On the early development of the common Japanese oyster. *Jap. J. Zool.*, 2, 3, 353–358.

Fujita, T. 1933. Note on the Japanese oyster larva. In: *Proc. V. Pacif. Sci. Congr. Canada, Toronto.* Univ. Toronto Press, vol. 5, 4111–4117.

Gage, J. 1966a. Observations on the bivalves *Montacute substriata* and *M. ferruginosa*, "commensals" with spatangoids. *J. Mar. Biol. Assoc. U.K.*, vol. 46, 49–70.

Gage, J. 1966b. The life history of the bivalves *Montacuta substriata* and *M. ferruginosa*, "commensals" with spatangoids. *J. Mar. Biol. Assoc. U.K.*, vol. 46, 499–511.

Gaginskaya, E.R., V.L. Kasyanov and E.S. Kornienko. 1983. Nekotorye osobennosti oogeneza morskoi zvezdy *Henricia* sp. [Some peculiarities of oogenesis of the sea star *Henricia* sp.]. *Tsitologiya*, 25, 2, 135–140.

Gal'perina, G.E. 1969. Ob opredélenii lichinok dvustvorchatykh mollyuskov Severnogo Kaspiya [On identification of larvae of bivalve mollusks of the Northern Caspian]. In: *Trudy Molodykh Uchenykh VNIRO*, vol. 1, 248–252.

Gemmill, J. F. 1912. The development of the starfish *Solaster endeca* Forbes. *Trans. Zool. Soc. London*, vol. 20, 1–17.

Gemmill, J.F. 1914. The development and certain points in the adult structure of the starfish *Asterina rubena* L. *Philos. Trans. Roy. Soc. London*, vol. 205, 213–294.

Gemmill, J.F. 1915a. The larva of the starfish *Porania pulvillus* (Q.F.M.). *Quart. J. Microsc. Sci.*, vol. 61, 27–50.

Gemmill, J.F. 1915b. Double hydrocoel in the development of the larva of *Asterias rubens*. *Quart. J. Microsc. Sci.*, vol. 61, 51–80.

Gemmill, J.F. 1916. Notes on the development of the starfishes *Asterias glacialis* Q.F.M., *Cribrella oculata* (Linck) Forbes, *Solaster roseus* (Q.F.M.) Capc. *Proc. Zool. Soc., Japan*, vol. 39, 553–567.

Gilbert, F. 1963. Brood protection in three southern Californian species of the pelecypod Cardita. *Wasmann J. Biol.*, 21, 2, 141–148.

Gilmour, T.H.J. 1985. Analysis of videotype recordings of larval feeding in the sea urchin *Lytechinus pictus*. *Can. J. Zool.*, 63, 6, 1354–1359.

Gilmour, T.H.J. 1986. Streamlines and particle path in the feeding mechanisms of larvae of the sea urchin *Lytechinus pictus* Verrill. *Exp. Mar. Biol., Ecol.,* 95, 1, 27–36.

Ginzburg, A.S. 1974. Oplodotvorenie yaits dvustvorchatykh mollyuskov pri razhykh usloviyakh osemeneniya [Fertilization of eggs of bivalve mollusks under different conditions of insemination]. *Ontogenez,* 5, 4, 341–348.

Gordon, I. 1962a. On the development of calcareous test of *Echinus miliaris. Philos. Trans. Roy. Soc.* London, vol. 214B, 259–312.

Gordon, I. 1926b. On the development of the calcareous test of *Echinocardium cordatum. Philos. Trans. Roy. Soc. London,* vol. 215B, 255–313.

Gordon, I. 1928. Skeletal development in *Arbacia, Echinarachnius* and *Leptasterias. Philos. Trans. Roy. Soc. London,* vol. 217B, 289–334.

Goto, S. 1986. The metamorphosis of *Asterias pallida. J. Col. Sci. Univ. Tokyo,* vol. 10, 239– 278.

Grave, B.H. 1928. Natural history of the shipworm *Teredo navalis* at Woods Hole, Massachusetts. *Biol. Bull.,* no. 55, 260–282.

Grave, C. 1898. Embryology of *Ophiocoma echinata* Agassiz. *Johns Hopkins Univ. Circ.,* vol. 18, 6–7.

Grave, C. 1902. Some points in the structure and development of *Mellita testudinata. Johns Hopkins Univ. Circ.,* 21, 157, 57–59.

Grave, C. 1916. *Ophiura brevispina. J. Morphol.,* vol. 27, pp. 413–452.

Grube, A.E. 1868. Über einen lebending gebârenden Seeigel. *Sber. Preuss. Akad. Wiss.,* pp. 178–180.

Gruffydd, Ll.D., D.J.W. Lane and A.R. Beaumont. 1975. The glands of the larval foot in *Pecten maximux* L. and possible homologies in other bivalves. *J. Mar. Biol. Assoc. U.K.,* vol. 55, 463–476.

Gustafson, R.G. and R.G.B. Reid. 1986. Development of the pericalymma larva of *Solemya reidi* (Bivalvia: Cryptodonta; Solemyidae) as revealed by light and electron microscopy. *Mar. Biol.,* vol. 93, 411–427.

Gustafson, R.G., D. O'Foighil and R.G.B. Reid. 1986. Early ontogeny of the septibranch bivalve *Cardiomya pectinata* (Carpenter, 1865). *J. Mar. Biol. Assoc. U.K.,* 64, 4, 943–950.

Gustafson, T. 1963. Mesenchymal distribution and ectodermal cell contacts in the sea urchin gastrula. *Zool. Bidr. Uppsala,* vol. 35, 425–431.

Gustafson, T. 1964. The role and activities of pseudopodia during morphogenesis of the sea urchin larva. In: *Primitive Motile Systems in Cell Biology.* Acad. Press, N.Y., pp. 333–348.

Gustafson, T. 1975. Cellular behaviour and cytochemistry in early stages of development. In: *The Sea Urchin Embryo. Biochemistry and Morphogenesis* (ed. G. Czihak). Springer-Verlag, Berlin — New York, pp. 233–266.

Gustafson, T. and L. Wolpert. 1967. Cellular movement and contact in sea urchin morphogenesis. *Biol. Rev.,* 42, 3, 442–498.

Hagström, B.E. and S. Lonning. 1961. Morphological and experimental studies on the genus *Echinus. Sarsia,* vol. 4, 21–31.

Hamada, T. 1927. On the artificial parthenogenesis of the oyster. *Zool. Mag.,* vol. 39.

Hansen, B. 1953. Brood protection and sex ratio of *Transenella tantilla* (Gould) — a Pacific bivalve. *Dansk. Naturhist. Foren. Videnskab. Medd.,* vol. 115, 313–324.

Harvey, E.B. 1956. *The American Arbacia and Other Sea Urchins.* Princeton Univ. Press, Princeton.

Hatanaka, M. and M. Kosaka. 1958. Biological studies on the population of the starfish, *Asterias amurensis,* in Sendai Bay. *Tohoku J. Agr. Res.,* 9, 3, 159–173.

Hatschek, B. 1880. Über Entwicklungsgeschichte von *Teredo. Arb. Zool. Inst. Univ. Wien und Zool. Stat., Triest.,* no. 3(1), 1–44.

Havinga, B. 1957. The settling of mussel seed in the Dutch Waddensea. Intern. Counc. Explor. Sea Shellfish Comm., pp. 1–5.

Hayashi, T. and K. Terai. 1964. Study on the larvae and young of Japanese surf clam, *Spisula sachalinensis* (Schrenck), at Shikuzu, Muroran City. Taxonomy of the Pelecypoda's veliger larvae in plankton. *Sci. Rep. Hokkaido Fish. Exp. Sta.,* 39, 2, 7–38.

Henderson, J.A. and J.S. Lucas. 1971. Larval development and metamorphosis of *Acanthaster planci* (Asteroidea). *Nature,* vol. 232, 655–657.

Hendler, G. 1975. Adaptational significance of the patterns of ophiuroid development. *Amer. Zool.,* vol. 15, 691–715.

Hendler, G. 1977. Development of *Amphioplus abditus* (Verrill) (Echinodermata: Ophiuroidea). 1. Larval biology. *Biol. Bull.,* vol. 152, 51–63.

Hendler, G. 1978. Development of *Amphioplus abditus* (Verrill) (Echinodermata: Ophiuroidea). 2. Description and discussion of ophiuroid skeletal ontogeny and homologies. *Biol. Bull.,* vol. 154, 79–95.

Hickman, R.W. and L1.D. Gruffydd. 1971. The histology of the larva of *Ostrea edulis* during metamorphosis. In: *IV Europ. Mar. Biol. Symp. Bangor, Wales, 1969.* Cambridge Univ. Press, Cambridge, pp. 281–294.

Hidu, H. and H.H. Haskin. 1978. Swimming speeds of oyster larvae, *Crassostrea virginica,* in different salinities and temperatures. *Estuaries,* 1, 4, 252–253.

Highsmith, R.C. 1982. Induced settlement and metamorphosis of sand dollar *(Dendraster excentricus)* larvae in predator-free sites: adult sand dollar beds. *Ecology,* vol. 63, 329–337.

Hill, C.L. and C.A. Kofoid. 1927. Marine borers and their relation to marine construction on the Pacific coast. San Francisco Bay Marine Pilling Comm., 1–357.

His, E. and N. Kriaria. 1972. Un essai en laboratoire d'élevage larvaire de *Crassostrea gigas*. In: *XIII Congr.-Assemblee Pléniere de la CIESM Athénes,* 1–3.

Höbaus, E. 1979. Skin excretion in sea urchins. *Naturwissenschaften,* 66, 3, 160–161.

Holland, D.L. 1978. Lipid reserves and energy metabolism in the larvae of benthic marine invertebrates. In: *Biochemical and Biophysical Perspectives in Marine Biology.* Acad. Press, London — N.Y., vol. 4, 85–125.

Holland, D.L. and B.E. Spenser. 1973. Biochemical changes in fed and starved oysters, *Ostrea edulis* L., during larval development, metamorphosis and early spat growth. *J. Mar. Biol. Assoc. U.K.,* vol. 53, 287–298.

Holland, D.L. and P.J. Hennant. 1974. Biochemical changes during growth of the spat of oyster *Ostrea edulis* L. *J. Mar. Biol. Assoc. U.K.,*vol. 54, 1007–1016.

Holland, N.D. 1979. Electron microscopic study of the cortical reaction of an ophiuroid echinoderm. *Tissue and Cell,* 11, 3, 445–455.

Hori, I. 1926. Notes on the full-grown larva of the Japanese common oyster, *Ostrea gigas* Thunberg. *J. Imp. Fish. Inst.,* 21, 1, 1–7.

Hörstedius, S. 1939. Entwicklung von *Astropecten auranciacus. Pubbl. Staz. Zool. Napoli,* vol. 17, 222–312.

Howard, A.D. 1953. Some viviparous pelecypod mollusks. Wasmann J. Biol., 11, 2, 233–240.

Hylander, B.L. and R.G. Summers. 1977. An ultrastructural analysis of the gametes and early fertilization in two bivalve molluscs, *Chama macrophylla* and *Spisula solidissima*, with special reference to gamete binding. *Cell. Tissue Res.*, vol. 182, 469–489.

Hyman, L.H. 1955. *The Invertebrates. Echinodermata.* McGraw-Hill, N.Y. vol. 4, 763 pp.

Imai, T. and M. Hatanaka. 1949. On the artificial propagation of Japanese common oyster, *Ostrea gigas* Thunb. by noncolored naked flagellates. *Bull. Inst. Agr. Res. Tohoku Univ.*, 1, 4, 33–46.

Imai, T.M. Hatanaka and R. Sato. 1950. Breeding of marine timber borer *Teredo navalis* L. in tanks and its use for antiboring test. *Tohoku J. Agr. Res.*, 1, 2, 199–208.

Inaba, D. 1930. Notes on the development of a holothurian *Caudina Chilensis* (J. Müller). *Sci. Rep. Tohoku Univ. Sendai,* vol. 5, pp. 215–248.

Ingle, R.M. 1962. Spawning and settling of oyster in relation to seasonal environmental changes. *Bull. Mar. Sci. Gulf. Carib.,* vol. 1, no. 2.

Ino, T., F. Sagara, S. Hamada and M. Tamakawa. 1955. On the spawning season of the starfish *Asterias amurensis* in Tokyo Bay. *Bull. Jap. Sec. Sci. Fish.,* 25, 1, 32–36.

Isham, L.B. and J.Q. Tierney. 1953. Some aspects of the larval development and metamorphosis of *Terede (Lyrodus) pedicellata* de Quatrfages. *Bull. Mar. Sci. Gulf. Carib.,* vol. 2, pp. 574–589.

Ivanova-Kazas, O.M. 1975. Sravnitel'naya embriologiya bespozvonochnykh zhivotnykh. Prosteishieinizshie mnogokletochnye [Comparative Embryology of Invertebrates. Protozoa and Lower Multicellular Organisms]. Nauka, Novosibirsk, 372 pp.

Ivanova-Kazas, O.M. 1977. Sravnital'naya embryologiya bespozvonochnykh zhivotnykh. Trokhofornye, shupal'tsevye, shchetinkochelyustnye, pogonofory [Comparative Embryology of Invertebrates. Trochophores, Tentaculats, Chaetognatha and Pogonophora]. Nauka, Moscow, 312 pp.

Ivanova-Kazas, O.M. 1978. Sravnital'naya embriologiya bespozvonochnykh zhivotnykh. Iglokozhie i polukhordovya [Comparative Embryology of Invertebrates. Echinodermata and Hemichordata). Nauka. Moscow, 166 pp.

Jagersten, G. 1972. *Evolution of the metazoan Life Cycle.* Acad. Press, London-New York, pp. 1–281.

Jangoux, M. 1978. Functions des caecums rectaux chez l'stoile de mer, *Asterias rubens* L. *Thalassia Jugosl.,* 12, 1, 181–186.

Jenner, C. and A. McCrary. 1968. Sexual dimorphism in erycinacean bivalves. *Amer. Malacol. Union Ann. Rep. Bull.,* vol. 35, 43.

Johnson, M.W. and R.C. Miller. 1975. Seasonal settlement of shipworms, barnacles and other wharf-pile organisms at Friday Harbor. *Publ. Oceanogr. Wash. Univ.,* no. 2, 1–18.

Jørgensen, C.B. 1946. Lamellibranchiata. *Medd. Komm. Danm. Fish Havunders, Ser. Plankton,* 4, 1, 277–311.

Kaestner, A. 1965. Lehrbuch der speziellen Zoologie. T.l. Fischer, Jena, 845 s.

Kano, J.T. and M. Komatsu. 1978. Development of the sea star, *Asterina batheri* Goto. *Develop., Growth and Differ.,* 20, 2, 107–114.

Kasyanov, V.L. 1977. Razvitie morskoi zvezdy *Patiria pectnifera* [Development of the sea star *Patiria pectnifera*]. In: *I Vees. Knoff. po Mor. Biol.* Izd-vo DVNTs AN SSSR, Vladivostok, pp. 68–69.

Kasyanov, V.L. 1987. Kakie morakie zvezdy imeyut planktotrofnuyu lichinku? [which sea stars have Planktotrophic larvae?] In: *Issledovaniya Iglokozhikh Dal'nevostochnykh Morei,* Izd-vo DVD AN SSSR, Vladivostok, pp. 125–'43.

Kasyanov, V.L. 1989. Reproduktivnaya strategiya morskikh dvustvorchatykh mollyuskov i iglokozhikh [Reproductive Strategy of Marine Bivalves and Echinoderms]. Nauka, Leningrad, 183 pp.

Kasyanov, V.L., A.F. Kukin, L.A. Medvedeva, and Yu. M. Yakovlev. 1976. Sroki razmnozheniya i sostoyanie gonad v nerestovyi period u massovykh vidov dvustvorchatykh mollyuskov i iglokozhikh zaliva Vostok Yaponskogo morya [Periods of reproduction and state of gonads in the spawning period of mass species of bivalve mollusks and echinoderms from Vostok Bay of the Sea of Japan]. In: *Biologicheskie Issledovaniya Zaliva Vostok.* Izd-vo DVNTs AN SSSR, Vladivostok, pp. 156–157.

Kasyanov, V.L., N.K. Kolotukhina, G.A. Kruchkova, and S.N. Yakovlev. 1977. Times of spawning of mass echinoderm species inhabiting the Sea of Japan. In *Proc. 3rd Japan-Soviet Joint Symp. Aquacult. Nov. Tokyo*, pp. 181–184.

Kasyanov, V.L., L.A. Medvedeva, Yu.M. Yakovlev and S.N. Yakovlev. 1980. Razmnozhenie iglokozhikh i dvustvorchatykh molluskov [Reproduction in Echinoderms and Bivalve Mollusks]. Nauka, Moscow, 204 pp.

Kaufman Z.S. 1968. Postembryonal'nyi period razvitiya nekotorykh zvezd Belogo morya [Postembryonal period of development in some sea stars of the White Sea]. *Dokl. AN SSSR*, 181, 4, 1009–1012.

Kaufman, Z.S. 1977. Osobennosti polovykh tsiklov belomorskikh bespozvonochnykh [Peculiarities of Sexual Cycles of the White sea Invertebrates]. Nauka, Leningrad, 265 pp.

Kawamura, K. 1970. On the development of the planktonic larvae of Japanese sea urchins *Strongylocentrotus intermedius* and *Strongylocentrotus nudus. Sci. Rep. Hokkaido Fish. Exp. Sta.,* no. 12, 25–32.

Kawamura K. and Y. Taki. 1965. Ecological studies on the sea urchin *Strongylocentrotus intermedius* on the coast of Fundomari in the north region of Rebun Island. *Sci. Rep. Hokkaido Fish. Exp. Sta.,*vol. 4, pp. 22–40.

Kilias, R. 1969. *Urania Tierreich.* Berlin, vol. 1, 565–566.

Kim, J.S. 1968. Histological observations of the annual change in the gonad of the starfish *Asterias amurensis* Lütken. *Bull. Fac. Fish. Hokkaido Univ.* 19, 2, 97–108.

Kinosita, T. 1938. A study on the spawning season of *Stichopus japonicus. Hokkaido Suisan Schinenjyo Junpo.,* vol. 373, 1–7.

Kirk, H.B. 1916. On the much-abbreviated development of a sand star (*Ophionereis senayeri*). Preliminary note. *Trans. N. Z. Inst.*, vol. 48, 383–384.

Kiselev, I.A. 1969. Plankton morei i kontinental'nykh vodoemov (Plankton of Seas and Continental Water Bodies) Nauka, Leningrad, vol. 1, 658 pp.

Kiseleva G.A. 1970. Osedanie i metamorfoz lichinok mollyuska-kamnetochtsa *Pholas dactylus* Linné [Settling and metamorphosis of larvae of the stone-boring mollusk *Pholas dactylus* Linné]. In: *Ekol-morfol. Issled. Donnykh Organizmov*. Naukova Dumka, Kiev, pp. 102–113.

Kniprath, E. 1979. The functional morphology of the embryonic shell gland in the conchiferous molluscs. *Malacologia*, vol. 18, 549–552.

Knudsen, I. 1961. The bathyal and abyssal Xylophaga (Pholadidae, Bivalvia). *Galathea Rep.* vol. 5, 163–209.

Kobayakawa, J. and N. Satoh. 1978. Induction of the wrinkled blastula formation in the starfish, *Asterina pectinifera*, by modified developmental conditions, *Biol. Bull.*, 155, 1, 150–160.

Koehler, R. 1926. Echinodermata: Echinoidea. *Sci. Rep. Austral. Antarct. Expand., Ser. C.*, vol. 8, 1–134.

Kofoid, C.A. and R.C. Miller, 1927. Biological section. In: *Marine Borers and Their Relation to Marine Construction on the Pacific Coast/San Francisco Bay*. Mar. Piling Comm., San Francisco, pp. 188–343.

Komatsu, M. 1972. On the wrinkled blastula of the sea star, *Asterina pectinifera. Zool. Mag.*, vol. 81, 227–231.

Komatsu, M. 1975a. On the development of the sea star, *Astropecten latespinosus* Meissner. *Biol. Bull.*, 148, 1, 49–54.

Komatsu, M. 1975b. Development of the sea star *Asteria coronata japonica* Hayashi. *Proc. Jap. Soc. Syst. Zool.*, no. 11, 42–48.

Komatsu, M. 1982. Development of the sea star *Ctenopleura fisheri. Mar. Biol.*, vol. 66, 199–205.

Komatsu, M., J. Kano, H. Joshizava *et al.* 1979. Reproduction and development of the hermaphroditic sea star *Asterina minor* Hayashi. *Biol. Bull.*, vol. 157, 258–274.

Komatsu, M., Y.T. Kano and C. Oguro. 1982. Development of the sea star *Luidia quinaria* von Martens. In: *Internat. Echinoderm Conf. Tampa,* pp. 37–39.

Kominami, T. and N. Satoh. 1980. Temporal and cell-numerical organization of embryos in the starfish, *Asterina pectinifera. Zool. Mag.*, 89, 3, 244–251.

Konstantinova, M.I. 1966. Kharakteristika dvizheniya pelagicheskikh lichinok morskikh bespozvonochnykh [Characteristics of the locomotion of pelagic larvae of marine invertebrates]. *Doki. AN SSSR,* vol. 170, 726–729.

Korringa, P. 1957. Water temperature and breeding throughout the geographical range of *Ostrea edulis. Ann. Biol.*,33, 1/2, 1–17.

Kowalewsky, A.O. 1867. Beiträge zur Entwicklungsgeschichte der Holothurien. *Mem. Acad. Imp. Sci. St. Petersbourg*, 7, 6, 1–8.

Kryuchkova, G.A. 1976. Morfologiya lichinochnogo skeleta morskikh ezhei zaliva Vostok Yaponskogo morya [Morphology of the larval skeleton of

sea urchins from Vostok Bay of the Sea of Japan]. *Biol. Morya,* no. 4, 45–54.

Kryuchkova, G.A. 1977. Gibridnye lichinki ploskikh morskikh ezhei [Hybrid larvae of sand dollars]. *Biol. Morya,* no. 5, 78–81.

Kryuchkova, G.A. 1979a. Obrazovanie amnioticheskoi polosti i razvitie definitvnogo skeleta u plostikh morskikh ezhei [Formation of the amniotic sac and development of the definitive skeleton in sand dollars]. *Biol. Morya,* no. 3, 50–56.

Kryuchkova, G.A. 1969b. Formirovanie definitivnogo skeleta u morskikh ezhei roda *Strongylocentrotus* [Formation of definitive skeleton in sea urchins of the genus *Strongylocentrotus*]. *Biol. Morya,* no. 4, 38–46.

Kryuchkova, G.A. 1979c. Razvitie definitivnogo skeleta u *Echinocardium cordatum* [Development of the definitive skeleton in *Echinocardium cordatum*]. *Biol. Morya,* no. 6, 35–43.

Kryuchkova, G.A. 1981. Morfologicheskie osobennosti lichinok *Stichopus japonicus* [Morphological peculiarities of *Stichopus japonicus* larvae]. In: *VI Vses Sovesch. Embriologov/Tez. Dokl.* Nauka, Moscow, p. 97.

Kryuchkova, G.A. 1988. Razvitie ofiur *Ophiura sarsi* i *Amphipholis kochii* [Development of brittle stars *Ophiura sarsi* and *Amphipholis kochii*]. *Biol. Morya,* no. 1. 33–40.

Kulikova, V.A. 1975. Lichinki massovykh vidov dvustvorchatkh mollyuskov v planktone laguny Busse (Sakhalin) [Larvae of massive species of bivalves in the plankton of Busse Lagoon (Sakhalin]. In: *Mollyuski. Ikh Sistema, Evolyutsiya i Rol' v Prirode* Nauka, Leningrad, vol. 5, 130–132.

Kulikova, V.A. 1978. Morfologiya, sezonnaya dinamika chislennosti i osedanie lichinok dvustvorchatogo mollyuska *Musculista senhousia* v lagune Busse (Yuzhnoi Sakhalin) [Morphology, seasonal dynamics of population and settling of larvae of the bivalve *Musculista senhousia* in Busse Lagoon (South Sakhalin)]. *Biol. Morya,* no. 4, 133–135.

Kulikova, V.A. 1979. Osobennosti razmnozheniya dvustvorchatykh mollyuskov v lagune Busse v svyazi s temperaturnymi usloviyami vodoema [Peculiarities of reproduction of bivalves in Busse Lagoon in relation to temperature conditions of the water body]. *Biol. Morya,* no. 1, 34–38.

Kulikova, V.A. and V.D. Tabunkov. 1974. Ekologiya, razmnozhenie, rost i produktsionye svoistva populyatsii grebeshka *Mizuhopecten yessoensis* (Dysodonta, Pectinidae) v lagune Busse (zaliv/Aniva) [Ecology, reproduction, growth and production properties of the population of the scallop *Mizuhopecten yessoensis* (Dysodonta, Pectinidae) in Busse Lagoon (Anive Bay)]. *Zool. Zhurn.,* 53, 12, 1767–1774.

Kulikova, V.A., L.A. Medvedeva and G.M. Guide. 1981. Morfologiya pelagicheskikh lichinok trekh vidov dvustvorchatykh mollyuskov semeistva Pectinidae zaliva Petra Velikogo (Yaponskoe more) [Morphology of pelagic

larvae of three species of bivalves of the family Pectinidae in Peter the Great Bay (Sea of Japan)]. *Biol. Morya,* no. 4, 75–77.

Kulikova, V.A., S.A. Kalashnikova and N.A. Aizdaicher. 1987. Razvitie i morfologiya rakoviny lichinok *Arca boucardi* (Mytilida, Arcidae) poluchennykh v kul'ture [Development and morphology of larval shell of *Arca boucardi* (Mytilida, Arcidae) obtained in culture]. *Zool. Zhurn.,* 66, 5, 770–773.

Kume, M. and K. Dan. 1968. *Invertebrate Embryology.* Nolit, Belgrade, 605 pp.

La Barbera, M. 1975. Larval and postlarval development of the giant clams, *Tridacna maxima* and *Tridacna squamosa* (Bivalvia, Tridacnidae). *Malacologia,* 15, 1, 69–79.

Lacaze-Duthiers, H.M. 1870. Sur l'organization de L'arrosoir *Aspergillum javanicum. C.R. Acad. Sci. Paris,* Vol. 70, 268–271.

Lane, D.J.W. and J.A. Nott. 1970. A study of the morphology, fine structure and histochemistry of the foot of the pediveliger of *Mytilus edulis* L. *J. Mar. Biol. Assoc. U.K.* Vol. 55, 477–495.

Lawson-Kerr, C. and D.T. Anderson. 1978. Reproduction, spawning and development of the starfish *Patiriella exigua* Lamarck) (Asteroidea. Asterinidae) and some comparisons with *P. calcer* (Lamarck). *Austral. J. Mar. and Freshwater Res.,* 29, 1, 45–54.

Lebour, M.V. 1938a. Notes on the breeding of some lamellibrancha from Plymouth and their larvae. *J.'Mar. Biol. Assoc. U.K.,* 23, 1, 119–145.

Lebour, M.V. 1938b. The life history of *Kellia suborbiculais. J. Mar. Biol. Assoc. U.K.*, vol. 22, 447–452.

Lender, T. and R. Delavault. 1968. Proiskhozhdenie i razvitie polevykh kletok u iglokozhikh [Origin and development of sex cells in enchinoderms]. In: *Proiskhozhdenie i Razvitie Polovykh Kletok v Ontogeneze Pozvonochnykh i Nekotorykh Grupp Bespozvonochnykh.* Meditsina, Leningrad, pp. 163–172.

Le Pennec, M.V. 1980a. Premiéres observations sur la morphogenese de la coquille larvaire de *Spisule subtruncata* (Da Costa) an élevage expérimentale. *Cah. Biol. Mar.*, 21, 4, 403–408.

Le Pennec, M.V. 1980b. The larval and postlarval hinge of some families of bivalve mollusks. *J. Mar. Biol. Assoc. U.K.*, 60, 3, 601–617.

Liao, Chengyi and Tiekai Qio. 1987. A preliminary study of the artificial rearing of the larvae and juveniles of the purple sea urchin. *J. Fish. Chin.*, 11, 4, 277–283.

Lillie, F.R. 1895. The embryology of the Unionidae. *J. Morphol.*, vol. 10, 1–100.

Lindahl, P.E. 1932. Zur Kenntnis des Ovarialeis bei dem Seeigel. *Roux' Arch. Entwicklungamech.*, vol. 126, 373–390.

Longo, F.J. and E. Anderson. 1969a. Cytological aspects of fertilization in the lamellibranch, *Mytilus edulis.* I. Polar body formation and development of the female pronucleus. *J. Exp. Zool.*, 172, 1, 69–96.

Longo, F.J. and E. Anderson. 1969b. Cytological aspects of fertilization in the lamellibranch, *Mytilus edulis.* II. Development of the male pronucleus and the association of maternally and paternally derived chromosomes. *J. Exp. Zool.*, 172, 1, 97–119.

Longwell, A.C. and S.S. Stiles. 1968. Fertilization and completion of meiosis in spawned eggs of the American oyster, *Crassostrea virginica* Gmelin. *Caryologia,* 21, 1, 65–73.

Lonning, S. 1976. Reproductive cycle and ultrastructure of yolk development in some echinoderms from the Bergen area, western Norway. *Sarsia,* no. 62, 49–72.

Loosanoff, V.L. 1969. Development of shellfish culture techniques. In: *Proc. Conf. Artificial Propagation Commerc. Valuable Shellfishes.* Newark Univ., Delaware, pp. 9–40.

Loosanoff, V.L. and H. C. Davis. 1963. Rearing of bivalve mollusks. *Adv. Mar. Biol.*, no. 1, 1–136.

Loosanoff, V.L., H.C. Davis and P.E. Chanley. 1966. Dimensions and shapes of larvae of some marine bivalve mollusks. *Malacologia*, 4, 2, 351–435.

Lucas, A. 1975. Sex differentiation and juvenile sexuality in bivalve molluscs. *Publ. Staz. Zool. Napoli,* vol. 39, 532–541.

Lutz, R.A. and H. Hidu, 1979. Hinge morphogenesis in the shells of larval and early postlarval mussels [*Mytilus edulis* L. and *Modiolus modiolus* (L.)]. *J. Mar. Biol. Assoc. U.K.,* vol. 59, 111–121.

MacDonald, D. Ch., R.K. Kohen, E.S. Balakirev, G.P. Manchenko, A.I. Puaduvkin, S.O. Sergievskii and K.V. Krutovskii. 1990. Vidovaya prinadlezhnost' s"edobnoi midii, obitayushchei v priaziatskoi chasti Tikhogo Okeana [Species affinity of edible mussels living in the Asiatic part of the Pacific Ocean]." *Biol. Morya,* no. 1, 13–21.

Malakhov, V.V. and L.A. Medvedeva. 1986. Embryonal'noa razvitie dvustvorchatykh mollyuskov *Patinopecten yessoensis* (Pectinida, Pectinidae) i *Spisula sachalinensis* (Cardiida, Mactridae) [Embryonal development of marine bivalves *Patinopecten yessoensis* (Pectinida, Pectinidae) and *Spisula sachalinensis* (Cardiida, Mactridae)]. *Zool. Zhurn.*, 65, 5, 732–740.

Maru, K. 1972. Morphological observation on the veliger larvae of a scallop, *Patinopecten yessoensis* Jay. *Sci. Rep. Hokkaido Fish. Exp. Sta.,* no. 14, 55–62.

Maruyama, Y.K. 1981. Development of swimming behaviour in sea urchin embryo. *J. Exp. Zool.*, 215, 2, 163–171.

Mason, J. 1972. The cultivation of the European mussel *Mytilus edulis* Linné. *Oceanogr. Mar. Biol. London,* 437–460.

Masterman, A.T. 1902. Early development of *Cribrella oculata. Trans. Roy. Soc. Edinburg,* vol. 40, 373–417.

Matsumoto, H. 1915. A new classification of the Ophiuroidea: with description of new genera and species. *Proc. Acad. Nat. Sci. Philadelphia,* vol. 57, pt. 1, 43–95.

Matveeva, T.A. 1948. Biologiya *Mytilus edulis* Vostochnogo Murmana [Biology of the *Mytilus edulis* of the eastern Murman]. *Tr. Murm. Biol. Stantsii,* vol. 1.

Matveeva, T.A. 1953. O sposobakh raxmnozheniya morskikh dvustvorchatykh mollyuskov [On the modes of reproduction in marine bivalves]. *Dokl. AN SSSR,* vol. 93, 923–924.

Matveeva, T.A. 1975. Prisposobleniya k vynashivaniyu yaits u nekotorykh morskikh dvustvorchatykh mollyuskov [Devices for carrying eggs in some marine bivalves]. In: *Mollyuski. Ikh Sistema, Evolyutsiya i Rol' v Prirode.* Nauka, Leningrad, vol. 5, 133–135.

Matveeva, T.A. 1979. Prisposobleniya k vynashivaniyu yaits u nekotorykh vidov dvustvorchatykh mollyuskov [Devices for carrying eggs in some species of bivalves]. *Tr. Zool. In-ta,* vol. 80, 39–43.

McBride, E.W. 1896. Development of *Asterina gibbosa. Quart. J. Microsc. Sci.,* vol. 8, 339–411.

McBride, E.W. 1903. The development of *Echinus esculentus* together with some points in the development of *E. miliaris* and *E. acutus. Philos. Trans. Roy. Soc. London,* vol. 195B, 285–327.

McBride, E.W. 1907. Development of *Ophiothrix fragilis. Quart. J. Microsc. Sci.,* vol. 51, 557–606.

McBride, E.W. 1914. The development of *Echinocardium cordatum.* pt. I. The external features of the development. *Quart. J. Microsc. Sci.,* vol. 59, 471–486.

McBride, E.W. 1918. The development of *Echinocardium cordatum.* Pt. II. The development of the internal organs. *Quart. J. Microsc. Sci.,* vol. 63, 259–282.

McClintock, P.S. and J.S. Pearse. 1986. Organic and energetic content of eggs and juveniles of antarctic echinoids and asteroids with lecithotrophic development. *Compar. Biochem. Physiol.,* 85A, 2, 341–345.

McEuen, F.S. and F.-S. Chia. 1985. Larval development of a molpadid holothuroid *Molpadia intermedia* (Ludwig, 1894) (Echinodermata). *Can. J. Zool.,* 63, 11, 2533–2559.

Medvedeva, L.A. 1981. Lichinochnoe razvitie dvuostvorchatogo mollyuska *Spisula sachalinensis* [Larval development in bivalve *Spisula*

sachalinensis]. Tez. Dokl. VI Vses. Soveshch. Embriologov. Nauka, Moscow, 116 pp.

Medvedeva, L.A. and V.V. Malakhov. 1983. Embrional'noe razvitie dvustvorchatogo mollyuska *Mactra chinensis* [Embryonal development of the bivalve *Mactra chinensis]. Zool. Zhurn.,* vol. 62.

Meek, A. 1927. Bipinnaria asterigera. *Proc. Zool. Soc. London,* vol. 1, 151–171.

Meisenheimer, J. 1901. Entwicklungsgeschichte von *Dreissensia polymorpha* Pall. *Ztschr. wiss. Zool.,* vol. 69, 1–137.

Meisenheimer, J. 1921. *Geschlecht und Geschlechter.* Verl. Fischer, Jena, 557 pp.

Metschnikoff, I.I. 1869. Studien über die Entwicklung der Echinodermen und Nemertinen. *Mem. Acad. Imp. Sci. St. Petersburg,* XIV, 8, 1–73.

Mileikovsky, S.A. 1960. O svyazi mezhdu temperaturnymi granitsami neresta vida i ego zeogeograficheskoi prinadlezhnost'yu u morskikh bespozvonochnykh [On the relationship between the temperature limits of spawning of a species and its zoogeographic affinity in marine invertebrates]. *Zool. Zhurn.*, 39, 5, 666–669.

Mileikovsky, S.A. 1973. Speed of active movement of pelagic larvae of marine bottom invertebrates and their ability to regulate their vertical position. *Mar. Biol.*, 23, 1, 11–17.

Mileikovsky, S.A. 1977. Lichinki donnykh bespozvonochnykh [Larvae of benthic invertebrates]. In: *Biologiya Okeana.* Nauka, Moscow, vol. 1, 96–106.

Mileikovsky, S.A. 1981. Ekologiya razmnozheniya morskogo bentoss [Reproductive Ecology of Marine Benthos]. Nauka, Moscow, 91 pp.

Miller, R.H. and P.J. Hollis. 1963. Abbreviated pelagic life of Chilean and New Zealand oysters. *Nature,* 197, 4866, 512–513.

Miner, R.W. 1950. *Field Book of Seashore Life.* Putnam, New York, 888 pp.

Mitsukuri, K. 1903. Notes on the habits and life history of *Stichopus japonicus* Selenka. *Ann. Zool. Jap.,* vol. 5, 1–21.

Miyasaki, I. 1933. Effects of temperature and salinity on the development of the eggs of a marine bivalve *Mactra sulcataria* Reeve. *Bull. Jap. Soc. Sci. Fish.,* 2, 4, 162–166.

Miyasaki, I. 1935. On the development of some marine bivalves with special reference to the shelled larvae. *J. Jap. Imp. Fish. Inst.,* 31, 1, 1–10.

Mladenov, P.V. 1979. Unusual lecithotrophic development of the Carribean brittle star *Ophiothrix oerstedi. Mar. Biol.*, vol. 55, 55–62.

Mladenov, Ph. V. 1985. Development and metamorphosis of the brittle star *Ophiocoma pumila*: evolutionary and ecological implications. *Biol. Bull.,* 168, 2, 285–295.

Mokretsova, N.D. 1975. Biologicheskie osnovy i biotekhnicheskaya skhema kul'tivinovaniya trepanga (v usloviyakh zaliva Pos'et Yaponskogo morya) [Biological bases and biotechnological scheme of culturing trepang (in conditions of Posjet Bay, Sea of Japan)]. In: *Biologicheskie Resursy Morei Dal'nego Vostoka, Tez. Dokl. Vses. Soveshch.* Vladivostok, pp. 82–84.

Mokretsova, N.D. 1977. Stadii rannego ontogeneza trepanga *Stichopus japonicus* var. *armatus* Selenka (Aspidochirota, Stichopodidae) pri kul'tivirovanii v iskustvennykh usloviyakh [The early ontogenesis stages of trepang *Stichopus japonicus* var. *armatus* Selenka (Aspidochirota, Stichopodidae) during culturing under artificial conditions]. *Zool. Zhurn.*, 6, 1, 79–85.

Monne, L. and S. Harde. 1951. On the formation of the blastocoel and similar embryonic cavities. *Ark. Zool.*, vol. 1, 463–469.

Moore, H.B. 1936. The biology of *Echinocardium cordatum. J. Mar. Biol. Assoc. U.K.*, 20, 3, 655–672.

Moore, H.B. 1966. Ecology of echinoids. In: *Physiology of Echinodermata.* Wiley, New York, pp. 73–85.

Moore, M.M. 1933. Notes on the development of the sea urchin *Temnopleurus hardwicki, Sci. Rep. Tohoku Imp. Univ. Ser. Biol.*, 8, 3, 263–276.

Mortensen, Th. 1894. Zur Anatomie und Entwicklung der *Cucumaria glacialis* (Ljungman). *Ztschr. wiss. Zool.*, vol. 57, 704–732.

Mortensen, Th. 1898. Die Echinodermen Larven der Plankton Expedition. *Ergeb. Plankton Exp. Humboldtstiftung,* vol. 2, 1–120.

Mortensen, Th. 1903. Echinoidea. *Dan. Ingolf. Exped.*, 4, 1, 1–193.

Mortensen, Th. 1909. Die Echinoiden. *Dt. Südpol. Exped.*, 11, 1, 1–113.

Mortensen, Th. 1913. On the development of some British echinoderms. *J. Mar. Biol. Assoc. U.K.*, vol. 10, 1–18.

Mortensen, Th. 1920. On hermaphroditism in viviparous ophiuroids. *Acta Zool.*, vol. 1, 1–18.

Mortensen, Th. 1921. *Studies of the Development and Larval Forms of Echinoderms.* G.E.C. Gad, Copenhagen, 266 pp.

Mortensen, Th. 1925. *Coniocidaris umbraculum,* a brood-protecting species. *N. Z. Sci. Technol.*, vol. 8, 192.

Mortensen, Th. 1927. On the postlarval development of some cidarids. *Kgl. Danske Vid. Selakab. Skr. Nat. Math.* Afd., 8 raekke, vol. 11, 367–387.

Mortensen, Th. 1931. Contribution to the study of the development and larval forms of echinoderms. I–II. *Mem. Roy. Acad. Sci. Let. Denmark,* 9 ser., 4, 1, 1–39.

Mortensen, Th. 1933. Echinoderms of South Africa. *Vid. Medd. Dansk. Naturhist. Foren. Kobenhavn,* vol. 93, 215–400.

Mortensen, Th. 1936. Echinoidea and Ophiuroides. *Discovery Reports,* vol. 12, 201–348.

Mortensen, Th. 1937. Contributions to the study of the development and larval forms of echinoderms. III. *Mem. Roy. Acad. Sci. Let. Denmark,* 9 ser., 7, 1, 1–65.

Mortensen, Th. 1938. Contributions to the study of the development and larval forms of echinoderms. IV. *Mem. Roy. Acad. Sci. Let. Denmark,* 9 ser., 7, 3, 1–59.

Mortensen, Th. 1948. Report on the Echinoidea collected by the *Albatross.* Philippine Archipelago and adjacent regions, pt. 3. *Bull. U.S. Nat. Mus.,* vol. 14, no. 3.

Mortensen, Th. 1950. Echinoidea. *Rep. B.A.N.Z. Antarct. Res. Exped.,* ser. B, 4, 10, 297–310.

Morton, B. 1973. The biology and functional morphology of *Galeomma (Paralepida) takii* (Bivalvia, Leptonacea). *J. Zool. (London),* vol. 169, pp. 133–150.

Morton, B. 1974. Some aspects of the biology, population dynamics and functional morphology of *Musculista senhousia* Benson (Bivalvia, Mytilidae). *Pacif. Sci.,* 28, 1, 19–35.

Morton, B. 1976. Secondary brooding of temporary dwarf males in *Ephippodonta (Ephippodontina) oedipus* n. sp. (Bivalvia, Leptonacea). *J. Conchol. (London),* vol. 29, 31–39.

Morton, B. 1980. Some aspects of the biology and functional morphology (including the presence of a ligamental lithodesma) of *Montacutona compacta* and *M. olivacea* (Bivalvia: Leptonacea) associated with coelenterates in Hong Kong. *J. Zool. (London),* vol. 192, 431–455.

Morton, B. 1981. The biology and functional morphology of *Chlamydoconcha orcutti* with a discussion on taxanomic status of the Chlamydoconchacea (Mollusca, Bivalvia). *J. Zool. (London),* vol. 195, 81–121.

Motavkin, P.A. and G.P. Novikova. 1971. Morfologiya i sintez deitoplazmy u amurskoi zvezdy [Morphology and synthesis of deutoplasm in the Amur sea star]. In: *Biologicheskie i Meditsinskie Issledovaniya na Dal'nem Vostoke.* Vladivostok, pp. 138–141.

Nachtsheim, H. 1914. Ueber die Entwicklung von *Echinaster sepositus. Zool. Anz.,* vol. 44, 600–606.

Nakajima, Y. 1986. Presence of a ciliary patch in the preoral epithelium of sea urchin plutei. *Devel., Growth and Differ.,* 28, 3, 243–249.

Nakajima, Y. 1987. Serotonergic nerve cells in starfish larvae. *Abstr. 6th Internat. echinoderm Confer. Victoria.* Victoria Univ. Press, Victoria.

Narasimhamurti, N. 1933. Development of *Ophiocoma nigra. Quart. J. Microsc. Sci.,* vol. 76, 63–88.

Newell, G.E. and R.C. Newell. 1963. *Marine Plankton: A Practical Guide.* Hutchinson Educational, London, 207 pp.

Nezlin, L.P. and S.Sh. Dautov, 1987. Nervnaya sistema planktotrofnykh lichinok iglokozhikh [The nervous system of planktotrophic larvae of echinoderms]. In: *Probl. Filogenii i Sist. Iglokozhikh, Tez. Dokl. 6 Vses. Simp. po Iglokozhim. Tallin.* Izd. AN SSSR, pp. 72–73.

Novikova, G.P. 1978. Polovye tsikly morskikh zvezd *Asterias amurensis* i *Patiria pectinifera* Zaliva Petra Velikogo Yaponskogo morya [Reproductive cycles of sea stars *Asterias amurensis* and *Patiria pectinifera* from Peter the Great Bay, Sea of Japan]. *Biol. Morya,* no. 6, 33–40.

Ockelmann, K.W. 1958. The zoology of east Greenland. Marine Lamellibranchia. *Med. Grønland,* 122, 4, 1–256.

Ockelmann, K.W. 1962. Developmental types in marine bivalves and their distribution along the Atlantic coast of Europe. In: *Proc. Europ. Malac. Congr. London,* pp. 25–35.

Odhner, N.H. 1914. Notizen über die Fauna der Adria bei Rovigno Beiträge zur Kenntnis der marinen Molluskenfauna von Rovigno in Istrien. *Zool. Anz.*, 44, 4, 156–170.

O'Foighil, D. 1985. Sperm transfer and storage in the brooding bivalve *Mysella tumida. Biol. Bull.,* 69, 3, 602–614.

Oguro, Ch., M. Komatsu and Y. Kano, 1976. Development and metamorphosis of the sea star, *Astropecten scoparius* Valenciennes. *Biol. Bull.,* 151, 3, 560–573.

Ohshima, H. 1921, On the development of *Curcumaria echinata. Quart. J. Microsc. Sci.,* vol. 65, 173–246.

Ohshima, H. 1925. Notes on the development of the sea cucumber. *Thyone briareus. Science,* vol. 61, 420–422.

Okada, K. 1936. Some notes on *Sphaerium japonicum biwaense* Mori, a freshwater bivalve. IV. Gastrula and fetal larva. *Sci. Rep. Tohoku Imp. Univ., Ser. Biol.* vol. 11, 49–68.

Okazaki, K. 1960. Skeleton formation of sea urchin larvae. II. Organic matrix of the spiculae. *Embryologia,* 5, 7, 283–320.

Okazaki, K. 1963. Skeleton formation of sea urchin larvae. *Embryologie,* 7, 1, 21–38.

Okazaki, K. 1975. Normal development to metamorphosis. In: *The Sea Urchin Embryo. Biochemistry and Morphogenesis* (ed. G. Czihak). Springer-Verlag, Berlin-New York, pp. 177–232.

Okazaki, K. and K. Dan. 1954. The metamorphosis of partial larvae of *Peronella japonica* Mortensen, a sand dollar. *Biol. Bull.,* vol. 106, 83–99.

Oldfield, E. 1955. Observations on the anatomy and mode of life of *Lasaea rubra* (Montagu) and *Turtonia minuta* (Fabricius) *Proc. Malacol. Soc. London,* vol. 31, 226–249.

Oldfield, E. 1964. The reproduction and development of some members of the Erycinidae and Montacutidae (Mollusca, Eulamellibranchiata). *Proc. Malacol. Soc. London,* vol. 36, 79–120.

Olsen, H. 1942. Development of *Ophiopholis aculeata. Bergens Mus. Aarbok. Naturviol. Rekke,* no. 6, 5–107.

Onoda, K. 1931, Development of *Heliocidaris crassispina. Mem. Coll. Sci. Kyoto Imp. Univ.,* vol. 7, 103–134.

Onoda, K. 1936. Development of some Japanese echinoids. *Jap. J. Zool.,* vol. 6, 637–654.

Onoda, K. 1938. Notes on the development of some Japanese echinoids with special reference to the structure of the larval body. *Jap. J. Zool.,* vol. 8, 1–13.

Pain, S. L., P.A. Tyler and J.D. Gage, 1982. The reproductive biology of the deep-sea asteroids *Benthopecten simplex* (Torrier), *Pectinaster filholi* and *Pontaster tenuispinus* Düben a Koren (Phanerozonia: Benthopectinidae) from the Rockall Trough. *J. Mar. Biol., Ecol.,* 65, 2, 195–271.

Patent, D.H. 1970a. The early embryology of the basket star, *Gorgonocephalus caryi* (Echinodermata, Ophiuroidea). *Mar. Biol.,* 6, 3, 262–267.

Patent, D.H. 1970b. Life history of the basket star, *Gorgonocephalus eucnenis* (Müller and Troschel) (Echinodermata, Ophiuroidea). *Ophelia,* vol. 8, 145–159.

Pelseneer, P. 1906. Mollusca. In: *A Treatise on Zoology* (ed. E. Ray Lankaster). Adam and Charles Black, London, 355 pp.

Pelseneer, P. 1911. Les lamellibranches de l'expedition du Siboga. *Siboga Expéd.* I. 61, *Monogr.* 53a, 1–125.

Pelseneer, P. 1926. Notes d'embryologie malacologique: Ponte de *Cyprea europea, Triforis perversa* et *Lucina lactea. Bull. Biol. France Belg.,* vol. 60, 88–112.

Pelseneer, P. 1935. Essai d'ethologie zoologique d'aprés l'étude des mollusques. *Acad. Roy. Belg.,* no. 1, 416–596.

Pérès, J.M. 1937. Sur trois espéces du genre *Montacuta. J. Tra. Sta. Biol. Roscoff,* vol. 15, 5–28.

Piatigorsky, I. 1975. Gametogenesis. In: *The Sea Urchin Embryo* (ed. G. Czihak). Springer-Verlag, Berlin-New York.

Poggiani, L. 1968. Note sulle larva planctoniche di alcuni Malluschi dell Adriatico medio-occidentale e sviluppo postlarvale di alcuni di essi. *Not. Lab. Biol. Mar. Pesca. Fano,* 2, 8, 137–180.

Quayle, D.B. 1961/1953. The larva of *Bankia setacea* Tryon. *Rep. Brit. Columbia Dep. Fish.,* pp. 92–104.

Quayle, D.B. 1955. The British Columbia shipworm. *Rep. Brit. Columbia Dep. Fish.,* pp. k92–k104.

Quayle, D.B. 1959. The early development of *Bankia setacea* Tryon. In: *Proc. Friday Harbor Symp. Marine Boring and Fouling Organisms,* pp. 157–177.

Raff, R.A. 1987. Constraint, flexibility and phylogenetic history in the evolution of direct development in the sea urchin. *Devel. Biol.,* 119, 1, 6–19.

Rakov, V.A. 1974. Morfologiya lichinki tikhookeanskoi ustritsy *(Crassostrea gigas* Thunberg) [Morphology of the giant Pacific oyster *(Crassostrea gigas* Thunberg)]. In: *Issled. po Biol. Ryb i Promyslovoi Okeanografii.* Vladivostok, no. 5, 15–18.

Rakov, V.A. 1975. Dinamika chilennosti i raspredelenie lichinok tikhokeanskoi ustritsy v zalive Pos'eta [Dynamics of population and distribution of Pacific oyster in Posjet Bay]. In: *Materialy po Biologii Ryb i Promyslovoi Okeanografii.* Vladivostok, no. 6.

Ramorino, L. and B. Campos. 1979. Desarrollo larval y postlarval de *Perumytilus purpuratis* (Lamarck, 1819): Bivalvia: Mytilidae. *Ann. Mus. Hist. Natur. Valparaiso,* vol. 12, 207–218.

Raes, C.B. 1950. The identification and classification of lamellibranch larvae. *Hull. Bull. Mar. Ecol.,* no. 3 (19), 73–104.

Riisgard, H.U., A. Randlov and P.S. Kristensen. 1980. Rates of water processing, oxygen consumption and efficiency of particle retention in veligers and young postmetamorphic *Mytilus edulis. Ophelia,* 19, 1, 37–47.

Rowley, R.J. 1987. Settlement and recruitment of the purple urchin *Strongylocentrotus purpuratus* in a kelp bed and urchin barrens. *Abstr. 6th Internat. Echinoderm Confer. Victoria.* Victoria Univ. Press, Victoria.

Runnström, S. 1927/1928. Entwicklung von *Leptosynapta inhaereus. Bergons Mus. Aarbok.,* no. 1, 1–80.

Runnström, J. and S. Runnström. 1918/1919. Ueber die Entwicklung von *Cucumaria fronodosa* und *Psolus phantapus. Bergens Mus. Aserbok.,* no. 5, 1–99.

Ruppert, E.E. and E.J. Balser. 1986. Nephridia in the larvae of hemichordates and echinoderms. *Biol. Bull.,* 171, 1, 188–196.

Russo, A. 1891. Embryologia dell *Amphiura Aquamata. Atti. Acad. Fis. Nat. Napoli,* 2, 5, 1–24.

Ryabchikov, P.I. 1957. Rasprostranenie drevotochtsev v moryakh SSSR [Distribution of wood-borers in the seas of the USSR]. Nauka, Moscow, pp. 3–229.

Ryberg, E. 1973. The localization of cholinesterases and non-specific esterases in the echinopluteus. *Zool. Scr.,* vol. 2, 162–170.

Ryberg, E. 1977. The nervous system of the early echinopluteus. *Cell and Tissue Res.,* vol. 179, 157–167.

Ryberg, E. and B. Lundgren. 1977. Extra-ectodermal strands in the ciliated bands of the echinopluteus. *Develop., Growth and Differ.,* 19, 4, 299–308.

Ryberg, E. and B. Lundgren. 1979. Some aspects on pigment cell distribution and function in the developing echinopluteus of *Psammechinus miliaris*. *Develop., Growth and Differ.*, 21, 2, 129–140.

Sachs, M.I. 1971. A cytological analysis of artificial parthenogenesis in the surf clam *Spisula solidissima*. *J. Ultrastruct. Res.*, 36, 5/6 806–823.

Salvini-Plawen, L. 1972. Zur Morphologie und Phylogenie der Mollusken. Die Beziehungen der Candofeveata unds der Solenogastres als Aculifera, als Mollusca und als Spiralia (nebst einem Beitrag Zur Phylogenie der coelomatischen Räume). *Ztschr. viss. Zool.*, vol. 184, 205–394.

Salvini-Plawen, L. 1973. Zur Kläring des "Trochophora" Begriffes. *Experientia*, vol. 20, 1434–1435.

Sastry, A.N. 1979. Pelecypoda (excluding Ostreidae). In: *Reproduction of Marine Invertebrates* (eds. A.C. Giese and J.S. Pearse). Acad. Press, New York, vol. 5, 113–292.

Schechter, V. 1941. Experimental studies upon the egg cells of the clam, *Mactra solidissima*, with special reference to longevity. *J. Exp. Zool.*, 86, 3, 461–479.

Schmekel, L. 1975. Egg and embryo ultrastructure. In: The *Sea Urchin Embryo* (ed. G. Czihak). Springer-Verlag, Berlin – New York, p. 8.

Schweinitz, E. and R.A. Lutz. 1976. Larval development of the northern horse mussel, *Modiolus mediolus* (L.), including a comparison with the larvae of *Mytilus edulis* L. as an aid in planktonic identification. *Biol. Bull.*, 150, 3, 348–360.

Selenka, E. 1880. Keimblätter und Organanlagen der Echiniden *Ztschr. wiss. Zool.*, vol. 33, 39–54.

Selenka, E. 1883. *Studien über Entwicklungsgeschichte der Thiere.* 2. *Die Keimblätter der Echinodermen.* Wiesbaden, pp. 28–61.

Sellmer, G.P. 1967. Functional morphology and ecological life history of the gem clam, *Gemma gemma* (Eulamellibranchia, Veneridae). *Malacologia*, 5, 2, 137–223.

Semon, R. 1888. Die Entwicklung der *Synapta digitata* und die Stammengeschichte der Echinodermen. *Jen. Ztschr. Naturwissen*, vol. 22, 175–309.

Sentz-Braconnot, E. 1968. Relation entre le larves planctoniques et les jeunes stades fixés chez les Lamellibranches dans la rads de Ville-franche-sur-mer (Aples-maritimes). *Vie et Milieu*, 19, 1-B, 85–108.

Shepel', N.A. 1979. Ekologiya midii *M. edulis* v svyazi s ee kul'tivirovaniem v zalive Pos'eta (Yaponskoe more) [Ecology of *M. edulis* in connection with its culturing in Posjet Bay (Sea of Japan)]. In: *Promyslovye Dvustovorchatye Mollyuski Midii i ikh Rol'v Ekosistemakh.* Izd-vo Zool. In-ta AN SSSR. Leningrad, pp. 126–127.

Skarlato, O.A. 1981. Dvustvorchatye mollyuski umerennykh shiret zapadnoi chasti Tikhogo Okeana (Bivalves of the Temperate Latitudes of the Western Pacific Ocean). Nauka, Leningrad, 480 pp.

Skarlato, O.A. and Ya. I. Starobogatov. 1979. Osnovnye cherty evolyutsii i sistema klassa Bivalvia [Main features of evolution and systematics of the class Bivalvia]. *Tr. Zool. In-ta,* vol. 80, 5–38.

Smiley, S. 1986. Metamorphosis of *Stichopus californicus* (Echinodermata; Holothurioidea) and its phylogenetic implications. *Biol. Bull.,* 171, 3, 611–631.

Stancyk, S.E. 1973. Development of *Ophiolepis elegans* (Echinodermata; Ophiuroidea) and its implications in the estuarine environment. *Mar. Biol.,* vol. 27, 7–12.

Starobogatov, Ya.I. 1979. Evolyutsiya pelegicheskikh lichinok pervichnorotykh zhivotnykh i problema osnovnykh komponentov tels [Evolution of pelagic larvae of protostomians and the problem of the main body parts.] *Zool. Zhurn.,* 58, 2, 149–160.

Strathmann, R.R. 1971. The feeding behaviour of planktotrophic echinoderm larvae. Mechanisms, regulations and rates of suspension feeeding. *J. Exp. Mar. Biol. and Ecol.,* no. 6, 109–160.

Strathmann, R.R. 1974. Introduction to function and adaptation in echinoderm larvae. *Thalassia Jugosil,* 10, 1/2. 321–339.

Strathmann, R.R. 1975. Larval feeding in echinoderms. *Amer. Zool.,* vol. 15, 717–730.

Strathmann, R.R. 1978a. Larval settlement in echinoderms. In: *Settlement and Metamorphosis of Marine Invertebrate Larvae.* Elsevier, New York, pp. 235–246.

Strathmann, R.R. 1978b. Length of pelagic period in echinoderms with feeding larvae from the Northeast Pacific. *J. Exp. Mar. Biol. Ecol.,* vol. 34, 23–27.

Strathmann, R.R. 1978c. The evolution and loss of feeding larval stages of marine invertebrates. *Evolution,* 32, 4, 894–906.

Strathmann, R.R. and E. Leise. 1979. On feeding mechanisms and clearance rates of molluscan veligers. *Biol. Bull.,* vol. 157, 524–535.

Strathmann, R.R., T.L. Jahn and J.R.C. Fonseca. 1972. Suspension feeding by marine invertebrate larvae: clearance of particles by ciliated bands of a rotifer, pluteus and trochophore. *Biol. Bull.,* vol. 142, 505–519.

Sullivan, C.M. 1948. Bivalve larvae of Malpeque Bay, Prince Edward Island. *Bull. Fish. Res. Board Can.,* vol. 77, 1–36.

Tabunkov, V.D. 1971. Biologiya *Spisula sachalinensis* (Schrenck) v bukhte Lososei (zal. Aniva) [Biology of *Spisula sachalinensis* (Schrenck) in Lossosei Inlet (Aniva Bay)]. In: *Mollyuski: Puti, Metody i Itogi ikh Izucheniya.* Nauka, Leningrad, pp. 57–58.

Tanaka, G. 1958. Seasonal changes occurring in the gonad of *Stichopus japonicus. Bull. Fac. Fish. Hokkaido Univ.,* 9, 1, 29–36.

Tattersall, W.M. and E.M. Sheppard. 1934. Observations on the bipinnaria of the asteroid genus *Luidia.* In: *J. Johnstone Memorial Volume.* Univ. Press, Liverpool, pp. 35–61.

Thomson, C.W. 1878. Notice of some peculiarities in the mode of propagation of certain echinoderms of the Southern Sea. *J. Linn. Soc. Zool.,* vol. 13, 55–79.

Thorson, G. 1936. The larval development, growth and metabolism of Arctic marine bottom invertebrates. *Medd. Grønland,* vol. 100, 1–155.

Thorson, G. 1946. Reproduction and larval development of Danish marine bottom invertebrates, with special reference to the planktonic larvae in the Sound (Oresund). *Medd. Komm. Danm. Fish Havunders, Ser. Plancton,* 4, 1, 1–529.

Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. *Biol. Rev.,* vol. 25, 1–45.

Turner, H.J. and C.J. George. 1955. Some aspects of the behaviour of the quahog, *Venus mercenaria,* during the early stages. *Mass. Dep. Nat. Resour. Div. Mar. Fish. Invest. Shellfish Rep.,* no. 8, 5–14.

Turner, R.D. 1966. *Survey and Illustrated Catalogue of the Teredinidae. Mus. Comp. Zool.* Cambridge, Harvard Univ., 265 pp.

Turner, R.D. 1971. Australian shipworms. *Austral. Natur. Hist.,* 17, 4, 139–145.

Turner, R.D. 1975. Bivalve larvae: their behaviour, dispersal and identification. In: *Ecology of Fouling Communities,* pp. 23–26.

Turner R.D. 1976a. Fixation and preservation of molluscan zooplankton. In: *Zooplankton Fixation and Preservation.* UNESCO, Paris, pp. 290–304.

Turner, R.D. 1976b. Some factors involved in the settlement and metamorphosis of marine bivalve larvae. In: *Proc. III. Intern. Biodegradation Symp.,* pp. 409–416.

Turner, R.D. and A.C. Johnson. 1971. Biology of marine boring molluscs. In *Marine Borers, Fungi and Fouling Organisms of Wood.* UNESCO, Paris, pp. 259–301.

Turner, R.D. and P.J. Boyle. 1974. Studies of bivalve larvae using the scanning electron microscope and critical point drying. *Bull. Amer. Malacol. Union.* pp. 59–65.

Turner, R.D. and J.H. Deerborn. 1979. Organic and inorganic composition of postmetamorphic stages of *Ophionotus hexactis* (E.A. Smith) (Echinodermata: Ophiuroidea) during intraovarian incubation. *J. Exp. Mar. Biol. and Ecol.,* 36, 1, 41–51.

Turner, R.D. and Yu. M. Yakovlev. 1981. Zhiznennyi tsikl *Zachsia zankewitchi* teredenidy a karlikovymi samtsami [Life cycle of teredenid *Zachsia*

zenkewitchi with dwarf males]. In: *Genetika i Razmnozhenie Morskikh Zhivotnykh.* Izd-vo DVNTs AN SSSR, Vladivostok, pp. 215–219.

Turner, R.D. and Yu. M. Yakovlev. 1983. Dwarf males in the Teredinidae (Bivalvia, Pholadacea). *Science,* vol. 219, 1077–1078.

Tyler, P.A. 1980. Deep-sea ophiuroids. *Oceanogr. Mar. Biol. Ann. Rev.,* vol. 18, 125–153.

Ubisch, L. 1913. Die Anlage und Ausbildung des Skeletsystem einiger Echiniden und die Symmetrieverhältnisse von Larven und Imago. *Ztschr. Wiss. Zool.,* vol. 104, 119–156.

Ukeles, R. 1969. Nutritional requirements in shellfish culture. In: *Proc. Confer. Artificial Propagation Commerc. Valuable Shellfishes.* Univ. Delaware, Newark.

Ukeles, R. 1975. Views on bivalve larvae nutrition. In: *Proc. First Intern. Conf. on Aquacult. Nutrition,* pp. 127–162.

Vasetskii, S.G. 1973. Dinamika delenii sozrevaniya v yaitsakh gigantskoi ustritsky *Ostrea gigas* [Dynamics of maturation division in eggs of the giant oyster *Ostrea gigas]. Ontogenez,* 4, 5, 453–460.

Voeltzkow, A. 1891. *Entovalva mirabilis,* eine schmarotzende Muschel aus den Arm einer Holothurie. *Zool. Jb. Abt. System. Ökol.,* vol. 5, 619–628.

Vorob'ev V.P. 1938. Midii Chernogo morya [Mussels of the Black Sea]. *Tr. Az CherNIRO,* 2, 11, 27–41.

Vyshkvartsev, D.I. and Yu. I. Sorokin. 1978. Ob intensivnosti pitaniya nekotorykh morskikh bespozvonochnykh restvorennym organicheskim veshchestvom [On the intensity of feeding on soluble organic matter by some marine invertebrates]. In: *Biol. Issl. Dal'nevost. Morei.* Izd. DVNTs AN SSSR, Vladivostok, pp. 27–31.

Wada, S.K. 1953. Larviparous oysters from the tropical west Pacific. *Rec. Oceanogr. Works Jap. N.S.,* vol. 1, 66–72.

Waller, Th. R. 1981. Functional morphology and development of veliger larvae of the European oyster, *Ostrea edulis* Linné. *Smithsonian Contribs. Zool.,* no. 328, 1–70.

Walne, P.R. 1965. Observation on the influence of food supply and temperature on the feeding and growth of the larvae *Ostrea edulis* L. *Fish. Invest. Min. Agr. Fish. Food London,* ser. II, vol. 24, 1–45.

Wear, R.G. 1966. Physiological and ecological studies on the bivalve mollusc, *Arthritica bifurca,* living commensally with the tubicolous polychaete *Pectinaria australia. Biol. Bull.,* vol. 130, 141–149.

Werner, B. 1939. Über die Entwicklung und Artunterscheidung von Muschellarvan des Nordseeplanktons unter besonderer Berücksichtigung der Schalenentwicklung. *Zool. Jb.,* 66, 1, 1–54.

Werner, B. 1959. Das Prinzip des endlosen Schleimfilters beim Nahrungserwerb wirbelloser Meerestiers. *Intern. Rev. Hydrobiol.,* vol. 44, 181–215.

Wilbur, K. 1964. Shell formation and regeneration. In: *Physiology of the Mollusca.* Acad. Press, New York, vol. 1, 243–282.

Wilson, D. 1978. Some observations on bipinnariae and juveniles of the starfish genus *Luidia. J. Mar. Biol. Assoc. U.K.,* vol. 58, 467–478.

Wood, L. and W.Y. Hargis. 1971. Transport of bivalve larvae in a tidal estuary. In: *Fourth Europ. Mar. Biol. Symp.* Cambridge Univ. Press, London, pp. 29–44.

Yakovlev, Yu. M. 1988. Morfologiya i zhiznennyi tsikl dvustvorchatogo mollyuska *Zachsia zenkewitschi* (Cardiida: Teredinidae) [Morphology and life cycle of the bivalve *Zachsia zenkewitschi* (Cardiida: Teredinidae)]. Avtoref. Diss. Kand. Biol. Nauk. In-t Biologii Morya, Vladivostok, 24 pp.

Yakovlev, Yu. M. and V.V. Malakhov. 1985. The anatomy of dwarf males of *Zachsia zenkewitschi. Asian Marine Biol.,* vol. 2, 47–55.

Yamamoto, G. 1951. Ecological study of the spawning of the scallop *Pecten (Patinopecten) yessoensis* in Muysu Bay. *Bull. Jap. Soc. Sci. Fish.,* 17, 2, 53–56.

Yamamoto, G. 1964. Studies on the propagation of the scallop *Patinopecten yessoensis* (Jay) in Muysu Bay. *Nihon Suisanhigen Hogokyokai, Suisan Zoshoku Sosho,* no. 6, 1–77.

Yamashita, M. 1985. Embryonic development of the brittle star, *Amphipholis kochii,* in laboratory culture. *Biol. Bull.,* vol. 169, 131–142.

Yonge, C.M. 1926. Structure and physiology of the organs of feeding and digestion in *Ostrea edulis. J. Mar. Biol. Assoc. U.K.,* 14, 2, 295–386.

Yonge, C.M. 1969. Functional morphology and evolution within the Carditacea (Bivalvia). *Proc. Malacol. Soc. London,* vol. 38, 493–527.

Yoshida, H. 1935. On the full-grown veligers and early young shell-stages of *Venerupis philippinarum* (Adams at Reeve). *Venus,* 5, 5, 264–273.

Yoshida, H. 1938. Notes on the veligers and the young shells of *Mya arenaria japonica. Venus,* 8, 1, 13–21.

Yoshida, H. 1953. Studies on larvae and young shells of industrial bivalves in Japan. *J. Shimonoseki coll. Fish.,* 3, 1, 1–106.

Young, C.M. and J.L. Cameron. 1987. Larval forms and developmental rates of some bathyal echinoderms. *Abstr. 6th Internat. Echinoderm Confer. Victoria.* Victoria Univ. Press, Victoria.

Zakhvatkina, K.A. 1959. Lichinki dvustvorchatykh mollyuskov Sevastopol'skogo raiono Chernogo morya [Larvae of bivalve mollusks of the Sevastopol' region of the Black Sea]. *Tr. Sevast. Biol. St.,* no. 11, 108–152.

Zeuthen, E. 1947. Body size and metabolic rate in the animal kingdom, with special regard to the marine microfauna. *C. R. Trav. Lab. Carlsberg, Ser. Chim.,* vol. 26, 17–161.