A COMPARATIVE STUDY OF POST-LARVAL FEEDING MECHANISMS IN THE BIVALVIA

JOAN E. MORTIMER

Submitted in fulfilment of the requirements
for the degree of
Doctor of Philosophy

Department of Zoology
The University, Glasgow, Scotland
1962

ProQuest LLC.
789 East Eisenhower Parkway
P.O. Box 1346
Ann Arbor, MI 48106 – 1346

TABLE OF CONTENTS

Page

Page

LIST OF FIGURES

Following page

PART I: SUB-CLASS PROTOBRANCHIA

---

* Photographs of shell valves.

PART II: SUB-CLASS LAMELLIBRANCHIA

Note: Post-larvae are arbitrarily designated as 'early', 'mid' or 'late' according to size: 'early' are up to 500 μ in length, 'mid' from 500 to 900 μ in length and 'late' are longer than 900 μ.

---

* Photographs of living specimens.

Following Page

Following Page

ABSTRACT

Post-larval development in the two sub-classes of the Bivalvia, the Protobranchia and the Lamellibranchia, differs so markedly that it was necessary to deal with each separately. A description is given of post-larvae of three species of Nucula, belonging to the protobranch Family Nuculidae, ranging in length from 160 μ, with test newly shed, to 650 μ, with both ctenidia and palps well developed. This post-larval phase persists at least a year and contrasts with the short larval phase of 60 hours recorded by Drew (1899 b and 1901) for Nucula proxima. The post-larval feeding mechanisms are of particular interest since they differ radically from that of the adult.

Feeding activities begin in post-larvae approximately 170 μ long and are executed by the foot which, extended beyond the shell, waves to and fro, the cilia encircling its sole wafting particles into the mantle cavity and onto the pedal walls. A curious feature, located on the inner mantle surface, is an arc of cilia whose beat may help to draw in particles and certainly throws them onto the proximal wall of the foot where adoral ciliary tracts carry them to the mouth. In post-larvae exceeding 200 μ the activity of the pallial ciliated arc wanes as the ctenidia and palps develop.

With two filaments in each inner demibranch the ciliary feeding mechanism begins to resemble that of lamellibranchs. Particles enter the mantle cavity in the respiratory water current produced by the ctenidia, collect on its surface, and proceed to the filament tips and along the underlying adoral pedal tract. Below this

adoral tract the foot develops an antagonistic ciliary tract carrying rejected particles out of the mantle cavity. The palp lamellae of post-larvae 500 μ long establish a functional contact with the first filament of the inner demibranch and particles travel directly from one to the other. This type of feeding continues until the post-larva is 650 μ long when the palp proboscides probably become functional. The posible phylogentic significance of the post-larval feeding mechanisms is discussed.

Amongst the Lamellibranchia post-larvae belonging to five familes of the Anisomyaria and twelve families of the Eulamellibranchia were examined. In each of the anisomyarian families (Anomiidae, Pectinidae, Limidae, Ostreidae and Mytilidae) the post-larval feeding mechanism is distinctive and in the first four families tends to show a certain complexity. In these four families the monomyarian condition has considerable effect on ctenidial development and hence on the post-larval feeding mechanism. While in the Anomiidae and Pectinidae these effects appear somewhat disadvantageous, in the Limidae and Ostreidae they are modified by progressive changes in the pattern of ctenidial development. Consideration of the differences in rate and sequence of development reveals a common pattern of development in the four families. One characteristic of this developmental pattern is the disposition and period of activity of certain localized growth zones, the 'embryonic zones', which provide for the elongation and reflection of the filaments.

In the Mytilidae the post-larval feeding mechanism exhibits a simplicity not found in other Anisomyaria. The basic

pattern of ctenidial development is also distinctive particularily in regard to the locations and times of activity of the embryonic zones.

In contrast to the Anisomyaria little variety was encountered amongst the twelve eulamellibranch families. The post-larval feeding mechanism closely resembled that of the Mytilidae but the basic pattern of ctenidial development was distinct from that of the latter. Siphon development was examined in the Eulamellibranchia and found to embody two principles: growth from a localized proximal zone and progressive fusion of the mantle folds. The method of siphon extension and withdrawal is described.

ACKNOWLEDGMENTS

This investigation was made possible through a grant from the Ontario Research Foundation for which the author expresses her appreciation.

The research was carried out in the Department of Zoology of the University of Glasgow and at the Marine Station of the Scottish Marine Biological Association at Millport. Grateful acknowledgment is extended to Mr. E. Ford, Past Director of the Marine Station, and also to the staff of the Marine Station and of the Department of Zoology of the University for facilities and assistance. The author is also indebted to the staff of the Fisheries Experiment Station of the Ministry of Fisheries, Agriculture and Food at Conway, Wales for preserved specimens of Ostrea edulis spat and for facilities provided during a short visit there in 1955.

Examination of the spat of Crassostrea virginica was made possible through the co-operation of the staff of the Biological Station of the Fisheries Research Board of Canada at Ellerslie, Prince Edward Island. Facilities for completion of the thesis were furnished by the Department of Zoology of the University of Western Ontario.

Grateful acknowledgment is expressed to Dr. G.L. Wilkins (British Museum of Natural History) for assistance in identification of certain species, to Dr. R.H. Millar (Marine Station, Millport) for advice on culture methods for rearing lamellibranch

larvae, to Dr. H. F. Steedman (Zoology Department, Glasgow University) for assistance in microtechnique, and also to Dr. D. B. Quayle (Fisheries Research Board of Canada, Naniamo, British Columbia) for aid in the identification of the Anomiidae.

The author is most appreciative of the generosity of all those who agreed to correct this manuscript at various stages in its preparation: Dr. G. W. Bartlett (Biology Department, Memorial University of Newfoundland), Mr. H. Squires and Dr. J. C. Medcof (Fisheries Research Board of Canada at St. John's, Newfoundland and St. Andrews, New Brunswick respectively). Special thanks are extended to Dr. Helen I. Battle (Zoology Department, University of Western Ontario) who gave so unstintingly of her time and advice to further the preparation of this manuscript. The author is particularly indebted to Dr. G. Owen (Zoology Department, Glasgow University) for his many helpful suggestions and constructive criticisms at all stages of this work.

It is a privilege to express my deepest gratitude to Professor C. M. Yonge, C.B.E., F.R.S., for the suggestion of this problem, and for his continued encouragement and guidance throughout this investigation.

PART I

SUB-CLASS PROTOBRANCHIA

INTRODUCTION

The Nuculidae are the most primitive living bivalves; and a nuculoid type has long been considered to be the ancestor from which the Bivalvia arose (Pelseneer, 1888, 1911; Stempell, 1898a, 1898b; and Odhner, 1912). In an attempt to elucidate the evolutionary process which produced this very successful molluscan class, much interest has centred around the study of protobranch morphology and biology (Heath, 1937; Hirasaka, 1927; and Yonge, 1939).

Although the first description of a protobranch larva was given in 1898 by Bernard when he figured the larva of Nucula nucleus (Linne), Drew (1899a, 1899b, and 1901) provided the first full descriptive account of development in the protobranchiate molluscs. His studies were conducted mainly on Yoldia limatula Say and Nucula delphinodonta (Mighels) but included brief comparisons of the young stages of both species with those of Nucula proxima Say. Despite the interest stimulated in this fascinating group of bivalves by the work of Drew and others (Stempell, 1898a, 1898b, 1899; and Morse, 1913, 1919), there were no further studies of the developmental stages until 1938 when Lebour reported fertilizations of Nucula turquida Leckenby and Marshall and Nucula nucleus, and was able to rear embryos to free-swimming larvae of the type described by Drew. Sullivan (1948) showed a photomicrograph of a post-larval shell of Yoldia limatula but she did not encounter the larvae. Jørgensen (1946) and Rees (1952) described

the bivalve larvae found in the plankton tows taken in the Sound between the Baltic and Kattegat, and in the North Sea respectively; neither encountered any protobranch larvae or post-larvae in their collections. The only other information to be gleaned from the literature consists of data on the egg size and breeding seasons of various protobranchs reported by Thorson (1936) and Allen (1953, 1954).

Drew's work (1899a, 1899b, 1901) remains today as the only detailed descriptive account of the embryology and post-larval development of the protobranchs; since it provides the background for the present investigation, a brief summary of his findings will help to clarify the observations to be described below.

The three species which Drew described belong to two different families of the Protobranchia, namely: Nucula delphinodonta and N. proxima of the Nuculidae, and Yoldia limatula of the Nuculanidae. The early stages of development in N. delphinodonta take place while the larva is retained in the parental brood-sac whereas development in the other two species is free. Nevertheless, the process is remarkably similar in all three species. The fertilized egg develops into a 'barrel-shaped' larva consisting of a tiny embryo enclosed in an envelope of ciliated cells. These cells constitute the test --- a structure homologous to the velum of other lamellibranchs. At the close of a short planktonic life the larva sheds its test and drops to the bottom. At metamorphosis the organization of the larva is very simple; it comprises a short digestive tract, an anterior adductor muscle, a ventral mass of cells destined to become the foot, and the mantle/shell. After casting the test, the foot slowly assumes the shape and structure of the adult foot by the formation of a 'heel' posteriorly, thus

leaving an anterior portion or 'sole' which later becomes bilobed. Ventrally the whole foot acquires cilia which are long and active. The gill anlagen do not appear immediately following metamorphosis and their subsequent development is slow. The anlagen first appear as posterior thickenings of the mantle on each side; they grow to form blunt ciliated projections and eventually each divides into two filaments, the ventral of which continues to form new filaments. Soon after the formation of the fourth pair of inner filaments, the outer filaments develop opposite them. When the second inner filament is present the palps begin to form as ciliated areas on the walls of the foot and body, lateral to the mouth. The lamellae of the upper, then of the lower, palp form at about the same time as the fourth and fifth gill filaments respectively. Their growth is slow and only when the sixth inner filament has formed do the palp appendages commence to develop; by the time nine or ten inner filaments are present the proboscides have attained their characteristic form.

Drew's remarks concerning the living post-larvae are mainly confined to the foot which develops slowly in Nucula, in contrast to Yoldia where burrowing begins almost immediately after casting. He postulated that the prolonged inactivity of N. delphinodonta following metamorphosis was attributable to an altered development resultant upon having been reared in a protected brood-sac; but N. proxima was found to be equally sluggish. He also suggested that since the digestive diverticula are ruptured by the sudden closure of the shell valves following casting, feeding is interrupted for a few days.

Drew emphasized the slow rate of development noting that the late larval stages of N. delphinodonta removed from

the brood-sac had reached only the second gill filament stage in a month. Admittedly, growth may not be optimum under laboratory conditions, but even making allowance for this, it would be several months before the palp proboscides were sufficiently well formed to permit the post-larva to feed in the manner of the adult. At the same time, it is inconceivable that the post-larvae fast for several months and yet grow from a length of approximately 200μ to 400μ --- an eight-fold increase in volume. The question then arises, "How does the young post-larva feed during the several months following metamorphosis and prior to the formation of functional palp proboscides?".

Despite the primitive ancestral characteristics attributed to the protobranchs the implications of Drew's work on their position in the phylogenetic tree of bivalves have been largely overlooked. Moreover, recent work on the stomach and digestive diverticula of the Nuculidae (Owen, 1956) has suggested that these organs also show indications of specialization. It was therefore considered that further developmental studies might add more information to clarify this position.

The examination of living specimens ranging from the newly metamorphosed post-larvae to the stage at which the palp proboscides could begin to function has demonstrated that there is a feeding mechanism in these young stages.

MATERIALS AND METHODS

Collection of Living Material

Protobranch larvae were never present in plankton tows; although infrequently one or two newly metamorphosed Nucula, in which the test had been recently shed, appeared in the surface tows, they were more abundant in the deep tows taken regularly off Garroch Head (Fig. 1, Station 1). Subsequently, deep tows were made over areas where Nucula was known to occur (Station 2 in the Cumbrae-Bute Deep off Kilchattan Bay, and in Loch Fyne at Station 4 off Skat Mhor, Station 5 in the Tarbert Deep, and Station 6 south of the Otter Spit and Loch Gilp); these yielded up to 50 post-larvae in a 20-minute tow.

Despite the occurrence of such large numbers of post-larvae in these tows, it was obvious that they were not planktonic stages but bottom-living forms. There was the possibility that some individuals might have shed their tests between the time of capture and examination; but since older stages became more abundant in later months, the presence of the post-larvae could not be accounted for in this way. When young stages of Nucula were kept in the laboratory the reason for their presence in the tows soon became apparent. The post-larvae have a remarkably low specific gravity --- being only slightly greater than that of sea water --- and the least disturbance of the water in the breffit was sufficient to swirl them off the bottom. Similarly any currant passing over the bottom on which they had settled would lift them from the surface of the mud.

FIGURE 1

Map of the Clyde sea area showing distribution of *Nucula sulcata* (S), *N. tenuis* (Te), *N. turgida* (Tu), and *N. nucleus* (N) in relation to the stations (1 to 6) at which tows or trawl hauls were made.

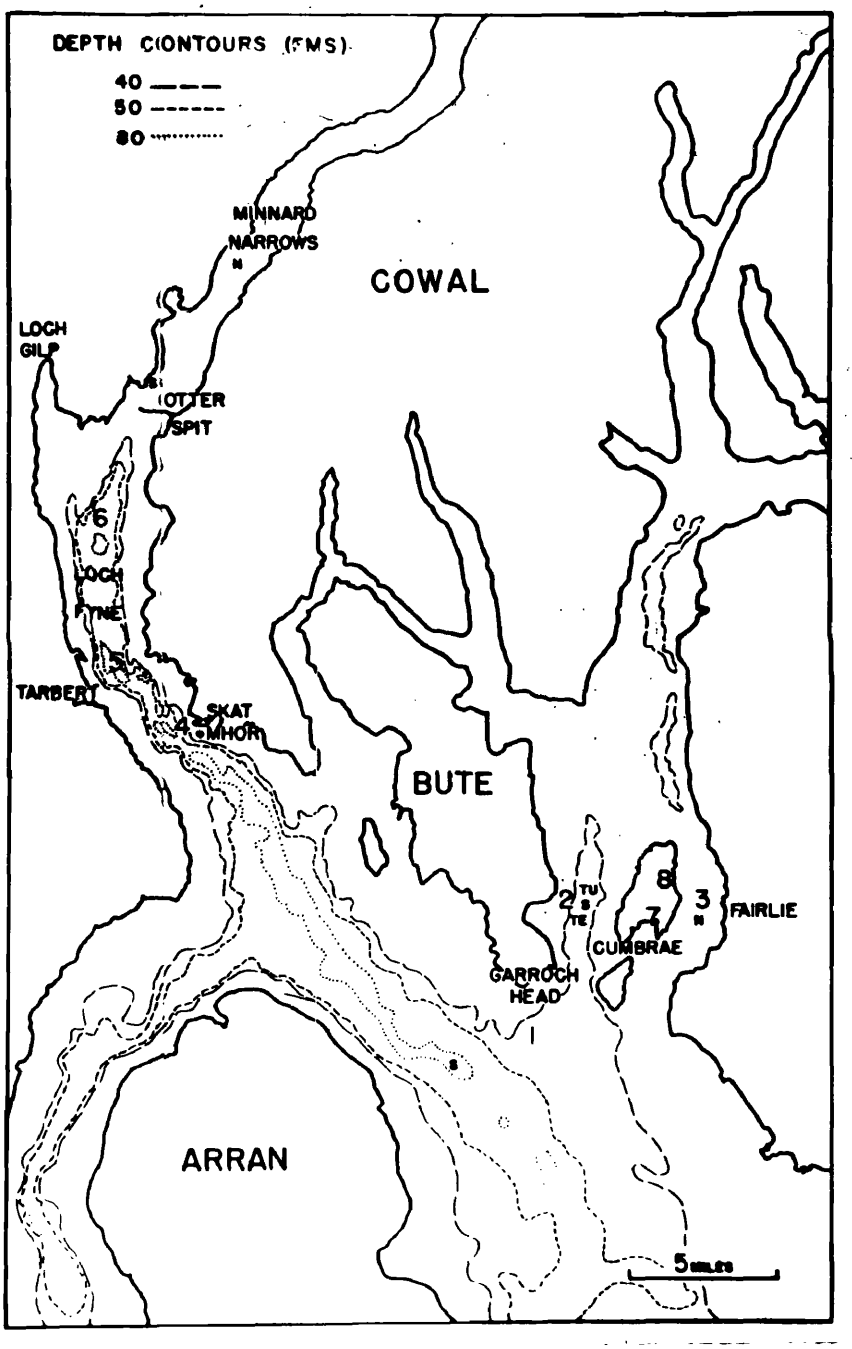

DEPTH CONTOURS (FMS)
40
50
80
MINNARD NARROWS N
COWAL
LOCH GILP
OTTER SPIT
6
LOCH FYNE
TARBERT
SKAT GMHOR
4
BUTE
2
TU S TE
8
7
3 N
FAIRLIE
CUMBRAE
GARROCH HEAD
1
ARRAN
5 MILES

FIGURE 1

The tows in which they were most abundant always contained a small quantity of fine mud particles, indicating that the net had passed close enough to the bottom to disturb the superficial layer of mud.

The extremely low density of Nucula post-larvae and the ease with which they could be swirled off the bottom suggested another method of collection, by which still later developmental stages were obtained. A sledge trawl was fitted with two small nets of fine bolting silk (6 inches in diameter at the mouth and 15 inches long) lashed to the top of the framework inside the mouth.* The trawl, lowered into the water until it was just off the bottom, was towed at a minimum speed for 20 minutes. Soft mud filled the coarse net of the trawl but only small quantities of fine mud entered the small nets. Large numbers of Nucula post-larvae were obtained in this way from hauls taken at Stations 2, 3, 4, and 6 (Fig. 1).

Culture Methods

Several attempts to carry out fertilizations of Nucula sulcata in the laboratory in November 1955 were unsuccessful. Since the young post-larvae of this species were later found to be most plentiful in February it is unlikely that the gametes were ripe in November. The young stages in the tows at this time were identified later as the post-larvae of N. turgida and N. tenuis.

Attempts made to rear post-larvae by feeding

---

* The author is indebted to Dr. J. Mauchline for suggesting and designing this apparatus.

them μ-flagellates and organic detritus were unsuccessful. Nevertheless, all stages could be reared very easily in about 1 inch of mud in the bottom of a breffit, providing the mud contained no large organisms which might die and foul the water. These cultures could be maintained for as long as three to four months by changing the water about once a month. Post-larval stages collected in fine townettings could be kept for approximately one month in the breffit of plankton. They appeared to feed on the detritus formed as the planktonic organisms died and sank to the bottom.

Examination of Living Material

While the transparency of the majority of lamellibranch larval and post-larval shells greatly facilitates direct observation of living specimens, this was almost impossible with the protobranchs. Not only were observations on living material hindered by the opacity of the shell but also by the extremely small size of the younger spat. Thus, whenever possible the shell valves were removed, with a minimum of injury to the soft parts, to enable a more accurate observation of the intricate ciliary mechanisms. The use of dissections means that the animals were not observed feeding in the normal manner; the ciliary currents of the organs of the mantle cavity have been described from dissections, and the method of feeding inferred from them. This technique has been applied by many workers to the study of ciliary currents and feeding in adult lamellibranchs, and as will be indicated below, can be relied upon to give a true interpretation of the feeding mechanism. Feeding

experiments such as those employed by Owen (1955b, 1956) would be valuable to verify the findings reported here, but were beyond the scope of this investigation.

The difficulties encountered in detecting the minute details of the ciliary tracts made it imperative to examine large numbers of specimens. Consequently, the developmental sequence described here is, of necessity, a composite picture emerging from the details observed in many specimens. The direction and distribution of ciliary currents was determined by the use of a colloidal carbon preparation, 'Aquadag'. Since the dissections did not lend themselves to photomicrography, drawings, on which the ciliary currents could be marked, were prepared using squared paper in conjunction with a graticuled ocular.

Study of Preserved Material

A series of representative stages of Nucula post-larvae were narcotized wtih propylene phenoxetol (Owen, 1955a) and fixed in Bouin's and Bouin-Duboscq's fluids (Atkins, 1937). Specimens were embedded in 60 - 62° C. Fisher Tissuemat and serial sections cut at thicknesses of 2 to 5 μ; the thinnest sections showed the cilia to best advantage. Sections were cut in all planes, but transverse and slightly oblique sagittal sections were the most satisfactory. Heidenhain's iron haematoxylin, alcian blue 8GS (Steedman, 1950), and orange G in clove oil were used in combination in staining.

IDENTIFICATION OF SPECIES

As methods were devised to capture more post-larvae it soon became apparent that they were not all of one type. Two distinctly different forms were noted among the smallest stages in which the prodissoconch alone is present. Older post-larvae showed that one of these types also included two species, distinguished by the character of the early dissoconch. The characteristic features of the prodissoconch and dissoconch of these three species, Nucula sulcata, N. turgida, and N. tenuis, are given in Appendix I.

SEASONAL OCCURRENCE AND FREQUENCY OF POST-LARVAE

Newly metamorphosed post-larvae of N. turgida and N. tenuis were common in the deep townettings as early as mid-November, but by January their numbers had dwindled considerably. The early post-larvae were most numerous in January and February. N. sulcata appeared first in January, reached a peak abundance in February, and the early post-larval stages were common from March to May.

While tows were taken regularly throughout the year, trawl collections were made only in the months from October to May; post-larvae were always present in these samples.

Post-larvae kept in the laboratory grew slowly. A mud sample from the North Tarbert Deep, collected on February 15 when the N. sulcata were all newly metamorphosed (length approximately 165μ), was examined on June 28. Thirty-one N. sulcata showed a

mode between 240 and 250μ while twenty-two N. turgida and N. tenuis were fairly equally distributed over the range from 185 to 410μ.

CILIARY CURRENTS IN THE MANTLE CAVITY OF THE POST-LARVA

Post-larval development was found to be identical in each of the three species of Nucula described in the preceding section. Since the rate of development in N. sulcata differed slightly from that in N. turgida and N. tenuis, measurements of each post-larval stage are given separately for the former species. In every other respect the following description applies to each of the three species.

Synopsis of Developmental Stages

The 'barrel-shaped' larvae described so vividly by Drew (1899a, 1901) and reared from the fertilized eggs of N. turgida and N. nucleus by Lebour (1938) were never encountered in this investigation. Representative series of stages, from newly metamorphosed post-larvae of 165μ to nearly mature stages of approximately 600μ, were collected and examined with particular regard to the ciliary currents.

It is convenient to subdivide the post-larval period, between metamorphosis and maturity, into four arbitrarily defined stages according to the feeding mechanism involved. The four stages are characterized by the following morphological features:

Post-metamorphic Stage (Fig. 2)

With the exception of the complete digestive tract there is little structural differentiation in the newly metamorphosed

FIGURE 2

Nucula sulcata. Post-metamorphic stage.

Size - 0.16 x 0.11 mm.

DD - digestive diverticula, F - foot, MC - mantle cavity,
MM - mantle margin, P - prodissoconch, U - umbone.

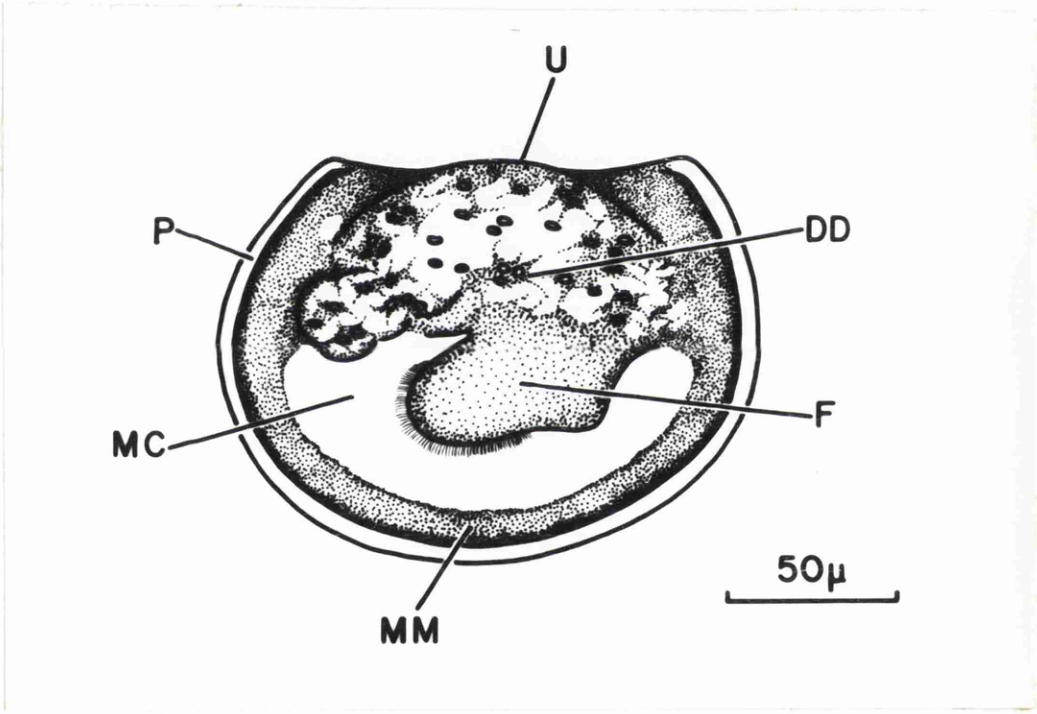


FIGURE 2

post-larva. Although, during the day or two passed in this stage, little or no growth occurs, the pedal anlage becomes differentiated into a recognizable foot. Both ctenidia and palps are absent.

N. turgida and N. tenuis - The length of the prodissoconch averages 162μ but varies between 155 and 185μ.

N. sulcata - The length of the prodissoconch averages 164μ but varies from 160 to 169μ.

Pre-ctenidial Stage (Fig. 3)

The ctenidium is represented solely by its anlage; the palps by the ciliated oral area or presumptive palpal region. In addition to the marginal cilia the mantle bears a ciliated arc, the pallial arc, which extends from the region of the gill anlage to the mouth. Distally the foot is differentiated into a posterior 'heel' and an anterior 'sole' which later becomes bilobed, the long pedal cilia circumscribing the disc so formed. Short cilia cover the lateral walls of the foot proximally. Although longer than the preceding one, this period is relatively short and growth is limited.

N. turgida and N. tenuis - The length increases from 178 to 185μ.

N. sulcata - The length increases from 169 to 194μ.

Proto-palpal Stage

A. Upper Palpal Stage (Fig. 4 & 5)

The palps are represented by a small upper lamella and

FIGURE 3

Nucula tenuis. Pre-ctenidial stage.

Broken arrow indicates direction of the metachronal wave of pallial ciliated arc. Solid arrows indicate direction of ciliary currents.

Size - 0.18 x 0.14 mm.

AA - anterior adductor muscle, DD - digestive diverticula, GA - gill anlage, H - heel of foot, MC - marginal cilia of mantle, MO - position of mouth, PA - posterior adductor muscle, PG - pedal ganglion, PCA - pallial ciliated arc, S - sole of foot, ST - statocyst.

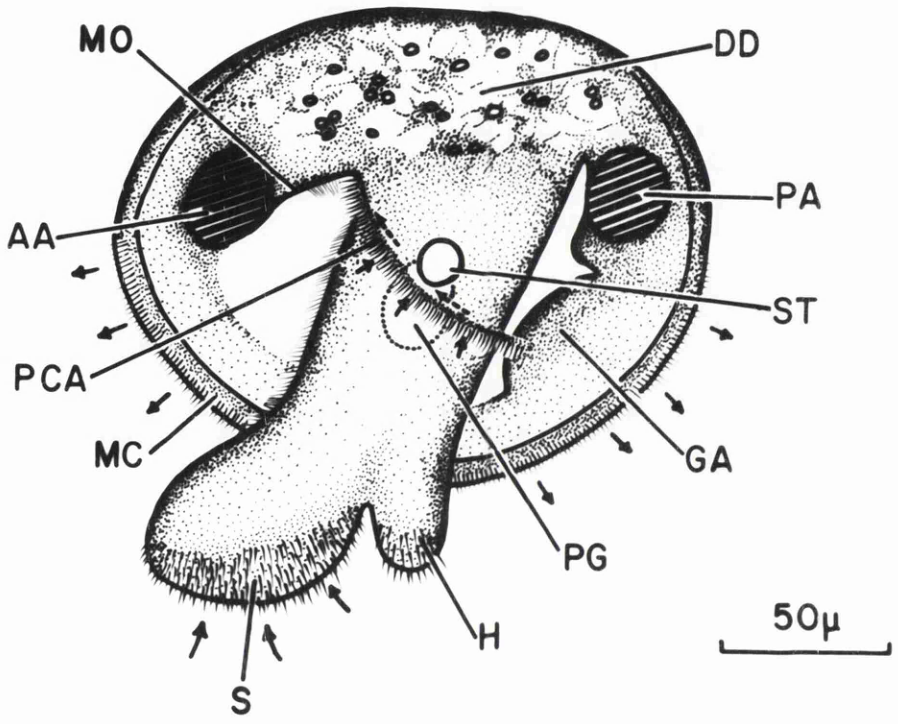


FIGURE 3

FIGURE 4

Nucula turgida. Proto-palpal stage (upper palpal) with pallial ciliated arc still present.

Long arrows indicate position of inhalant current; short arrows show the direction of the ciliary current along the adoral pedal tract.

Size - 0.21 x 0.16 mm.

APT - adoral pedal tract, C - ctenidium, COR - circumoral region, PCA - pallial ciliated arc.

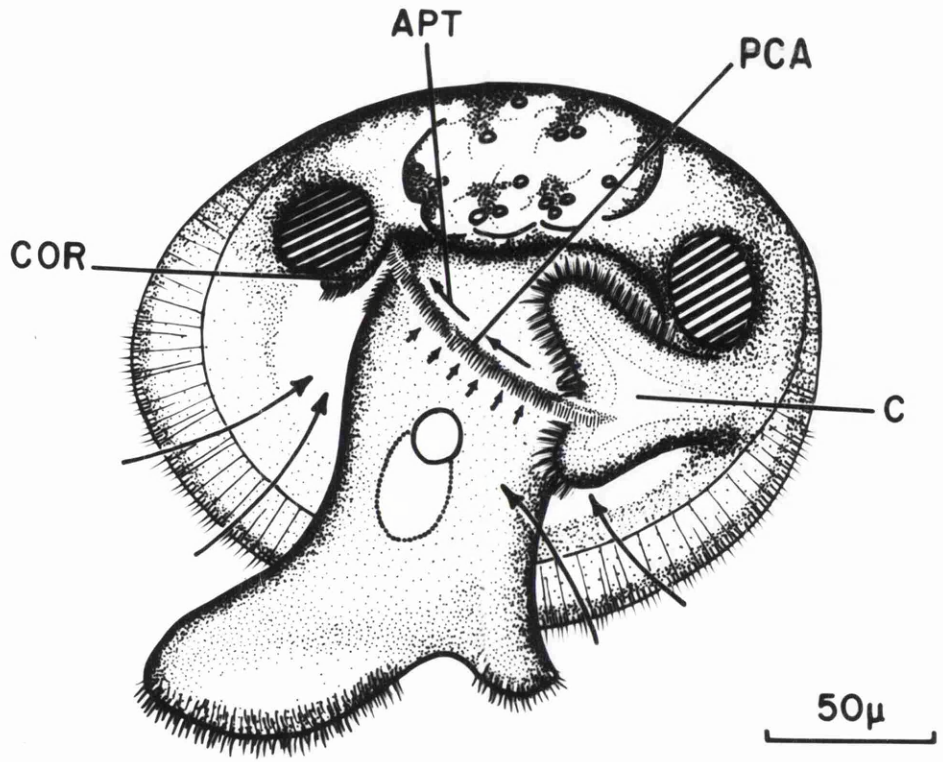


FIGURE 4

FIGURE 5

Nucula turgida. Proto-palpal stage (upper palpal) with pallial ciliated arc no longer present.

Single solid arrows indicate direction of ciliary currents; double-line arrows indicate position and direction of ciliary current along the pedal rejection tract.

Size - 0.28 x 0.23 mm.

APT - adoral pedal tract, P - prodissoconch, PRT - pedal rejection tract, UPL - upper palp lamella.

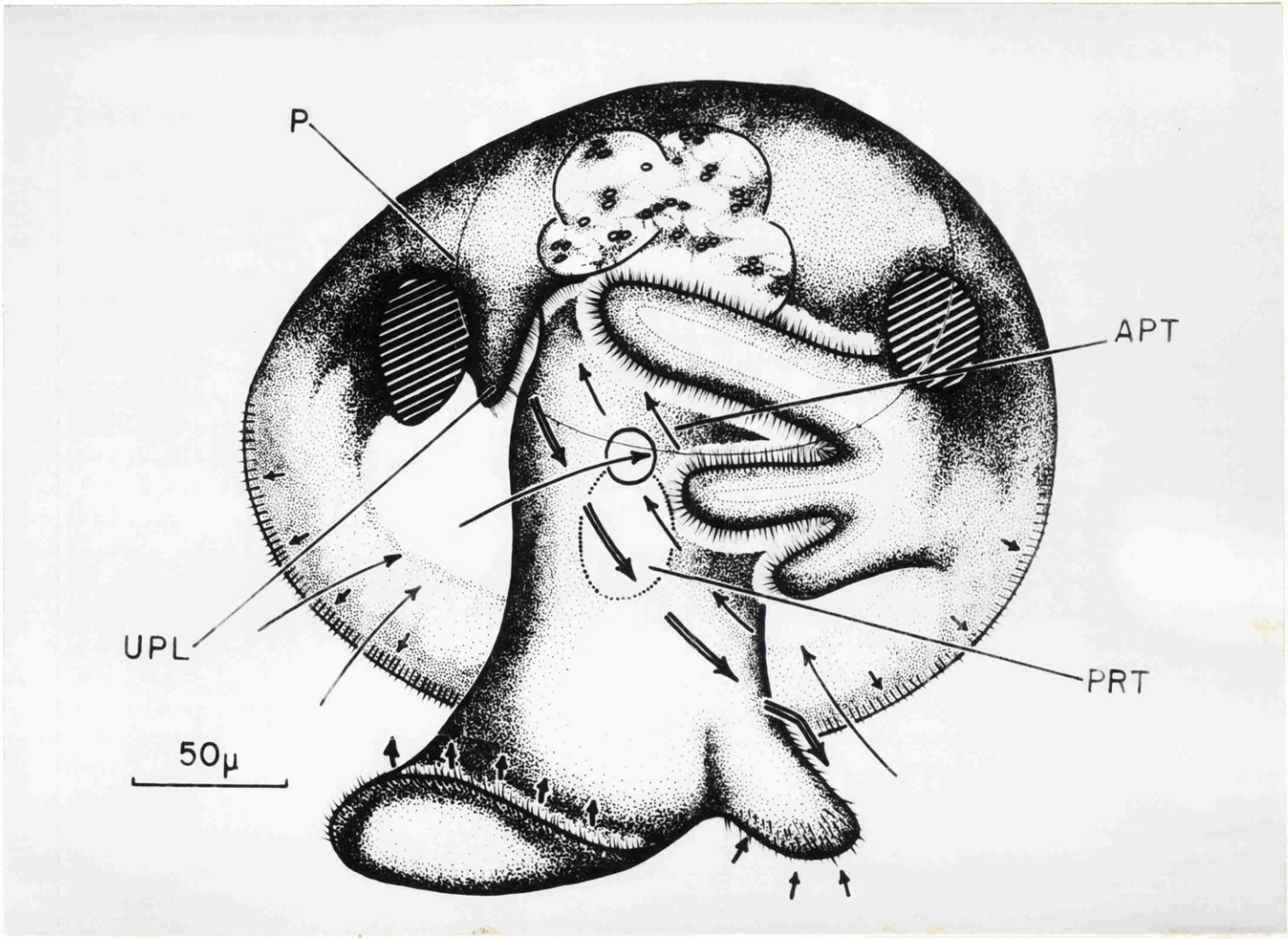


FIGURE 5

an underlying ciliated area, the precursor of the lower palp. Although the pallial ciliated arc persists in the early stages with two gill filaments it is not evident in later stages. The ctenidia have been differentiated and exhibit from two to six inner, and up to five outer filaments; they are functional and bear the full complement of cilia. Adjacent antagonistic ciliary currents traverse the foot diagonally from the posterior distal portion to the mouth and palps. During this period the post-larva feeds actively and exhibits a marked growth.

N. turgida and N. tenuis - The length increases from 185 to 500μ.

N. sulcata - The length increases from 194 to 500μ.

B. Lower Palpal Stage (Fig. 6)

The ciliated area underlying the upper palp becomes differentiated into the lower palp and direct contact is established between the palps and the first ctenidial filament. This filament is proportionately longer than the others and its tip lies between the two palps. In other respects this stage is similar to A.

N. turgida and N. tenuis - The length increases from approximately 500 to 600μ.

Proboscidean Stage (Fig. 8)

The palp proboscides, developing from the outer tip of the upper palp lamella, elongate rapidly. When they are of sufficient length to be functional the post-larva may be

FIGURE 6

Nucula tenuis. Proto-palpal stage (lower palpal). Arrows as before.

Size - 0.56 x 0.49 mm.

AAC - axial adoral current, APT - adoral pedal tract, FC - frontal current of ctenidial filaments, LPL - lower palp lamella, MO - position of mouth, PRT - pedal rejection tract, TC - position and direction of current of terminal cilia of ctenidial filaments, UPL - upper palp lamella, 'Y'G - 'Y'-shaped groove of upper palp lamella.

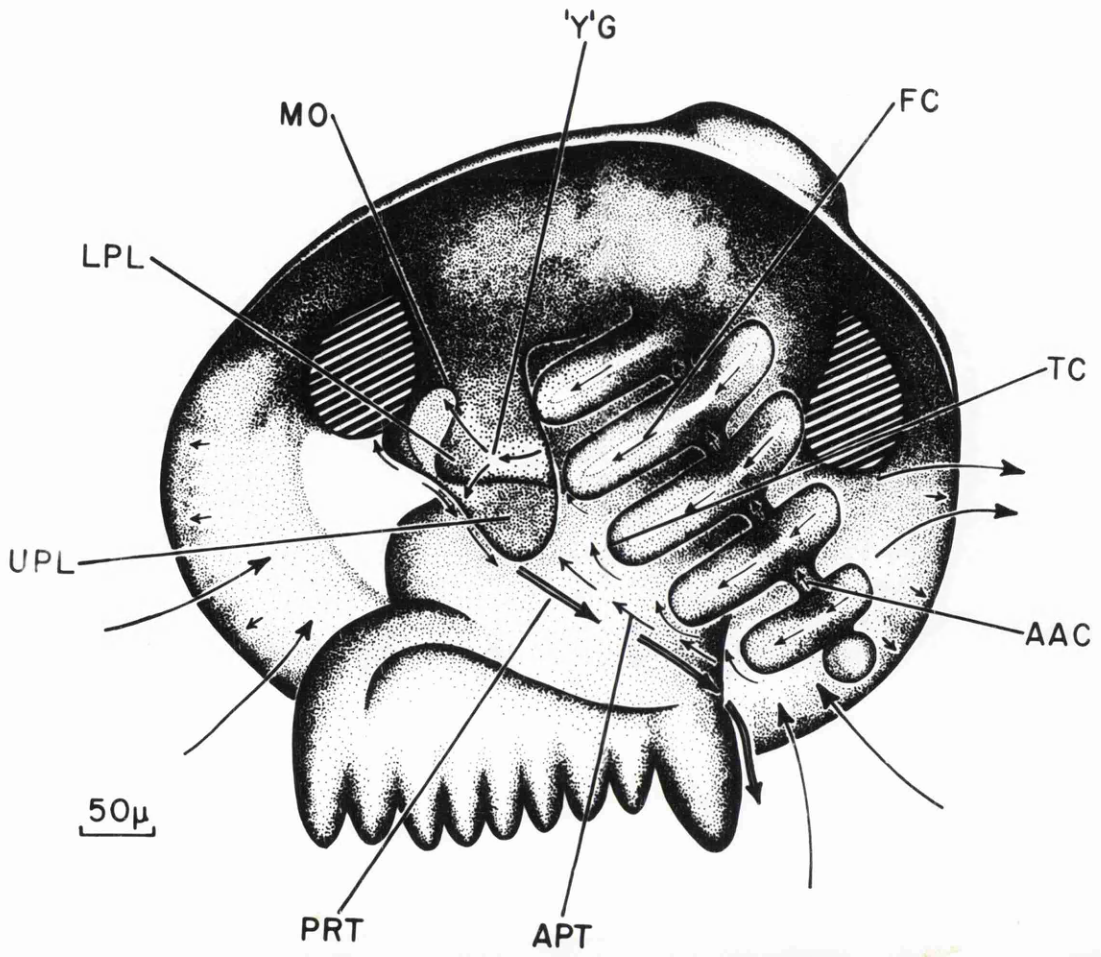


FIGURE 6

said to be fully developed; only further growth of the organs now formed is necessary for maturity.

N. turgida and N. tenuis - The length increases from approximately 600 to 650μ.

Ciliary Currents of the Mantle Cavity

The development of ciliary tracts in the mantle cavity will be considered separately for each organ with reference to the four developmental stages.

The post-metamorphic stages were remarkably lacking in any visible structure. At first they appeared opaque, the cavity between the shell valves being filled by a loose mass of apparently unorganized cells. Not until they had disappeared was any internal structure perceived. Unfortunately, post-larvae with such dispersed cells were not fixed and consequently neither the origin nor fate of these cells was determined.

A. The Foot

Initially the only apparent structure in the post-metamorphic stage is a small outgrowth protruding ventrally into the mantle cavity from the dorsal body mass. As this protuberance enlarges and becomes recognizable as the foot, it acquires a sparse covering of cilia. These cilia become more concentrated in the ventral and anterior regions and were seen beating weakly within the shell (Fig. 2, F).

In the pre-ctenidial stage, the foot continues to elongate and ~~very~~ long cilia (8 - 10μ)* make their appearance on

* Lengths of cilia were all measured from serial sections and are thus only approximate.

the 'sole', especially anteriorly; the beat of these cilia is strong and directed proximally. On its lateral walls the foot is clothed with short fine cilia (Fig. 4, APT), which create an adoral current; the limits of the adoral pedal tract were exceedingly difficult to define, both in living material and in sections. The tract appears to be dorsal to the pallial ciliated arc (Fig. 3 & 4, PCA) which is located on the mantle overlying the foot. In a few specimens a dorsal current was noted along the posterior margin of the foot.

The lateral cilia of the foot assume a greater prominence in the proto-palpal stage, two separate tracts now being readily distinguishable (Fig. 5). The first, already present in the pre-ctenidial stage, is the adoral pedal tract (Fig. 5, APT). These short cilia are now restricted to a more definite, somewhat triangular area on the proximal portion of the foot. The dorsal margin of this area lies along the line of junction between the foot and mantle; the posterior limit extends almost to the posterior margin of the foot. The third side of the triangle forms a diagonal line across the foot, beginning at a point a little dorsal to the heel and terminating near the mouth. Anteriorly where the foot joins the body wall, the tract broadens to form the ventral portion of the circum-oral region (Fig. 4, CMOR). The tract is covered posteriorly by the developing ctenidium; the ends of the filaments overlie most of the triangular area, but leave a band of cilia uncovered at their free ends. This band runs along the diagonal margin of the adoral ciliated area.

A second tract of moderately coarse cilia (6 - 8μ)

lies adjacent to the diagonal margin of the adoral pedal tract; it traverses the foot from a position just ventral to the mouth to a point dorsal to the heel. This tract, which will be referred to as the pedal rejection tract (Fig. 5, PRT), exhibits an aboral current. Thus the lateral walls of the foot bear two adjacent, antagonistic ciliary currents: the pedal rejection tract --- current aboral --- and the adoral pedal tract.

B. The mantle

Early in the post-metamorphic stage, probably shortly after the test is shed, the mantle acquires cilia along its inner margin (Fig. 3, MC). These cilia were prominent in all sectioned material, even in the smallest stages of approximately 180μ. They appear to be evenly distributed along the entire margin of the mantle, are ~~moderately~~ long (8 - 10μ), and beat out of the mantle cavity.

In the pre-ctenidial stage a second tract of cilia, the pallial ciliated arc, makes its appearance (Fig. 3 & 4, PCA). This peculiar structure occurs on either side of the mantle, overlying the ventral limit of the adoral pedal tract; it originates posteriorly at the gill anlage and curving antero-dorsally over the foot terminates near the mouth. The cilia comprising the pallial arc are ~~moderately~~ long (8 - 10μ) and their beat is dorsal, or centripetal along the radii of the arc. The extreme delicacy of this structure is demonstrated in sectioned material where it is seen that the arc consists of a single row of ciliated cells (~~Fig. 9, PCA~~); it is doubtful whether its presence would have been detected were it not for its most distinctive characteristic --- the strong

laeoplectic metachronal wave. The pallial ciliated arc was observed in living specimens up to 210μ long; in older individuals the opacity of the shell occluded it from view, but it was noted in sections of specimens up to 250μ.

In dissections of larger specimens, where the shell was removed to facilitate observations, the mantle was almost invariably destroyed. However, in one specimen of N. tenuis at the proto-palpal stage, 555μ x 487μ ~~in length~~, the mantle adhered closely to one shell valve, having been torn neatly across its junction with the body wall (Fig. 7). The margin of the mantle lay in its normal position still attached by the pallial muscles to the shell. In the intact animal the mantle is stretched tightly between the shell margin and its line of coalescence with the body wall; removal of the shell inevitably destroys this relationship. Hence the portion of the mantle between the two adductors was strongly contracted ventrally. Small isolated groups of cilia with a weak beat were distributed over the contracted area of the mantle (Fig. 7, IGC). Their arrangement was such that if the mantle were stretched to occupy its normal position, the cilia would lie in the region of the pallial arc of younger specimens. In addition to these isolated patches of cilia, other groups of cilia with a very strong beat directed out of the mantle cavity were located below the adductor muscles (Fig. 7, PRC & ARC). While those ventral to the posterior adductor were more prominent, both groups of cilia could be seen beating even in the intact animal; they were readily demonstrated in sectioned material.

FIGURE 7

Nucula tenuis. Internal view of left valve of specimen in Fig. 6 with left mantle adhering to shell.

Arrows indicate direction of ciliary current.

Size - 0.56 x 0.49 mm.

AAS - anterior adductor muscle scar, ARC - anterior rejection cilia, IGC - isolated groups of cilia, possibly representing remnants of the pallial ciliated arc, MJB - position of mantle junction with body, MM - mantle margin, PAS - posterior adductor muscle scar, PRC - posterior rejection cilia.

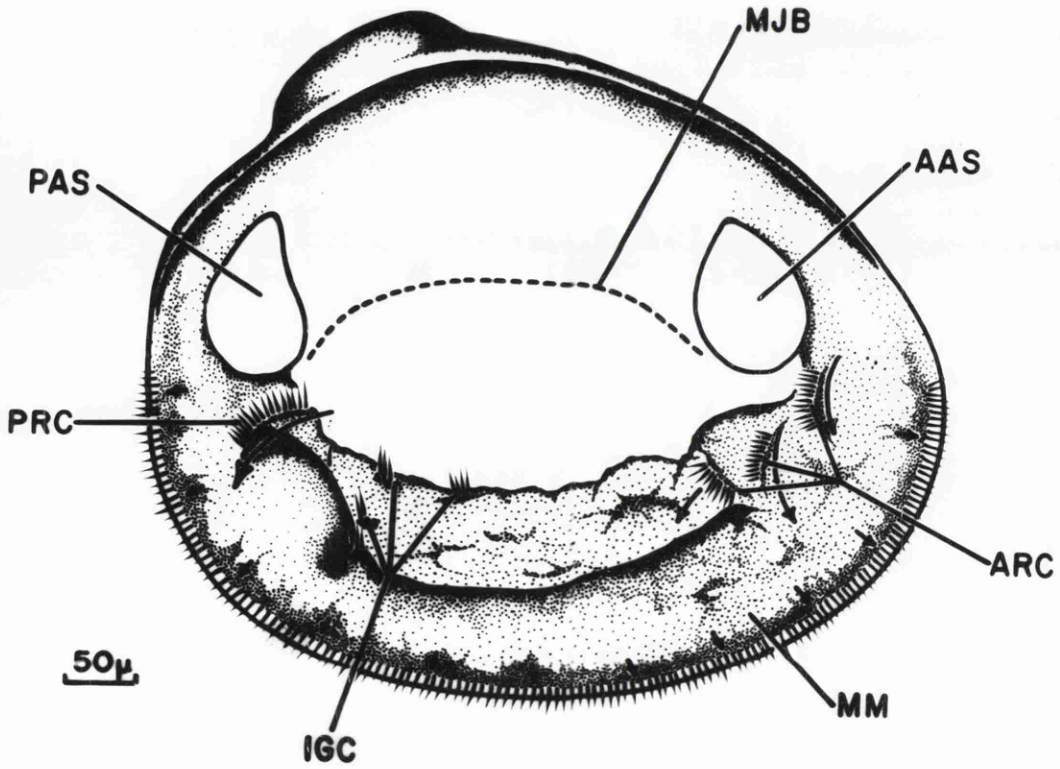


FIGURE 7

C. The Ctenidia

Initially in the proto-palpal stage the first two filaments are short and stubby, the upper one barely extending forward over the foot (Fig. 4, C); the sole representatives of the gill cilia are the lateral cilia. Due to their restricted numbers and limited distribution these cilia produce a weak and rather ineffectual inhalent current.

During the upper palpal stage the two primary filaments increase in length and diverge from one another distally to form a 'V': the first, projecting slightly dorsally, the second a little ventrally. As the filaments of both ctenidia now extend over the sides of the foot, their free ends project laterally, so that the two ctenidia also diverge from one another distally. Meanwhile, the filaments have acquired their full complement of cilia --- both eu-latero-frontals and frontals are present --- while the lateral cilia are now sufficiently numerous to create a moderately strong current.

Throughout the proto-palpal stage the development of the ctenidium proceeds by the addition of more filaments by the cleavage of the posterior one. When three inner filaments are present, the formation of the outer demibranch begins with the appearance of two short projections along the ctenidial axis exactly opposite the second and third filaments; there is never an outer filament formed opposite the first. Subsequently, new filaments are added to both demibranchs simultaneously. The filaments of the outer demibranch extend postero-dorsally from the axis, at the same time

projecting a little laterally into the mantle cavity to form an obtuse angle with the filaments of the inner demibranch.

The frontal currents on all filaments are directed towards the ventral surface or the ends of the inner filaments, where a current across the tips of the inner filaments carries particles from the tip of one filament to that of the adjacent anterior one. Along the ctenidial axis there is a weak adoral current but that on the frontal surfaces of the filaments is almost continuous across the axis from the outer to the inner demibranch and this current is much stronger than the axial one (Fig, 6).

D. The Labial Palps

Formation of the palps does not commence until the proto-palpal stage of post-larval development, but prior to this the presumptive palpal regions, comprising the portions of the foot and body wall adjacent to the mouth, have become ciliated. The distribution of these circum-oral cilia (Fig. 4, CmOR) is continuous with the adoral pedal ciliary tracts; the beat over the entire area is adoral. Despite the continuity of these areas, their cilia are easily distinguishable in sections; those of the circum-oral area are decidedly longer (5 - 6μ) and hence more conspicuous. The cilia of the adoral pedal tract are sparsely distributed and short (2 - 3μ) (Fig. 4, APC).

Development of the palps is slow; their various parts arising successively, not simultaneously. The first palpal component to appear is the upper lamella which arises as a 'U'-shaped ridge projecting ventrally, as a small hood, to enclose the mouth

anteriorly and laterally (Fig. 5, UPL). The ciliated epithelium, now restricted to the inner surface of the ridge, lies in apposition to the underlying ciliated area of the foot; both are derivatives of the circum-oral region.

As the palp lamellae enlarge they assume a triangular shape, two edges of which are free, while the third is broadly attached to the body wall dorsally (Fig. 6, UPL). One of these free edges forms the posterior limit of the lamella, while the antero-ventral edge is continuous anteriorly with its counterpart of the opposite palp lamella. From a point midway along the posterior edge, a depression or groove traverses the inner surface of the lamella to meet a similar depression, arising near the midpoint of the antero-ventral edge, to form the 'V' of a 'Y'-shaped groove; the stem of the 'Y' leads anteriorly and medially to the mouth (Fig. 9). Along the posterior arm and stem of the 'Y' the ciliary stroke is adoral, but in the ventral arm it is toward the free antero-ventral edge and hence aboral. Likewise, the beat of the cilia on the remainder of the lamella is directed aborally, or across the current in the adoral groove, and is such that particles tend to converge in the ventral arm of the 'Y' groove whence they travel rapidly to the free antero-ventral edge. The margin of the latter exhibits a strong posterior current leading to the apex of the palp lamella, except for a short region anteriorly where the current is reversed.

The 'Y'-shaped groove was shallow in sectioned material and not nearly as prominent as in living specimens. The cilia over the inner surface of the upper palp lamella were evenly

FIGURE 8

N. tenuis

Proboscidean Stage. Ventral view of right palps showing ciliary currents of upper and lower palp lamellae, palp pouch, and palp proboscis.

From specimen 0.66 mm. in length.

AG - adoral tract along groove of lower lamella;
AP - adoral current along groove of proboscis;
GU - groove of upper palp exhibiting adoral current;
LL - lower lamella; O - oesophagus; PO - palp pouch;
PP - palp proboscis; RL - ridges of lower lamella;
RT - rejection tract along margin of upper lamella;
RU - ridge of upper lamella bearing rejection tract.

FIGURE 9

N. tenuis

Proto-palpal stage (lower palpal). Detail of oral area showing ciliary tracts of left upper palp lamella. Note intimate relationship between palps and first filament of ctenidium.

From specimen 0.53 mm. in length.

AA - anterior adductor muscle; ARC - anterior rejection current of mantle; FC - frontal current of first ctenidial filament; LP - lower palp lamella; MO - mouth; R - ridge of upper palp; R'Y' - rejection arm of 'Y'-shaped groove; RT - rejection tract along antero-ventral edge of palp leading to pedal rejection tract; UP - upper palp lamella; 'Y'A and 'Y'S - adoral currents along arm and stem of 'Y'-shaped groove of upper palp.

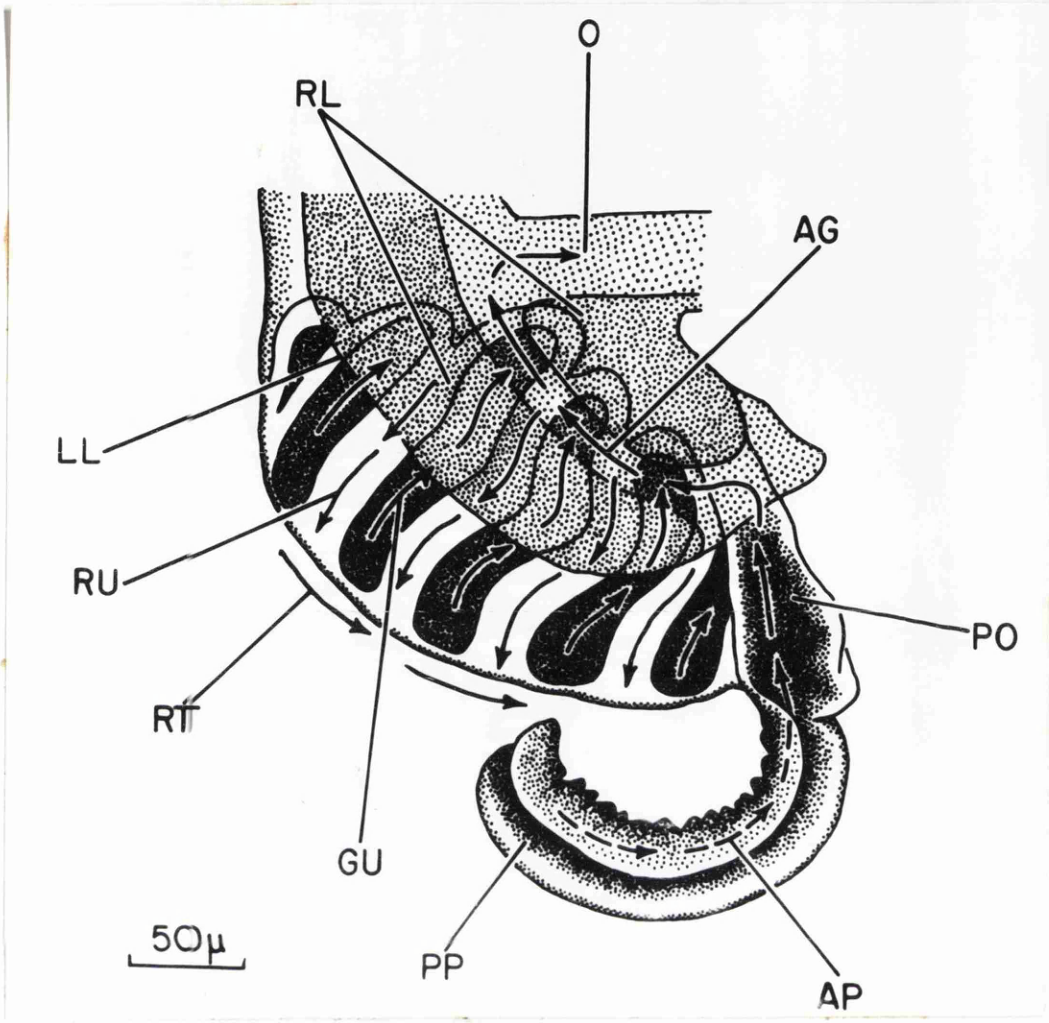


FIGURE 8

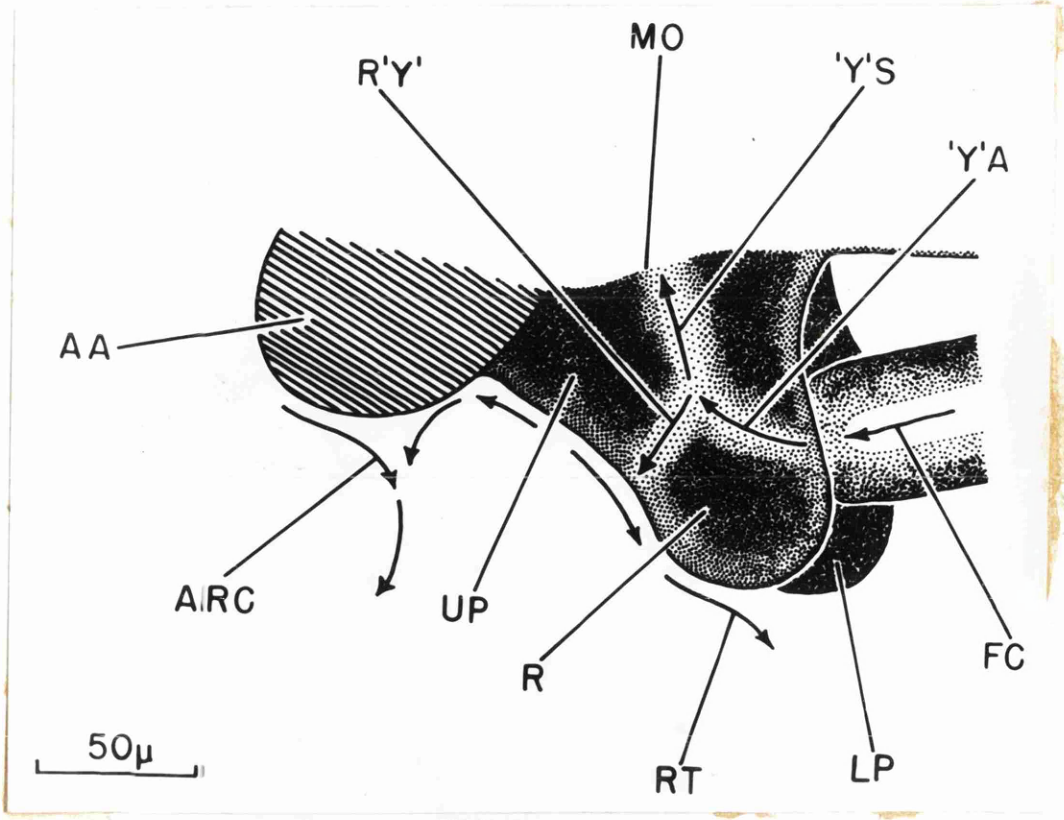


FIGURE 9

distributed and from 8 to 9μ in length; while those on the underlying surface of the foot were short, 5 to 6μ. In each instance they merged with the longer cilia of the oesophagus, 12μ in the antero-dorsal, and 6 to 8μ in the postero-ventral region.

As the post-larva approaches a length of 500μ (lower palpal stage) the presumptive lower palp, the pedal circum-oral region, commences its differentiation into a palp lamella; the ciliated epithelium is incorporated into the outer surface of the lamella. The lower palp is of the same shape as the upper but is little smaller, except where it extends beyond the posterior limit of the latter. Direct contact is now established between the ctenidia and the palps as the tip of the first filament comes to lie between the posterior edges of the palp lamellae (Fig. 6N+9).

At this stage of post-larval development the ~~directions of the~~ ciliary currents of the palp lamellae are identical to those on the palps of eulamellibranch post-larvae. ~~at a comparable stage~~. The protobranch palp lamellae closely resemble in shape, structure, and function those of a typical eulamellibranch. ~~or filibranch, such as Mytilus~~.

FEEDING MECHANISMS IN THE POST-LARVA

From the description of the ciliary currents, and their development and distribution on the organs within the mantle cavity, the integration of these currents can now be considered.

Post-metamorphic Stage

The newly metamorphosed post-larva is inactive. Only when it has reached the stage represented in Figure 3 are the first sluggish movements of the foot observed; these could not be construed as related to feeding.

Pre-ctenidial Stage

The first movements of the spat are executed by the foot; intermittently, it is protruded beyond the shell valves and waved gently back and forth before being withdrawn. Although such movements might be interpreted as indicative of locomotion, the young post-larva lies on its side and was never observed to make any attempt to right itself and burrow into the substratum.

While the foot is extended the long cilia on its sole are continually active; their beat is strong and directed proximally. As the foot waves back and forth small particles are caught by the long pedal cilia and thrown up onto the sides of the foot. Frequently, when the shell valves gape but the foot remains withdrawn in the mantle cavity, the activity of the long pedal cilia creates a moderately strong inhalant current. At such times

particles may be drawn into the mantle cavity even without the extrusion of the foot.

Once the sole of the foot has become bilobed, it acts even more efficiently in food collection. The lateral lobes are continually extended and then approximated as the foot is waved back and forth; this action, in conjunction with the beating of the long pedal cilia, is very effective in transferring particles to the walls of the foot.

Particles thrown onto the sides of the foot, or wafted into the mantle cavity, by the action of the long pedal cilia are directed onto the adoral pedal tract by the cilia of the pallial arc. The dorsal beat of these cilia serves in two capacities: first, to draw particles further dorsally, and second, to prevent particles from leaving the adoral pedal tract while in transit to the mouth.

Occasionally, particles may be carried dorsally along the posterior wall of the foot, then posteriorly below the posterior adductor muscle, and ventrally along the margin of the foot or carried out of the mantle cavity. This posterior pedal current could serve as a rejection tract, some particles being diverted posteriorly while the remainder travel across the base of the foot toward the mouth. Certainly, this is the only indication of a sorting mechanism, there being none in the oral region. The pedal rejection tract, adjacent and antagonistic to the adoral tract, is not present at this stage. Nevertheless, the small size of the post-larva means that the cilia of the mantle are probably adequate to

remove excess particles from the mantle cavity.

Proto-palpal Stage

A. Upper Palpal Stage

At an early stage in the development of the ctenidium, the lateral cilia of the two short gill filaments contribute to the inhalant current produced by the pedal cilia; but as these filaments elongate and the lateral cilia increase in number, they gradually take over the production of the inhalant current. When the first two filaments are well developed, the long pedal cilia become less active in food collection and the movements of the foot are largely restricted to locomotion. Initially, the main portion of the inhalant current enters the mantle cavity antero-ventrally, but as the ctenidia develop the current is shifted posteriorly since the large foot, when withdrawn, now blocks the anterior entrance.

Particles entering the inhalant stream are drawn to the posterior region of the mantle cavity by the lateral cilia. The foot and ctenidium combine to partition the mantle cavity; the ctenidia are still attached to the mantle along the axis while the tips of the filaments touch the lateral walls of the foot. Thus, particles either fall onto the surface of the foot or ctenidium. Particles impinging on the frontal surface of the filaments, or caught by the eu-latero-frontal cilia and thrown onto the frontal surface, travel to the tips of the filaments where terminal cilia direct them antero-dorsally (Fig. 6, TC). Due to the contact maintained between the free ends of the filaments and the foot,

particles carried by the terminal cilia are also influenced by the cilia of the adoral pedal tract and travel anteriorly along this tract together with the particles which fall directly onto the surface of the foot. In the oral region the particles pass between the inner surface of the upper lamella of the palps and the pedal circum-oral cilia; sorting on the lamella causes rejection of the larger particles and only the smaller ones enter the mouth. Rejected particles are quickly removed by the longer cilia of the pedal rejection tract to a point just dorsal to the heel of the foot, where they are transferred to the mantle to be ejected from the mantle cavity by the marginal pallial cilia.

As the complexity of the ctenidia increases from the simple two filament stage, they assume a more important rôle in food collection. Their area is greatly increased by the addition of more filaments to the inner demibranchs and later by the formation of the outer demibranchs; more particles now impinge on the surface of the ctenidia and fewer on the foot. Over the whole ctenidium the frontal currents are directed to the free ends of the inner filaments (Fig. 6). Despite the weak adoral axial current, particles are carried across the axis by the much stronger frontal current which is continuous except for a short interruption in the axial region, from the filaments of the outer demibranch to those of the inner. Due to the angle between the outer and inner demibranchs the axis lies in a groove; small particles probably fall into this groove and are carried adorally by the axial current. Along the ventral margin of the inner demibranch, where the filaments now lie close to one

another, particles are frequently passed by the terminal cilia from the tip of one filament to that of the adjacent anterior filament. Thus, particles may be carried anteriorly without resorting to the adoral pedal tract. Nevertheless, the latter is retained and continues to function, although in a more limited capacity, until the palp proboscides are well developed.

Simultaneously, both the complexity and size of the upper palp lamella has increased; the 'Y' groove is present and the posterior margin of the lamella lies in close proximity to the tip of the first filament, if not in contact with it. Transference of particles is now made directly from the end of the first filament to the posterior edge of the palp lamella where sorting occurs. Smaller particles pass along the groove directly to the mouth, while the larger ones are carried across the lamella into the ventral groove where they are directed to the antero-ventral edge of the lamella and fall onto the pedal rejection tract. A few particles reach the anterior end of the ventral edge of the palp lamella and travel anteriorly onto the mantle below the anterior adductor muscle; here they are ejected to the exterior by the strong pallial cilia (Fig. 7, ARC).

B. Lower Palpal Stage

The first gill filament now lies with its tip inserted between the lamellæ of the palps and particles are carried directly from the ctenidium to the palps. In other respects the ciliary currents and feeding mechanism remain unchanged.

Proboscidean Stage

Observations of the functioning of the palp proboscides during their development were impossible since they could only be made when the shell valves were removed and under these conditions do not function in food collection. It was only possible to note the ciliary currents (Fig. 8) which are identical to those in the adult. Throughout the development of the palp proboscides the pedal tracts remained; their cilia were active in transporting particles to and from the palps in excised specimens, even when the proboscides had reached full development.

DISCUSSION

Growth Rate

The peaks observed in the abundance of newly metamorphosed post-larvae, in November and December for N. turgida and N. tenuis and in February for N. sulcata, coincide with the breeding seasons listed by Lebour (1938) for Plymouth and Allen (1954) for Millport (Table I). These well-defined peaks indicate a fairly limited spawning period for each species; the only species of Nucula believed to have either an extended spawning period, or to spawn twice yearly, is N. nucleus (Lebour, 1938; Allen, 1954).

Since newly metamorphosed post-larvae first appear in November, the presence of post-larvae in October trawl collections is indicative of a slow rate of development. Measurements of spat from a mud sample collected in the North Tarbert Deep in mid February and kept in the laboratory until the ~~middle~~ end of June showed that N. sulcata had grown from approximately 165μ to an average length of 245μ in four and one-half months. While growth in the laboratory may not have been optimum, they had ~~merely~~ not doubled their length during that period. Drew (1901) emphasized the slow rate of development in N. delphinodonta.

The post-larval period, during which the young Nucula grow from a length of approximately 165 - 600μ, occupies the major portion of development, particularly in contrast to the short larval period as recorded by Drew (1899a, 1901): 60 hours from fertilization to metamorphosis in N. proxima and 90 - 120 hours in Yoldia limatula (Table I). Thus, both with regard to the duration of the

TABLE I

Summary of the Data Recorded in the Literature Concerning the Breeding Seasons and Development of the Protobranchia

NUCULIDAE

Nucula delphinodonta

Drew	1899b & 1901	Egg diameter 210μ. Development non-pelagic. Embryos reared in parental brood-sac.

Nucula proxima

Drew	1899b & 1901	Egg diameter 90μ. Development pelagic. Larval period from fertilization to metamorphosis is 60 hours.

Nucula nucleus

Bernard	1898	Prodissoconch 180μ (as measured from Figure).
Lebour	1938	Egg diameter 100μ. Breeds from spring to early autumn. Fertilizations carried out in July, September, October and November. No ripe spawn from December to March. Reared to 'barrel-shaped' larvae in July. Short free-swimming stage.
Jørgensen	1946	(From data of Thorson) Egg diameter in Kattegat approximately 180μ.
Allen	1954	Population studies indicated two maxima occur during the breeding season given by Lebour (1938).

Nucula hanleyi

Lebour	1938	Same breeding season as N. nucleus.

Nucula tenuis

Thorson	1936	Egg diameter 120 - 140μ. Development non-pelagic or very short pelagic.

TABLE I (Continued)

Nucula turgida		
Lebour	1938	Egg diameter 90μ. Development pelagic. Spawns in winter at Plymouth. Fertilized eggs reared to free-swimming larvae in February. Short free-swimming stage.
Allen	1954	Ripe spawn from October to February. Fertilizations unsuccessful.
Nucula sulcata		
Allen	1954	Ripe spawn in January and February. Fertilizations unsuccessful.
NUCULANIDAE		
Yoldia limatula		
Drew	1899a & 1899b	Egg diameter 150μ. Larval period from fertilization to metamorphosis is 90 - 120 hours. Size at metamorphosis is approximately 200μ.
Leda pernula		
Thorson	1936	Egg diameter 120 - 140μ. Development non-pelagic or very short pelagic.

post-larval period and the growth accomplished during it, this stage is a major one in the life history of Nucula.

Habits and Feeding during Development

A. Larval Period

Although no conclusive evidence is available, it is not unreasonable to assume that the young larva feeds actively during its short planktonic life. Structurally it is well adapted to feed efficiently; the mechanism is probably very similar to that employed by the veliger larva of lamellibranchs. Growth during this period is slight; in Yoldia limatula (Drew, 1899a) there is an increase of 50μ in length over the egg diameter of 150μ (Table I). Lebour (1938) gives the diameter of the egg of N. turgida as 90μ, and Thorson (1936) of N. tenuis as 120 - 140μ; there are no records of the egg diameter of N. sulcata. Prodissoconchs of these three species at Millport averaged approximately 165μ, which would suggest a larval growth corresponding to that of Yoldia limatula.

B. Post-metamorphic Period

It is doubtful that any food intake occurs during the short period following metamorphosis. Drew (1901) states that the sudden contraction of the adductor muscle upon casting causes the diverticula to rupture and the dorsal wall of the stomach to disintegrate. He concludes that no nutriment is taken in by the post-larva until the cells of the diverticula have been reorganized into pouches. In Yoldia limatula the reassemblage of the diverticula requires but a few hours, while in N. delphinodonta the process is

much slower, probably taking one to two days. While Drew's observations of the disintegration of the liver pouches could not be verified, the youngest spat of the three species dealt with here did give every appearance of containing isolated liver cells dispersed throughout the interior of the shell.

Thus, as far as can be determined, these early inactive stages do not feed; the only movements noted were slight twitches of the foot but never was it observed to be protruded.

C. Pre-ctenidial Period

It has already been noted that the young post-larva has an extremely low density, the adaptive value of which is obvious since it prevents the animal from being buried in the soft mud. It is therefore likely that, under natural conditions, as in the laboratory, the young Nucula lie on the surface of the mud and do not burrow. At this vulnerable point in development, it would undoubtedly be fatal for the animal to be buried.

Since the duration of this stage is short, growth is slight, involving an increase in length of 10μ in N. turgida and N. tenuis and approximately 30μ in N. sulcata.

The movements of the foot were observed to be concerned solely with feeding and were similar to those described by Drew (1901) for N. delphinodonta. It is noteworthy that all the ciliary currents, with the exception of the exhalant one produced by the marginal pallial cilia, are focused around the foot. The activity of the long pedal cilia, in conjunction with the characteristic movements of the foot, serve to collect particulate food;

the currents on the pedal walls lead to the mouth; the mantle overlying the foot bears the pallial ciliated arc which directs particles onto the adoral pedal tract. While the foot cannot be considered a particularly effective collector, it does show certain rather unique adaptations to the performance of this function. The most remarkable component of this pre-ctenidial feeding mechanism is the transitory pallial ciliated arc. Whereas shortly after the formation of the second gill filament it degenerates or becomes vestigial, the adoral pedal tract is incorporated into the ciliary feeding mechanism of the next stage and the long pedal cilia are utilized in burrowing.

D. Proto-palpal Period

Throughout this stage the post-larva utilizes a ciliary feeding mechanism. The efficiency of the mechanism is indicated by the fact that the young Nucula increases in length from 190μ to 600μ during this period, which extends over the greatest portion of post-larval development. As these stages comprised the majority of the specimens collected in the October trawl samples it is estimated that the duration of the proto-palpal period is almost one year.

The ciliary mechanism operative throughout this phase of post-larval development exhibits the following basic characteristics of the feeding mechanism of the eulamellibranchs:

1. The ctenidia are relatively large in comparison to other organs of the mantle cavity and to the ctenidia of the adult Nucula, although not relative to the size of the ctenidia in adult eulamellibranchs.

2. The frontal currents on both demibranchs carry all particles impinging on the gill surface to the free edge of the inner demibranch.
3. The terminal cilia at the tips of the filaments transport such particles anteriorly along the edge of the inner demibranch.
4. The tip of the first filament of the inner demibranch is inserted between the edges of the palp lamellae and particles are transferred directly to the surface of the latter.
5. Particles are sorted on the palp lamellae, some proceeding to the mouth while others are rejected.
6. A pedal* rejection tract removes particles not accepted for ingestion from the mantle cavity.

The primitive nature of the feeding mechanism is shown by the limited surface area of the ctenidia in comparison to that of adult lamellibranchs; the posterior position of the ctenidia; the incomplete partitioning of the mantle cavity into inhalant and exhalant chambers; and the anterior inhalant current. Nevertheless, while the post-larval mechanism is essentially simple in comparison with that characteristic of the lamellibranchs; it does show certain complexities, particularly in the presence of adjacent antagonistic ciliary tracts on the foot, and in the co-ordination of ciliary tracts on the ctenidia, foot, and palps.

---

* Pedal rejection tract of Nucula post-larvae is analogous to the recurrent path of the mantle in eulamellibranch post-larvae.

Post-larval Metamorphosis

The organization of the post-larva may be considered under three headings: those structures which are exclusive to the post-larva and are absent in the adult; those which are present in both the post-larva and the adult, but which undergo a functional metamorphosis during the transition between the two stages; and those which are characteristic of the adult only.

A. Structures which are exclusive to the post-larva include:

1. The adoral pedal ciliated area.
2. The pallial ciliated arc.
3. The long distal cilia circumscribing the bilobed sole of the foot.

These structures make their appearance in the early post-larva and degenerate late in post-larval or early in adult life.

B. Structures which are common to both post-larva and adult, but which show a functional metamorphosis, include:

1. The aboral rejection tract in the post-larva carries particles rejected by the palps, whereas in the adult it carries particles removed from the gills to the exterior. The position of this tract is altered so that in the adult it occupies the posterior margin of the foot (Yonge, 1939).
2. The ctenidia, which in the post-larva function as

feeding organs, are used solely for respiration in the adult. The metamorphosis of these organs involves three changes, two functional and one structural.

i. The frontal and terminal ciliary tracts are converted from temporary feeding to their primitive cleansing function. The frontal tracts remain unmodified and carry all particles to the free ventral edge of the inner demibranch; while the adoral tract of terminal cilia is retained only in the portions of the ctenidia posterior to the foot. Particles, accumulating at the ventral edge of the inner demibranch adjacent to the posterior margin of the foot, may either fall on the mantle, be removed by the palp proboscides (Atkins, 1936), or be transferred to the pedal rejection tract (Yonge, 1939).

ii. The functional contact between the ctenidia and palps is lost in the adult.

iii. The gill filaments of the post-larva are long and narrow resembling those of lamellibranch post-larvae; in the adult they are flat and leaf-like resembling those of the zygobranchiate gastropods.

3. Whereas in the post-larva the palp lamellae maintain

functional contact with the ctenidia, in the adult they are associated with the palp proboscides. The lamellae retain their sorting function throughout development and are always associated with feeding whether it be of the suspension or deposit type.

C. The only structures both morphologically and functionally peculiar to the adult are the palp proboscides; they appear late in post-larval development.

The post-larval period thus represents a distinct phase in the development of Nucula; it is terminated by the degeneration of exclusively post-larval structures, the functional metamorphosis of structures common to both post-larva and adult, and the utilization of the proboscides for food collection.

Phylogenetic Position of the Protobranchia

Since Pelseneer's time it has been generally recognized that the Protobranchia exhibit a number of primitive characters (Pelseneer, 1891; Stempell, 1898a & 1898b; Drew, 1899a, 1899b, 1901; Yonge, 1939, 1959), while within this Subclass the Family Nuculidae represent the most primitive group, the Nuculanidae and Solenomyidae being more specialized (Yonge, 1939, 1959). Consequently in attempting to elucidate the phylogenetic relationships of the bivalves most authors are unanimous in considering a nuculoid form as broadly ancestral to the Class Bivalvia.

Many phylogenetic trees have been errected on the basis of shell characters. Jackson (1890) postulated the origin of the 'Aviculidae and their allies' in the nuculids as follows: "It is extremely probable that Nucula or a Nuculoid form is the type we are

seeking as the early ancestral radical represented by the complete prodissoconch in the development of Avicula, Perna, Ostrea, Pecten, Anomia and their allies." Another palaeontologiest, Douvillé (Davies, 1933), considered the lamellibranchs to have evolved along three separate lines: a 'normal', a 'sedentary', and a 'burrowing' branch. The Nuculidae were ancestral to the 'normal' branch and the Solenomyidae to the 'burrowing' branch.

Other investigators have corroborated these conclusions by tracing phylogenetic relationships on the basis of anatomical characters. From such evidence Pelseneer (1888, 1911) derived his classification, which has been criticized for showing 'horizontal' as opposed to 'vertical' or phylogenetic relationships. However, his evolutionary scheme does illustrate these vertical relationships; the Nuculidae appear as the ancestral forms while the Solenomyidae are an offshoot from which no higher types have arisen. Based on the configuration of the kidney, Odhner (1912) constructed a bifurcating tree in which the Nuculidae, including the Nuculanidae, were ancestral to the Mytilacea, Ostreidae, Limidae, Pectinidae, Anomiidae, and Aviculidae; while the Solenomyidae gave rise to the remaining filibranchs and all the eulamellibranchs.

Theile (1935), combining shell and anatomical features, derived the Nuculacea and the Arcacea from a common ancestor, the latter giving rise to the remaining lamellibranchs.

Yonge (1939) points out that the investigation of the protobranch kidney by Burne (1903) refutes Odhner's conclusions. Yonge also elucidated the affinities between the Nuculidae and

Solenomyidae and showed conclusively that the latter could have given rise to no higher forms; this invalidates Odhner's and Douville's deduction that the Solenomyidae represent an ancestral type.

Atkins (1938) has divided the lamellibranchs into two major groups on the basis of the character of the latero-frontal cilia of the ctenidia. The Microciliobranchia are a monophyletic group and it is doubtful that they could have arisen from the protobranchs, which share with the remaining lamellibranchs the possession of eu-latero-frontal cilia. She stresses the improbability of structures so valuable in ciliary feeding --- especially since an attempt to regain them is found in the Ostreidae --- being lost in the course of the evolution of the Microciliobranchia. Yonge (1939), however, is unwilling to assess the value of the eu-latero-frontal cilia in ciliary feeding until more information is available concerning the part played by muscles and blood pressure in controlling the rate of filtration of water by the ctenidium. Moreover, he disagrees with Atkins' view that the eu-latero-frontals arose in connection with ciliary feeding, and states that they evolved with the need to prevent fouling of the supra-branchial cavity.

Phylogenetic Implications of Post-larval Development in Nucula

The bivalve Mollusca are characterized by the possession of a greatly extended mantle/shell which completely encloses the body. In these animals the mouth has lost contact with the substratum, and as pointed out by Yonge (1939, 1947, 1953), this has involved a complete change in feeding habits since, compared with the

univalve ancestor, the animal can no longer rasp off particles from a hard substratum by means of a radula. Yonge has suggested that as a consequence of this, the Bivalvia must have passed through an evolutionary stage corresponding to the condition exhibited by the modern Nuculidae in which the palp proboscides extend beyond the valve margins and function as feeding organs. The results obtained from this present study on the development of Nucula are of interest therefore in considering the possible role played by a "nucula stage" in the evolution of the Bivalvia, although it must be emphasized that the phylogenetic implications of such a study are not necessarily conclusive.

Speculation as to the possible significance of the ctenidial feeding mechanism in the post-larva of Nucula to the phylogeny of the bivalves has led to the formulation of three hypotheses.

A. The Ctenidial Feeding Mechanism Represents a Post-larval Innovation Which Appeared Subsequent to the Evolution of the Lamellibranchia

If the appearance of palp proboscides preceded the use of ctenidia as feeding organs in the bivalves, then it must be assumed that the ctenidial feeding mechanism of the post-larva represents an innovation which was incorporated into the life history of the Nuculidae after the lamellibranchs had evolved from this ancestral stock. Apparently, the ctenidial feeding mechanism arose independently in the post-larva of Nucula, and while not as highly evolved as in the lamellibranchs, does show convergence with the latter.

B. Ctenidial Feeding Mechanism Represents a Post-larval Innovation Which Appeared Prior to the Evolution of the Lamellibranchia

If, on the other hand, the post-larval innovation occurred before the evolution of the lamellibranchs, the latter may have arisen paedogenetically from the ancestral nuculoid type possessing a post-larval development of the type in modern Nucula. Thus, the lamellibranchs may have evolved through suppression of the adult deposit feeding stage followed by elaboration of the ctenidial feeding mechanism of the post-larva of the ancestral form.

For either of these hypotheses to be acceptable one condition must be satisfied. If the ctenidial feeding mechanism represents an innovation, it must have conferred some advantage on the post-larva. It is difficult to assess the conceivable advantages of such a feeding mechanism in the post-larval stages of modern Nucula. However, three possibilities are worthy of discussion.

1. The ctenidial feeding mechanism might be adaptive, permitting survival of the young post-larva in a habitat other than that occupied by the adult.

   The newly metamorphosed larva is inactive and probably does not feed for a least several days. During this period its density approximates that of sea water so that the slightest current is sufficient to lift it from the bottom. Such is the environment in which both post-larval and adult stages are found --- in deeper regions where the soft flocculent mud indicates little water disturbance. The method used

for collection of post-larval stages is additional proof of the effect of water currents in the passive transport of the young. Since the post-larva is relatively certain to reach the habitat of the adult, it requires no adaptive features for survival in any other habitat. Indeed, although the mechanism is a passive one, the young post-larvae of the three species studied here (N. sulcata, N. turgida, and N. tenuis) may be better adapted to selection of a permanently favourable substratum than are many lamellibranch larvae (Part III).

However, other species of Nucula such as N. nucleus occur in coarse muddy gravel (Allen, 1954) in areas where there is a considerable current. The relationship of the post-larvae to the environment in such species remains to be investigated.

2. The palp proboscides are possibly less efficient feeding organs for a small organism than are the ctenidia.

Palp proboscides attain a maximum efficiency in large animals; whereas ciliary feeding mechanisms, which depend for their efficiency on a large ratio of surface area to volume, are more advantageous in small organisms. The lamellibranchs have overcome this difficulty by an increase in surface area provided by the greater number and length of the gill filaments. It is difficult to assess the relative advantages of

the ctenidia and palp proboscides as organs of food collection in the post-larva of Nucula, particularly as the former cannot be considered efficient. The complexity of the ciliary feeding mechanism is puzzling, since any slight advantage which it may afford must be considered in relation to the simplicity of the deposit feeding method. In the latter, commencement of feeding would be dependent solely on the development of palp proboscides, and would seem to be beneficial to an organism with such a slow rate of development. Moreover, the methods employed for rearing young in the laboratory demonstrate that with the exception of particle size, the food of adults and post-larvae is identical.

3. The use of palp proboscides may be correlated with the ability of the post-larva to burrow.

Yonge (personal communication) has pointed out that the development of a temporary feeding mechanism may be associated with the early inadequacy of the foot for burrowing activities. Certainly, the early post-larvae do not burrow and palp proboscides developed at this time might be incapable of food collection. Moreover, the ability to burrow would also seem to be dependent on the development of effective respiratory and cleansing mechanisms, thus necessitating an initial hypertrophy of the ctenidia. If then, the palp

proboscides are only functional when the animal is embedded in the muddy substratum, the development of adoral ciliary tracts, adapting the ctenidia to temporary food collection, may represent a conservation of early developmental processes.

C. Ancestral Form with Undifferentiated Palps which Gave Rise Independently to the Lamellibranchia and the Protobranchia

A third hypothesis is that the ctenidial feeding mechanism of the post-larva is not an innovation, but rather represents the persistence of a similar stage in the life history of the ancestral form. Since it is necessary to postulate a transitional stage between radula and ctenidial feeding in the phylogeny of the Bivalvia, it has been suggested by Yonge (1959 b) that the ancestral type might have possessed "undifferentiated palps or lips on either side of the mouth" such as are found in Neopilina (Lemche, 1957) and that possibly the ctenidia served as accessory feeding organs, particularly in the young stages.

One of the first steps in the evolution of the bivalves must have been the extension and lateral compression of the mantle/shell so that the body became completely enclosed within the latter (Yonge, 1939 and 1953). The posterior mantle cavity would then have considerable lateral extensions ---on either side of the foot --- reaching forward to the mouth. Primitively the inhalant water current of the bivalves enters anteriorly (Yonge, 1939 and 1947) and therefore must pass to either side of the mouth as it is drawn into the mantle cavity by the posterior ctenidia. Thus the undifferentiated palps of the ancestral form, bathed by this water current, would be

in a position to collect, and hence utilize for food, some of the suspended matter carried in the inhalant stream. It is possible that initially co-operation between ctenidia and palps in feeding was the removal by the palps of suspended material from the respiratory water current produced by the ctenidia. Adaptation to this type of feeding probably involved lateral extension of the palps together with some differentiation of their apposed surfaces for sorting the particles collected. A roughly analogous feeding mechanism is seen in the post-larvae of the lamellibranch Tellinacea. Here the palps undergo a remarkable hypertrophy shortly after metamorphosis, so that in the young spat they are as large as --- or even somewhat larger than --- the ctenidia. The relative positions of the palps and ctenidia are strongly reminescent of those in Nucula and --- there being as yet no siphons --- the inhalant current enters anteriorly. It has frequently been observed that a large number of the particles carried by the inhalant stream impinge directly on the large palps. Such particles are sorted on the palps and either make their way to the mouth or are rejected.

Early in the evolution of this ancestral type specialization appears to have occurred along two separate lines. In one line, the palps enlarged considerably and then abandoned their utilization of the respiratory water current as a food source when they extended, by means of the newly developed proboscides, beyond the limits of the shell and were thus able to collect food directly from the substratum. In a second line, leading to the lamellibranchs, co-operation between the ctenidia and palps increased as the ctenidia extended forward in the mantle cavity to establish a direct contact

with the palps. Meanwhile, the ciliary tracts of the ctenidia, primitively concerned with cleansing, were recruited to form a part of the feeding mechanism while the palps became specialized as sorting organs.

In support of this hypothesis it should be noted that while the Nuculidae are undoubtedly the most primitive living bivalves (Yonge, 1939), they do show indications of both structural and functional specialization. Drew (1901) recognized the foot, once considered as being of primitive structure, as an organ specialized for life on a soft muddy bottom. From a study of the stomach and digestive diverticula, Owen (1956) has concluded that "the structure and physiology of the gut present many specialized features" which are possibly "correlated with the retention (or development?) of the labial palps as feeding organs and the ingestion of large quantities of inorganic material with the food." Nevertheless, it must be admitted that much of the evidence in favour of this hypothesis lies in the difficulty of explaining the adaptive value of the ciliary feeding mechanism of Nucula post-larvae on which the two alternative hypotheses are dependent.

SUMMARY

1. The post-larval development of Nucula sulcata, N. turgida, N. tenuis has been studied with particular reference to the feeding mechanisms; except for slight variations in size, development in the three species is identical.

2. On the basis of the feeding mechanisms the post-larval period may be divided into four stages: the post-metamorphic, the pre-ctenidial, the proto-palpal, and the proboscidean.

3. It is improbable that feeding occurs during the short post-metamorphic stage. The organization of the spat is extremely simple; the foot, mantle/shell, and visceral mass are the only discernable structures.

4. During the pre-ctenidial stage feeding is accomplished mainly by the activities of the foot. Particles are wafted into the mantle cavity by long pedal cilia, are drawn into the dorsal region of the mantle cavity through the activity of the pallial ciliated arc and transported to the mouth by adoral pedal tracts.

5. Ctenidia and palps begin their development during the pre-ctenidial stage, but are not sufficiently developed to take an active part in feeding.

6. During the proto-palpal stage food collection is performed by the ctenidia. Particles carried in the inhalant stream impinge on the gill filaments and are transported by the frontal tracts

to the ventral edge of the inner demibranch. Terminal cilia of the filaments, acting in conjunction with the adjacent adoral pedal tract, carry particles anteriorly. Since the first filament lies with its tip between the upper and lower palp lamellae, particles are transferred directly to the palps.

7. Sorting occurs on the palp lamellae. The upper palp bears on its inner surface a 'Y'-shaped groove; particles enter at the base of the 'Y' and are sorted at the point of bifurcation, particles destined for ingestion proceeding along the adoral arm, while others pass into the rejection arm to be carried to the free edge of the palp.

8. The lateral walls of the foot bear rejection tracts lying parallel and adjacent to the adoral tracts. The rejection tract commencing adjacent to the rejection point of the upper palp traverses the lateral wall of the foot diagonally, and terminates dorsal to the heel of the foot. Particles leaving the pedal rejection tract fall onto the mantle where the marginal cilia expel them from the mantle cavity.

9. During the proboscidean stage the palp proboscides develop from the posterior apex of the upper palp lamellae. Deposit feeding after the manner of the adult is not initiated until the proboscides are fully developed.

10. The termination of the post-larval period is marked by degeneration of the pallial ciliated arc and adoral pedal tract; functional metamorphosis of the pedal rejection tract and ctenidia; loss of

functional contact between ctenidia and palps; and the formation of, and commencement of food collection by the palp proboscides.

11. The phylogenetic implications of the ctenidial feeding mechanism of the post-larva are discussed.

BIBLIOGRAPHY

Allen, J.A. 1953. Observations on Nucula turgida Marshall and N. moorei Winckworth.
J. mar. biol. Ass. U.K., 31: 515-528.

_____ 1954. A comparative study of the British species of Nucula and Nuculana.
J. mar. biol. Ass. U.K., 33: 457-472.

Atkins, D. 1936. On the ciliary mechanisms and interrelationships of lamellibranchs. Part I. Some new observations on sorting mechanisms in certain Lamellibranchia.
Quart. J. micr. Sci., 79: 181-308.

_____ 1937. On the ciliary mechanisms and interrelationships of lamellibranchs. Part IV. Cuticular fusion, with special reference to the fourth aperture in certain lamellibranchs.
Quart. J. micr. Sci., 79: 423-445.

_____ 1938. On the ciliary mechanisms and interrelationships of lamellibranchs. Part VII. Latero-frontal cilia of the gill filaments and their phylogenetic value.
Quart. J. micr. Sci., 80: 345-436.

Bernard, F. 1898. Recherches ontogeniques et morphologiques sur la coquille des Lamellibranches. I. Taxodontes et Anisomyaires.
Ann. Sci. Natur. Zool., ser. 8, 8: 1-208.

Burne, R.H. 1903. On the renal organs of Nucula nucleus Linn.
Proc. malacol. Soc. Lond., 5: 300-304.

Davies, A.M. 1933. The bases of classification of the Lamellibranchia.
Proc. malacol. Soc. Lond., 20: 322-326.

Douvillé, H. 1912. Classifications des lamellibranches.
Bull. Soc. géol. Fr., 12: 419-467.

Drew, G.A. 1899a. Yoldia limatula.
Mem. biol. Lab. Johns Hopk. Univ., 4: no. 3.

_____ 1899b. Some observations on the habits, anatomy, and embryology of members of the Protobranchia.
Anat. Anz., 15: 493-518.

_____ 1901. The life history of Nucula delphinodonta (Mighels).
Quart. J. micr. Sci., 44: 313-391.

Heath, H. 1937. The anatomy of some protobranch mollusks.
Mem. Mus. Hist. nat. Belg., 2: 1-26.

Hirasaka, K. 1927. Notes on Nucula.
J. mar. biol. Ass. U.K., 14: 629-645.

Jackson, R.T. 1890. Phylogeny of the Pelecypoda, the Aviculidae and their allies.
Mem, Boston Soc. nat. Hist., 4: 277-394.

Jørgensen, C.B. 1946. Reproduction and larval development of Danish marine bottom invertebrates. Part 9. Lamellibranchia.
Medd. Komm. Danmarks Fisk. Havunders., Ser. Plankton, 4: 277-311.

Lebour, M. 1938. Notes on the breeding of some lamellibranchs from Plymouth and their larvae.
J. mar. biol. Ass. U.K., 23: 119-144.

Lemche, H. 1957. A new living deep-sea mollusc of the Cambro-Devonian Class Monoplacophora.
Nature, Lond., 179: 413-416.

Morse, E.S. 1913. Observations on living Solenomya.
Biol. Bull., Woods Hole, 25: 261-281.

_____ 1919. Observations on living lamellibranchs of New England.
Proc. Boston Soc. nat. Hist., 35: 139-196.

Odhner, N. 1912. Morphologische und phylogenetische Untersuchungen über die Nephridien der Lamellibrancien.
Z. wiss. Zool., 100: 287-391.

Owen, G. 1955a. Use of Propylene phenoxetol as a relaxing agent.
Nature, Lond., 175: 434.

_____ 1955b. Observations on the stomach and digestive diverticula of the Lamellibranchia. I. The Anisomyaria and Eulamellibranchia.
Quart. J. micr. Sci., 96: 517-537.

_____ 1956. Observations on the stomach and digestive diverticula of the Lamellibranchia. II. The Nuculidae.
Quart. J. micr. Sci., 97: 541-567.

Pelseneer, P. 1888. Report on the anatomy of the deep-sea Mollusca.
"Challenger" Rept., Zool., 27: 1-42.

_____ 1891. Contribution à l'étude des Lamellibranches.
Arch. Biol., 11: 147-312.

_____ 1899. Rescherches morphologiques et phylogénétiques sur les mollusques archaïques.
Mém. Acad. R. Belg., 57: 1-112.

_____ 1911. Les Lamellibranches de l'expédition du Siboga. Partie anatomique.
Siboga-Exped., 53a: 1-125.

Rees, C.B. 1950. The identification and classification of lamellibranch larvae.
Hull Bull. mar. Ecol., 3: 73-104.

Steedman, H.F. 1950. Alcian blue 8GS: A new stain for mucin.
Quart. J. micr. Sci., 91: 477-479.

Stempell, W. 1898a. Beiträge zur Kenntniss der Nuculiden.
Zool. Jb., Suppl. 4 (Fauna Chilensis): 339-430.

_____ 1898b. Ueber Solenomya togata Poli. (Vorläufige Mittheilung.)
S.B. Ges. naturf. Fr., Berl.: 82-85.

_____ 1899. Zur Anatomie von Solenomya togata Poli.
Zool. Jb., Abt. 2, 13: 89-170.

Sullivan, C.M. 1948. Bivalve larvae of Malpeque Bay, P.E.I.
Bull. Fish. Res. Bd. Can., 77: 1-36.

Theile, J. 1935. Handbuch der systematischen Weichtierkunde.
Teil 3, Classis Bivalvia.
Jena (G. Fischer).

Thorson, G. 1936. The larval development, growth and metabolism of Arctic marine bottom invertebrates, compared with those of other seas.
Medd. Grønl., 100: 1-155.

Winckworth, R. 1932. The British marine Mollusca.
J. Conchol., 19: 211-252.

Yonge, C.M. 1939. The protobranchiate Mollusca: a functional interpretation of their structure and evolution.
Phil. Trans. B, 230: 79-147.

_____ 1947. The pallial organs in the aspidobranch Gastropoda and their evolution throughout the Mollusca.
Phil. Trans. B, 232: 443-518.

_____ 1953. The monomyarian condition in the Lamellibranchia.
Trans. roy. Soc. Edinb., 62: 443-478.

_____ 1959a. The status of the Protobranchia in the bivalve Mollusca.
Proc. malacol. Soc. Lond. (in the Press).

_____ 1959b. Personal communciation.

APPENDIX I

Sub-Class Protobranchia - Family Nuculidae

Nucula sulcata Bronn

The prodissoconch is markedly 'D' shaped, the slightly concave hinge line breaking the curvature of the shell outline. The surface of the shell is shagreen-like (Fig. 4), bearing fine granulations, but its underlying texture is made up of concentric rectangular markings (Figs. 1 & 2).

The dissoconch continues to show the characteristic straight or slightly concave hinge line until, with the development of the umbone, the shell assumes a more rounded appearance dorsally. The shell is heavy and bears the close-set crescentic markings, radially disposed, which characterise the adult (Fig. 2). A typical post-larval shell of *N. sulcata* is shown in Figure 3.

Nucula turgida Marshall and Leckenby

The prodissoconch is egg-shaped; that is slightly pointed anteriorly and somewhat blunt posteriorly. The hinge line is convex, rather than concave, and continuous with the outline of the rest of the shell, resembling *N. delphinodonta* (Drew, 1901). The superficial texture of the shell resembles that of *N. sulcata* but lacks the underlying rectangular markings of the latter (Figs. 4, 5).

The dissoconch retains the same general shape as the prodissoconch and rapidly develops radial striations which remain prominent throughout its growth. At a length of approximately 1.2 mm. the inner margin of the shell becomes crenated. The shell

APPENDIX FIGURE 1

Nucula sulcata. Surface texture of prodissoconch showing ~~shagreen-like surface and~~ radially disposed rectangular markings.

X 800

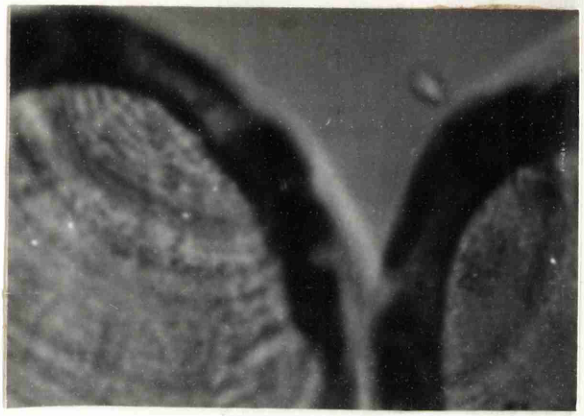
APPENDIX FIGURE 2

Nucula sulcata. Surface texture of early dissoconch showing radially disposed rectangular markings of prodissoconch (P) and crescentic markings of dissoconch (D).

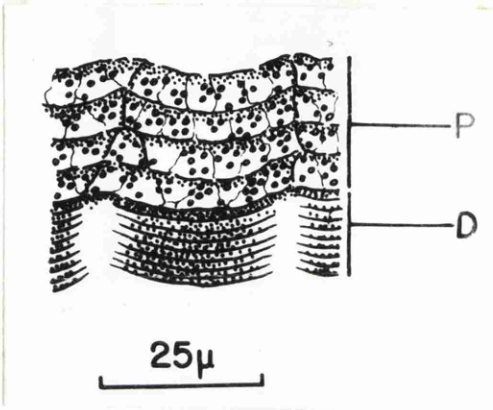
APPENDIX FIGURE 3

Nucula sulcata. Typical post-larval shell showing inner side of valves. The outline of the prodissoconch can be seen but the texture of the prodissoconch and dissoconch is not evident.

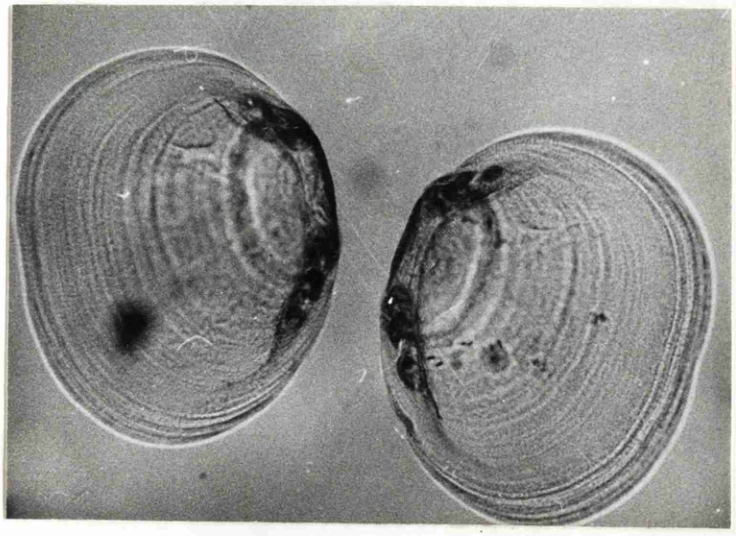
Size - 0.38 x 0.30 mm. X 250



APPENDIX FIGURE 1



APPENDIX FIGURE 2



APPENDIX FIGURE 3

APPENDIX FIGURE 4

Nucula turgida. Detail of surface texture of prodissoconch showing shagreen-like markings.

Size - 0.20 x 0.16 mm. X 800

APPENDIX FIGURE 5

Nucula turgida. Early post-larval shell, right valve, to show surface texture of prodissoconch.

Size - 0.20 x 0.16 mm. X 200

APPENDIX FIGURE 6

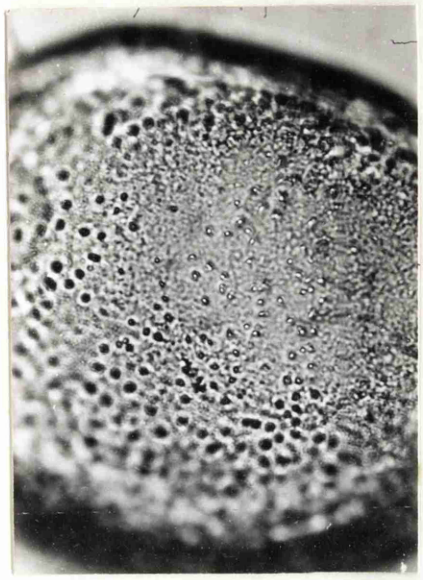
Nucula turgida. Hinge of right valve showing four taxodont teeth and central ligament.

Size 0.21 x 0.17 mm. X 800

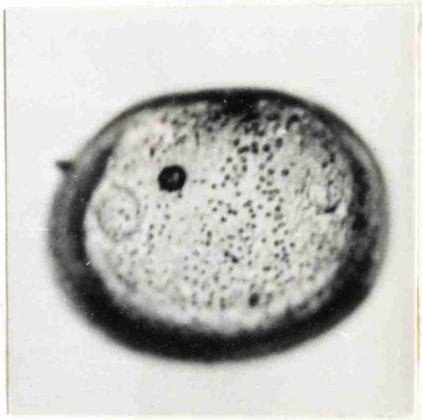
APPENDIX FIGURE 7

Nucula turgida. Right valve showing shape and texture of early dissoconch.

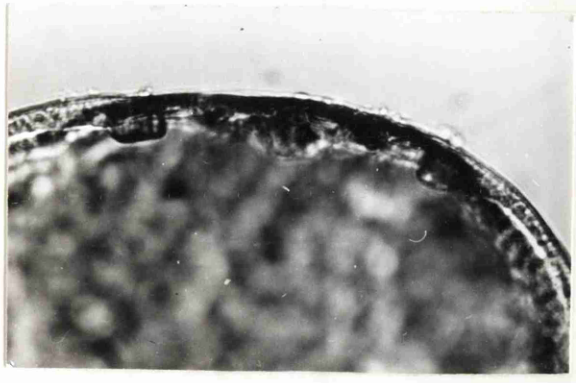
Size - 0.20 x 0.17 mm. X 200



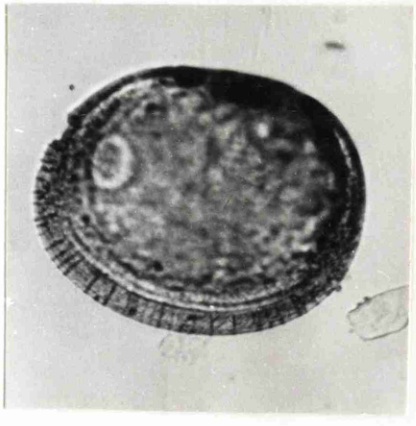
APPENDIX FIGURE 4



APPENDIX FIGURE 5



APPENDIX FIGURE 6



APPENDIX FIGURE 7

is intermediate in thickness between that of N. sulcata and N. turgida. Typical N. turgida shells are shown in Figures 7, 8, 10, and 11.

Nucula tenuis (Montagu)

The prodissoconch of N. tenuis was indistinguishable from that of N. turgida (Figs. 4, 5).

Initially the dissoconch resembles that of N. turgida (Fig. 7) but later the pointed anterior and truncated posterior ends become more accentuated (cf. Figs. 8, 9). Radial striations similar to those of N. turgida are present but are later dominated by the concentric markings which become progressively more conspicuous while the radial striations are rather weakly marked. The entire margin was retained in the largest specimens examined (approximately 4 mm.) and the shell is noticeably thinner and more delicate than that of N. turgida. The periostracum is glossy and olivaceous.

Allen (1954) found four of the five British species of Nucula listed by Winckworth (1932) in the Clyde Sea Area. N. sulcata and N. turgida are the most common (Part I, Fig. 1); while N. nucleus is found only in a few restricted areas, where the bottom is a coarse muddy gravel, such as Fairlie Channel and the Minnard Narrows in Loch Fyne. Since no townettings or trawl samples were taken in either area it is unlikely that this species would have been encountered in the collections. N. tenuis, the least common of the British species, overlaps the distribution of N. turgida and N. sulcata so it is probable that it would be taken along with

APPENDIX FIGURE 8

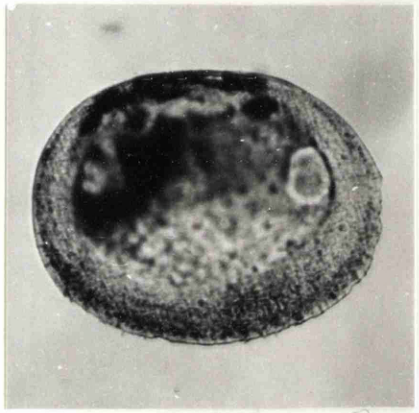
Nucula turgida. Left valve showing typical shape of early dissoconch.

Size 0.21 x 0.17 mm. X 200

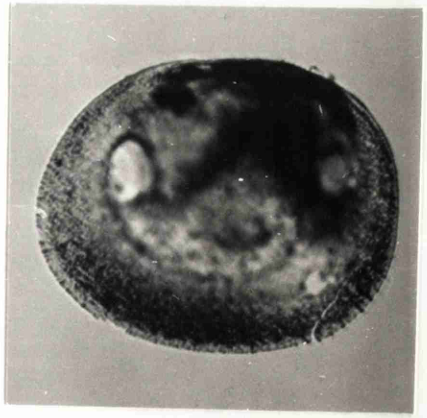
APPENDIX FIGURE 9

Nucula ~~turgida~~ tenuis. Right valve showing typical shape of early dissoconch.

Size - 0.22 x 0.18 mm. X 200



APPENDIX FIGURE 8



APPENDIX FIGURE 9

APPENDIX FIGURE 10

Nucula turgida. Left valve showing strong radial striations.

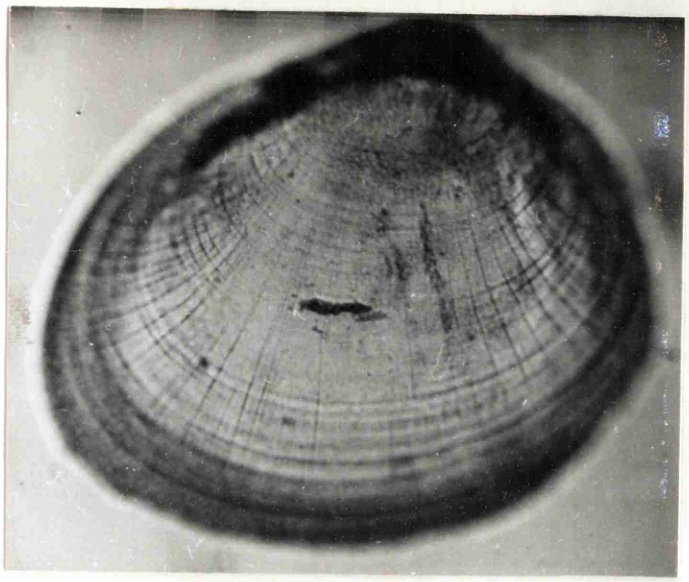
Size - 0.52 x 0.43 mm. X 150

APPENDIX FIGURE 11

Nucula turgida. Left valve showing typical shape, texture and internal crenated margin of shell.

(Black and white markings surrounding umbone and middle region of shell are artifacts due to preservation.)

Size - 1.4 x 11 mm. X 50



APPENDIX FIGURE 10

APPENDIX FIGURE 11

the latter. In addition, the entire margin and glossy periostracum clearly distinguish *N. tenuis* from *N. nucleus*.

PART II

SUB-CLASS LAMELLIBRANCHIA

INTRODUCTION

The investigations of Lacaze-Duthiers (1856) and Rice (1908) on Mytilus edulis, and Wasserloos (1911) and Herbers (1913) on fresh water lamellibranchs have contributed much to an understanding of the post-larval phases of lamellibranch development. However, since 1913 few additional contributions have been made, which is particularily regrettable in view of the functional interpretation of bivalve anatomy prevalent since the appearance in 1915 of Kellogg's paper on the ciliary mechanisms of bivalves. Moreover, in recent years advances in physiological and applied fields have rapidly outstripped those in the descriptive aspects of lamellibranch development. Biologists have made great progress in perfecting laboratory methods of rearing lamellibranch larvae (Bruce, Knight and Parke, 1940; Loosanoff and Davis, 1953; Loosanoff, Davis and Chanley, 1953 a & b; Loosanoff, 1954; Walne, 1956) and much has been learned of the environmental requirements of larval and post-larval stages. These methods are now being applied in large-scale culture techniques which will greatly increase shellfish production. Yet despite these advances, which have made it possible to rear all developmental stages in the laboratory, little attention has been directed to the biology of the newly metamorphosed spat. Many aspects of this problem urgently require investigation and while the present study is not of immediate practical value, it is hoped that it will increase the basic knowledge of post-larval development.

In the present investigation lamellibranch development is treated from the functional aspect, and is concerned solely with the feeding mechanisms during the post-larval period. Hence while emphasis is placed on the development of the ctenidia, supplementary observations on the palps, mantle and siphons are included to give a more complete understanding of the feeding mechanism. Moreover, in view of the detailed descriptions of post-larval development presented by Lacaze-Duthiers (1856), Rice (1908), Wasserloos (1911) and Herbers (1913), this study is presented from a comparative aspect, and post-larvae of a wide variety of species have been examined. No attempt is made to give a detailed account of development in any one species, but rather the similarities and differences in post-larval feeding mechanisms are stressed.

TERMINOLOGY

Since current terminology pertaining to the morphology and ciliary currents of the ctenidia is inconsistent and often confusing, it seemed advisable to adopt new terms in some instances and to restrict the use of others. Moreover, since a clear distinction must be made between ontogeny and phylogeny, certain terms are used exclusively with reference to the former.

Morphology

The lamellibranch ctenidium consists of a longitudinal axis bearing on either side a series of filaments, those on one side comprising the outer demibranch (Fig. 1, OD) while those

FIGURE 1

Diagrammatic cross section through a typical lamellibranch to show the position of proximal and distal lamellae of the inner and outer demibranchs. Dorsal and ventral frontal ciliary currents are illustrated by arrows on the right ctenidium.

LEGEND: CA - ctenidial axis, DFC - dorsal frontal ciliary current, DL - distal lamellae, F - foot, ID - inner demibranch, M - mantle, OD - outer demibranch, PL - proximal lamellae, VFC - ventral frontal ciliary current.

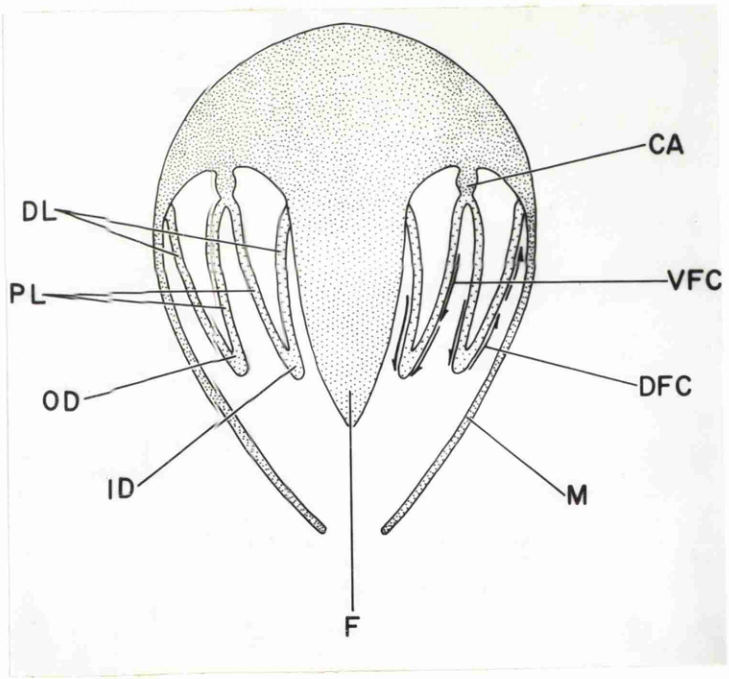


FIGURE 1

on the other make up the inner demibranch (ID). Adjacent filaments are united by ciliary or tissue junctions (filibranch and eulamellibranch conditions). In shape the filaments are elongate and bent to form a 'V' so that each demibranch has two surfaces which are named, with reference to the ctenidial axis, the 'proximal' (PL) and 'distal' (DL) lamellae.

The notation used by Wasserloos (1911) is followed here: filaments are numbered from anterior to posterior and designated as F_0 to F_n (Fig. 2 & 3). Filament F_0 possesses only one lateral surface, the other being fused with the body wall. The interfilamentary spaces are also numbered in a similar fashion; thus O_1 represents the first ostium or interfilamentary space between filaments F_0 and F_1 (Fig. 2 & 3).

Ciliary Currents

The frontal currents are described with respect to the orientation of the ctenidium in the heteromyarian Anisomyaria and in the Eulamellibranchia, where the ctenidial axis is dorsal and the demibranchs suspended from the axis in the dorso-ventral plane. Thus on the proximal lamella frontal currents directed towards the axis are designated as 'dorsal', those towards the free ventral margin as 'ventral'; on the distal lamella currents travelling to the free dorsal margin are 'dorsal', those to the ventral margin 'ventral' (Fig. 1, DFC & VFC). While these terms are not strictly applicable to the monomyarian Anisomyaria, they have been retained for the sake of simplicity. All ciliary currents travelling towards the mouth are 'adoral', those

directed away from the mouth are referred to as 'rejection' on the ctenidia and palps, but 'recurrent' on the mantle.

Development

'Primary' and 'secondary' refer to the sequence in which the lamellae or other structures appear in ontogeny. The processes of 'reflection' and 'perforation' are applicable only to ontogeny and have no phylogenetic implications.

NOMENCLATURE AND CLASSIFICATION

The nomenclature used is that of Winckworth (1932, 1951). The classification followed is that proposed by Yonge (1959) in which the Class Bivalvia is divided into two Sub-Classes, Protobranchia and Lamellibranchia.

REVIEW OF SALIENT FEATURES OF POST-LARVAL DEVELOPMENT

Ctenidial Development

Wasserloos (1911) gives a critical review of the work on ctenidial development in bivalves up to 1911, while the genesis of the molluscan gill is outlined by Raven (1958). It is sufficient therefore to emphasize those features of ctenidial development which are particularily relevant to this study.

The ctenidial anlage consists of a longitudinal ridge, attached along the line of union between the mantle and body wall, which is differentiated from anterior to posterior to form the proximal lamella of the inner demibranch. In lamellibranchs with

veliger larvae this process is initiated during the larval period, but the major portion of ctenidial development takes place during post-larval life. The inner demibranch appears first and its distal lamella is differentiated when development of the proximal lamella is fairly well advanced.

Proximal Lamella of the Inner Demibranch

Differentiation of the anlage may be accomplished by one of two methods: the 'papilla' method or the 'fold' method. In the former case, as described for Mytilus edulis by Lacaze-Duthiers (1856), the anlage is divided ventrally into a row of papillae attached dorsally to the ctenidial axis (Fig. 2, P). As they elongate their distal ends enlarge (Fig. 2, CP) and are secondarily fused with one another to form a marginal bridge (MB). In the fold method, described by Wasserloos (1911) for Cyclas cornea, the original ridge grows out into a fold which becomes perforated to form ostia (Fig. 3, O); the intervening filaments are never free from one another distally, the marginal bridge being here a primary and not a secondary structure. Whatever its origin, the marginal bridge grows medially, then dorsally. Its attachments to the lateral walls of the foot anteriorly, and to its counterpart from the opposite inner demibranch posteriorly, serve to partition the mantle cavity into supra and infra-branchial chambers.

Between 1856 and 1911 numerous descriptions of the early phases of ctenidial development appeared, some supporting the fold method and others confirming Lacaze-Duthiers' (1856) observations. As some workers inadvertently described stages somewhat later than the anlage, much confusion ensued, and it was not until 1911 that the

FIGURE 2

Papilla method of ctenidial differentiation as described by Lacaze-Duthiers (1856) for Mytilus edulis. Since the ctenidium is differentiated from anterior to posterior, the sequence of events may be seen by reading the diagram from left to right.

FIGURE 3

Fold method of ctenidial differentiation as described by Wasserloos (1911) for Cyclas cornea. As in Figure 2 the sequence of events may be seen by reading the diagram from left to right.

LEGEND: A - anlage of ctenidium, CA - ctenidial axis, CP - capitulum of filament, F_0 to F_4 - filaments, G - groove representing initial stage in formation of ostium, I - invagination formed as perforation of ostium begins, MB - marginal bridge, O_1 to O_4 - ostia or interfilamentary spaces, P - papilla.

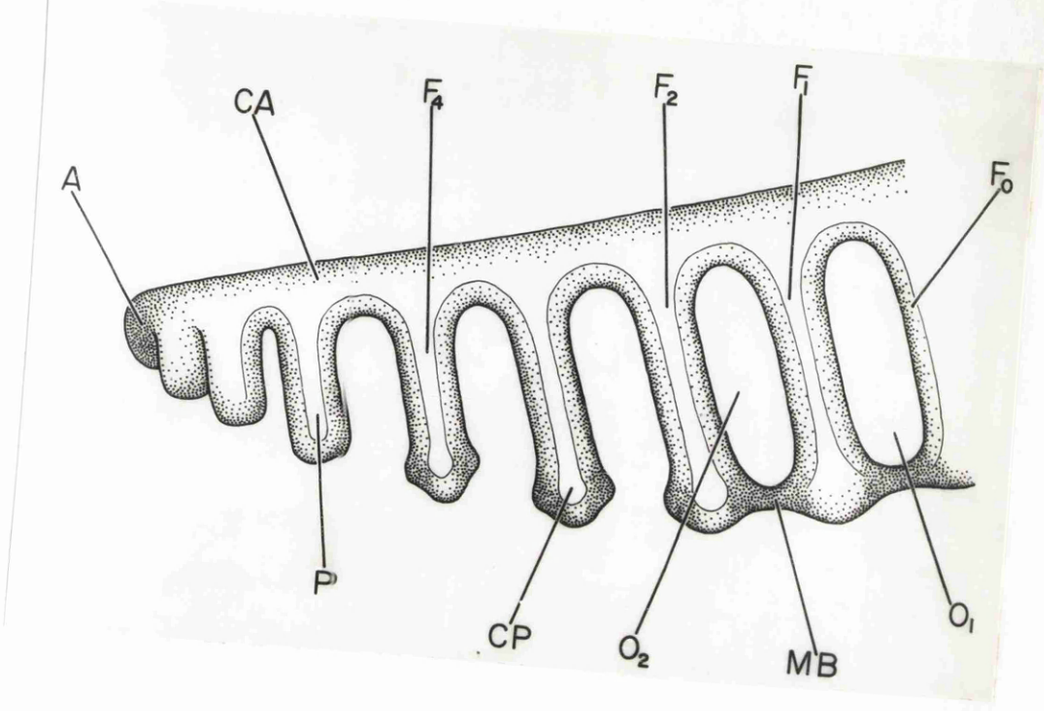


FIGURE 2

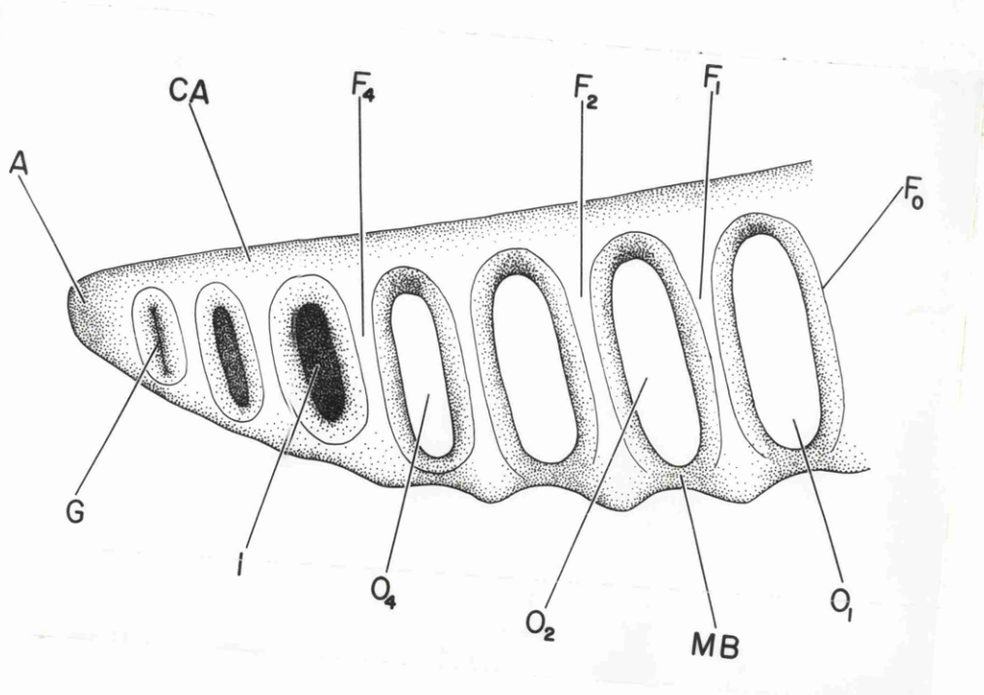


FIGURE 3

controversy was resolved when Wasserloos showed conclusively that both methods were valid.

Distal Lamella of the Inner Demibranch

Both Lacaze-Duthiers (1856), for Mytilus, and Wasserloos (1911), for Cyclas, described the development of the distal lamella of the inner demibranch as occurring by perforation of the marginal bridge (Fig. 4, Type I 4 & 5, Type II 4 a & 5 a). However, while Wasserloos agreed with Harms (1909) that in the Unionidae the filaments of the proximal lamella remain free distally (Fig. 4, Type III), he was skeptical of the latter's assertion that the filaments are reflected in the formation of the distal lamella (Fig. 4, Type III 4). Herbers (1913) disagreed with both earlier workers in maintaining that a marginal bridge is formed, but confirmed Harms' observations of the reflection of the proximal lamella to form the distal (Fig. 4, Type II 4b). Herbers stated that reflection of the proximal lamella to form the distal brings the marginal bridge to the free dorsal margin of the distal lamella Fig. 4, Type II 4 b).

Outer Demibranch

While Rice (1908) agreed with Lacaze-Duthiers (1856) that in Mytilus the first filaments of the outer demibranch are differentiated midway along the ctenidial axis, he discredited the latter's observations that new filaments are added both anteriorly and posteriorly from the middle. Rice maintained that addition of filaments anteriorly, if it occurs at all, is confined to the initial stages of development of the outer demibranch. In other respects Herbers (1913),

FIGURE 4

Diagram to show the successive steps in three types of ctenidial differentiation.

Type I - the fold method described by Wasserloos (1911) for Cyclas cornea.

Type II a - the papilla method described by Lacaze-Duthiers (1856) for Mytilus edulis.

Type II b - the papilla method described by Herbers (1913) for the Unionidae.

Type III - the papilla method described by Jackson (1890) for Anomia.

In each case the ctenidium is represented as seen in cross section.

Ctenidial axis is shown as solid black area.

Regions of continuity between adjacent filaments are shown stippled.

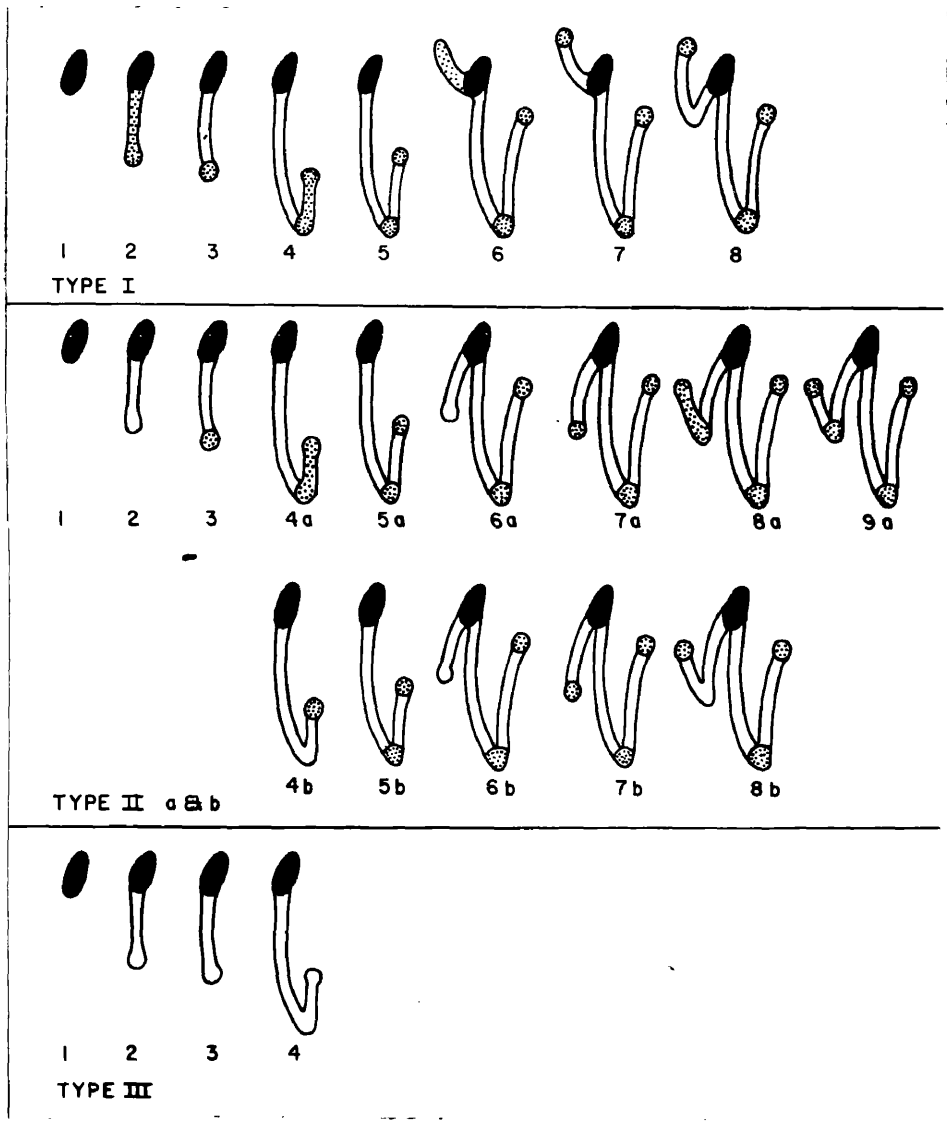

1 2 3 4 5 6 7 8
TYPE I
1 2 3 4a 5a 6a 7a 8a 9a
4b 5b 6b 7b 8b
TYPE II a & b
1 2 3 4
TYPE III

FIGURE 4

Lacaze-Duthiers and Rice found development of the outer demibranch to be similar to that of the inner.

In Cyclas, Calyculina and Pisidium Wasserloos (1911) observed a different method of formation of the outer demibranch. Initial differentiation is by the fold method, but when first formed the filaments are directed dorsally, instead of ventrally, and consist of the distal, rather than the proximal, lamella (Fig. 4, Type I 6 & 7). The proximal lamella is formed secondarily by outward, and later downward, growth of the portions of the filaments adjacent to the ctenidial axis (Fig. 4, Type I 8).

Later Differentiation from the Anlage

Rice (1908) observed that later differentiation of filaments from the anlage in Mytilus occurs simultaneously in the inner and outer demibranchs and departs from the initial pattern. Transverse ridges appear in the ctenidial axis; these become divided into two lobes representing inner and outer demibranchs (Fig. 5 B). Subsequently, each lobe "becomes perforated at its proximal end, thus becoming resolved into the two branches of a U-shaped filament, identical in form with those first developed" (Rice, 1905) (Fig. 5 C). All intermediate stages between the two methods of differentiation are found to occur in a sequence from anterior to posterior, so that the change from the first to the second method of differentiation is gradual. Later stages of ctenidial differentiation in Anomia, Arca, Modiola and Mya show the same condensed development, and Rice was led to the conclusion that this process is probably typical of all lamellibranchs.

FIGURE 5

Diagram to show three successive steps in condensed type of ctenidial differentiation described by Rice (1905 and 1908) for the late post-larval development of many lamellibranchs. Ctenidium is represented as seen in cross section. (Diagram is modified from Rice, 1908.)

A. Ctenidial anlage.

B. Anlage has divided into two lobes representing the inner and outer demibranchs.

C. A groove on either side of the ctenidial axis has divided each demibranch into proximal and distal lamellae.

LEGEND: CA - ctenidial axis, DL - distal lamella, ID - inner demibranch, OD - outer demibranch, PL - proximal lamella.

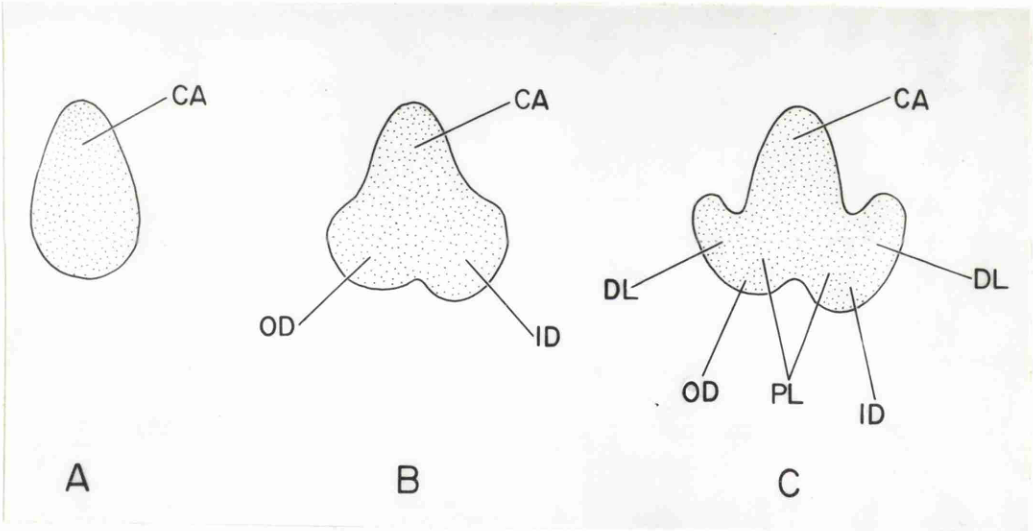


FIGURE 5

Types of Ctenidial Development

Thus, a review of the literature up to 1913 shows strong evidence in favour of three distinct methods of ctenidial formation, despite the disagreement as to the method of formation of the distal lamella in Type II. These may be summarized as follows.

Type I The ctenidial anlage is differentiated by the fold method in Cyclas, Calyculina, Pisidium (Wasserloos, 1911), Jousseaumiella (Bourne, 1906), Scioberetia (Bernard, 1895) --- fresh water forms which incubate their embryos in a parental brood pouch --- and in Teredo (Hatschek, 1880; Sigerfoos, 1896) --- a marine genus with veliger larvae. In the first three genera differentiation of the distal lamella of the inner demibranch is by perforation of the marginal bridge; the outer demibranch is represented initially by the filaments of the distal lamella which are directed dorsally (Fig. 4, Type I). Only the formation of the proximal lamella of the inner demibranch has been described for Jousseaumiella, Scioberetia and Teredo.

Type II The ctenidial anlage is differentiated by the papilla method in Dreissensia (Wasserloos, 1911), Mytilus (Lacaze-Duthiers, 1856; Rice, 1908), Mya (Rice, 1908) --- all having free swimming veligers --- and in the Unionidae (Harms, 1909; Wasserloos, 1911; Herbers, 1913) --- a fresh water family in which the larvae are parasitic glochidia. While Wasserloos and Harms held that the filaments remain free in the Unionidae, Herbers stated that their capitulae

unite to form the marginal bridge as described for the other three genera. Whereas Lacaze-Duthiers and Wasserloos recorded perforation of the marginal bridge to form the distal lamella in Mytilus and Dreissensia respectively (Fig. 4, Type II a), Herbers maintained that in Anodonta the filaments of the proximal lamella are reflected to form the distal lamella (Fig. 4, Type II b). Formation of the outer demibranch has been described by Lacaze-Duthiers and Herbers only, and is said to be identical to the formation of the inner in each case (Fig. 4, Type II, cf. 6 to 8 a with 6 to 9 b).

Type III The ctenidial anlage is differentiated by the papilla method and the ends of the filaments remain free ventrally in Nucula and Yoldia (Drew, 1898a, 1899b, 1901) --- protobranchs in which there is no differentiation of the demibranchs into proximal and distal lamellae --- and also in Anomia (Jackson, 1890). Jackson indicated that the free filaments of Anomia are reflected to form the distal lamella of the inner demibranch (Fig. 4, Type III). Harms' (1909) description of the Unionidae would also place them in this group, were his evidence not contradicted by the later work of Herbers (1913).

Palpal Development

Aside from ctenidial development few aspects of organogenesis are recorded for the post-larva.

In the trochophore larva of Cyclas, Wasserloos (1911) described the palps as arising from a ciliated area surrounding the mouth; since there is no veliger stage they develop directly. The upper palps originate first as triangular lobes projecting over the mouth on each side of the body; later the lower palps arise in a similar* margin of the ctenidium, so that the latter is in direct contact with the apposed ciliated faces of both palps.

Just as the mode of differentiation of the ctenidia aroused much controversy amongst early workers, much debate has centred around the origin of the palps in lamellibranchs possessing veliger larvae. The belief of Loven (1848) and Field (1922) that the palps arise from the velum has been confirmed by the more recent work of Cole (1938) on Ostrea edulis in which the upper palps are formed from the apical plate of the velum. Quayle (1952) affirmed the same origin in Venerupis.

Siphonal Development

In Cyclas (Wasserloos, 1911) the siphons arise by posterior fusion of the mantle lobes; the first junction is formed dorsal to the ctenidial axes and represents the siphonal septum. A short distance dorsal to this septum the mantle lobes fuse, delimiting an exhalant aperture. Small papillae appear on the mantle edge ventral to the septum and their fusion forms the inhalant aperture. The mantle surrounding the two apertures elongates posteriorly to form the two siphons which subsequently fuse along their adjacent surfaces.

Quayle (1952) has given the most complete description of siphon development. In Venerupis pullastra "the primary exhalant

*manner. A row of cilia extends posteriorly from the palps to the ventral

siphon develops from the inner lobes of the mantle edge as a thin-walled membraneous sac." Quayle also observed a similar siphon in living Mya spat which was "rapidly extruded and retracted, much like a proboscis." Ventral to the siphonal septum two series of tentacles develop by a grooving of the inner folds of the mantle; "the upper and lower ends of the two groups of tentacles fuse to form the margins of the inhalant siphon." The tentacles of the middle mantle fold appear later.

MATERIALS AND METHODS

Collection of Living Material

The majority of post-larvae used for this study were obtained by laboratory rearing of late larvae collected in fine plankton tows. Deep tows taken off Garroch Head (Part I, Fig. 1, Station 1) offered the greatest number and variety of veligers. Such townettings were usually taken twice weekly and continued throughout the year. Occasionally, tows from Fairlie Channel (Station 2) were also examined.

Later stages of development were provided by spat collected in the field. Mya arenaria, Venerupis pullastra and several species of Tellina and Venus were taken in the intertidal zones of Kames and Balloch Bays (Stations 3 & 4) on the Isle of Cumbrae. Pectinidae and Anomiidae were obtained from hydroids collected in Fairlie Channel (Station 2). Mysella bidentata, Mya arenaria and Hiatella arctica were found amongst the byssal threads of the nests of Lima hians. Mud samples from the Cumbrae-Bute Deep (Station 5) yielded post-larvae of Abra spp. and Thracia sp. Spisula solidissima were collected in abundance in the intertidal zone of a sandy beach near Charlottetown, Prince Edward Island, Canada. Spat of Ostrea edulis were examined at Conway, Wales and of Crassostrea viriginica at Ellerslie, Prince Edward Island, Canada.

Culture Methods

Larvae were reared in petri dishes (2" in diameter) covered by glass plates, or in glass shell vials (2½" high by 1½" in

diameter) provided with corks, and were kept partially immersed in running sea water. To minimize bacterial growth, penicillin and streptomycin (50 mgm. of each per litre) were added to sea water, which had been passed through a Berkfield Filter. μ-flagellates, Isochrysis galbana or Pyramimonas grossii* at a concentration of 50 cells per $mm.^3$ were used as food. The post-larvae were transferred to clean dishes with fresh sea water and food every three to four days, Although spat collected in the field required less frequent attention, they were maintained in the same way. Sand, sterilized by boiling in distilled water, was added to culture dishes containing Lima hians and burrowing species; mudstone** was used for cultures of Zirfaea crispata.

A fungus growth which accumulated on the shells of the post-larvae posed a considerable problem. When the mycelium entirely surrounded the young spat, reducing water circulation, it caused considerable mortality. Manual removal of the mycelium was laborious and inevitably left small traces of the fungus to begin a new growth. Eventually, the contamination was traced to the flagellate cultures where it appeared to persist in the form of spores; mycelial growth never appeared in such cultures unless they were several months old.

No attempt was made to rear embryos from artificially fertilized eggs. Although this would have greatly facilitated identification, it was impractical to rear a large number of species through the larval phases to metamorphosis.

---

* These cultures were kindly supplied by Dr. Mary Parke, Marine Biological Laboratory, Plymouth.

** The mudstone was procured through the kindness of Dr. J.J. Dodd, St. Andrews.

Examination of Living Material

Living post-larvae were examined in welled slides under a compound microscope. Sketches of the organs of the mantle cavity, particularly the ctenidia, and of the siphons were made at various stages of development. Ciliary currents were demonstrated by use of the colloidal carbon suspension 'Aquadag'.

In most newly metamorphosed spat the shell is sufficiently transparent to permit observation of the whole animal, but in later stages the shell of many species becomes opaque and dissections were necessary to elucidate further details of the ciliary currents in the mantle cavity.

Whenever the shells of the post-larvae were sufficiently transparent to reveal anatomical details, drawings were supplemented by photographs. Speed was essential in photography as the microscope light seemed to intensify the activity of the specimens. Thus, Kodak Super XX was found preferable to Kodak Panatomic X, and the slight loss of detail was more than compensated by the shorter exposure required. Panatomic X was employed in photographing the siphons where it showed details not apparent in photomicrographs made with Super XX. All photographs were taken using a microscope magnification of 150 unless otherwise noted.

Study of Preserved Material

Specimens were relaxed with propylene phenoxetol (Owen, 1955) before fixation. Post-larvae were very sensitive to any disturbance and the narcotizing solution (0.8 to 1.3 per cent in sea water) had to be introduced into the vial containing the specimens by

means of a wick of filter paper. The time required for narcotization varied from 30 to 90 minutes and although the results were not consistent no better method was found. A modified Bouin-Duboscq Fluid (Atkins, 1937c) gave the most satisfactory fixation.

Whole mounts of specimens stained in borax carmine were prepared for gross morphological studies. Other specimens stained in borax carmine were embedded in ester-wax (Steedman, 1947) and sectioned by hand under a stereoscopic microscope. Such sections, mounted in piccolyte, frequently revealed details of ctenidial structure to better advantage than thinner serial sections. However, some specimens embedded in 60 to 62° C. Fischer Tissuemat were serially sectioned at thicknesses of 2 to 5 μ and stained in Heidenhain's iron haematoxylin, alcian blue 8GN (Steedman, 1950) and orange G in clove oil. These were used only for fine details not shown by other methods.

Identification

Veliger larvae were identified by the method devised by Rees (1950), and excellent photomicrographs of the larval shells of all British species studied here, with the exception of Ostrea edulis, are to be found in his paper. Larvae of the two North American species, Crassostrea virginica and Spisula solidissima, have been described by Sullivan (1948). However, in certain instances where subsequent post-larval development showed Rees' identification to be false, notably Monia squama, Kellia suborbicularis, Mya arenaria and others, reference is made to the correct photomicrograph in Rees' paper. In cases where positive identification could not be made the specific name is given in parentheses, e.g. Chlamys (varia), while no specific name is given for

types which could only be assigned with certainty to a given genus, e.g. Venus sp. and Tellina sp.

POST-LARVAL DEVELOPMENT

Anomiidae

Two species of anomid post-larvae, Monia squama (Gmelin) and Heteranomia squamula (Linné), were examined. Monia squama ('Pectinid B', Rees, 1950)* veligers occurred in the plankton tows in October and November but were never abundant. Only 12 of the 32 veligers collected metamorphosed in laboratory cultures. The late larvae are eyed and have a conspicuous red pigment spot over the ctenidial axis on the right side; metamorphosis occurs at a length of 240 μ (Fig. 6). Heteranomia squamula (Rees, 1950)* was common in plankton tows from June to November. Metamorphosis occurs at a length of 270 μ; the late veligers are eyed but have no red pigment spot. The velar cilia of neither species exhibited a metachronal wave.

Ctenidial Development

Due to the scarcity of Monia larvae, ctenidial development is described for Heteranomia. However, as far as could be determined development of the ctenidia is initially similar in the two species (cf. Fig. 7 & 8), but in Heteranomia the demibranchs are never differentiated into proximal and distal lamellae. The development of these lamellae in Monia is probably similar to that of the pectinids described in the next section.

---

* Quayle (personal communication), while working at Millport, came independently to the same conclusion regarding the identification of the veligers of Heteranomia squamula and Monia squama, and the author is indebted to him for confirming the identification of these two species.

FIGURE 6

Monia squama. Mature veliger larva viewed from right side. This larva is described by Rees (1950) as 'Pectinid B'. The characteristic red pigment spot is not visible here but is clearly shown in Figures 14 and 15.

Length - 240 μ.

FIGURE 7

Heteranomia squamula. Early post-larva viewed from left side and showing alternation of the ctenidial filaments in the mid-ventral line.

Length - 340 μ.

FIGURE 8

Monia squama. Early post-larva viewed from left side and showing alternation of ctenidial filaments in the mid-ventral line.

Length - 280 μ.

All x 130

FIGURE 6

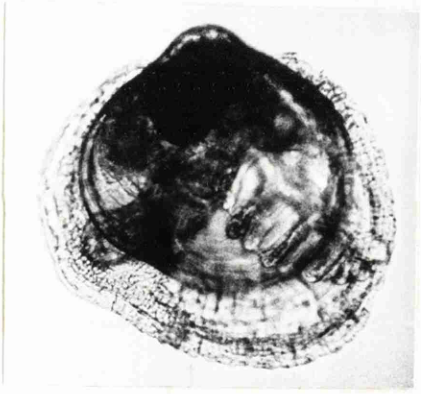


FIGURE 7

FIGURE 8

At metamorphosis Heteranomia has 3 ciliated ctenidial filaments in the inner demibranch (Fig. 9, CT); these and subsequent filaments are formed by the papilla method. Lateral cilia, appearing soon after the formation of the first filaments, are active prior to metamorphosis; micro-latero-frontal and probably frontal cilia, while developing after the laterals, are also present in the late veliger. The ctenidial anlagen are separate.

Forward rotation of the body, following loss of the velum, leaves the ctenidia free in the posterior mantle cavity. The short filaments of each demibranch are then seen to be connected at their ventral tips by long interlocking cilia, the interfilamentary junctions (Fig. 11 & 12, IFJ), but never become united by a marginal bridge. The demibranchs remain separate in the newly metamorphosed spat; but as the filaments elongate they also curve medially, and the tips of the filaments of each demibranch come to lie in the midline where they alternate with those of the opposite demibranch (Fig. 10, 11 & 12). Interctenidial junctions (Fig. 11 & 12, ICJ) are formed by the interlocking of cilia on the anterior and posterior faces of the tip of each filament, with cilia of filaments of the opposite demibranch immediately anterior and posterior to it. The cilia of these interctenidial junctions differ from those of the interfilamentary junctions in being much shorter (Fig. 12). The right demibranch is slightly distorted anteriorly by the displacement of the first filament by the foot and byssal muscle which lie between it and the palps. The tips of the filaments are never connected to the foot, but the interfilamentary and interctenidial junctions unite the filaments of both demibranchs into a single unit lying posterior to the foot (Fig. 10).

FIGURE 9

Heteranomia squamula. Mature veliger larva viewed from right side to show position of ctenidium overlying the foot prior to metamorphosis.

Length - 250 μ.

LEGEND: AA - anterior adductor muscle, CT - ctenidium, DD - digestive diverticula, F - foot, MO - mouth, PA - posterior adductor muscle, PS - pedal sinus of left valve, RE - rectum, V - velum.

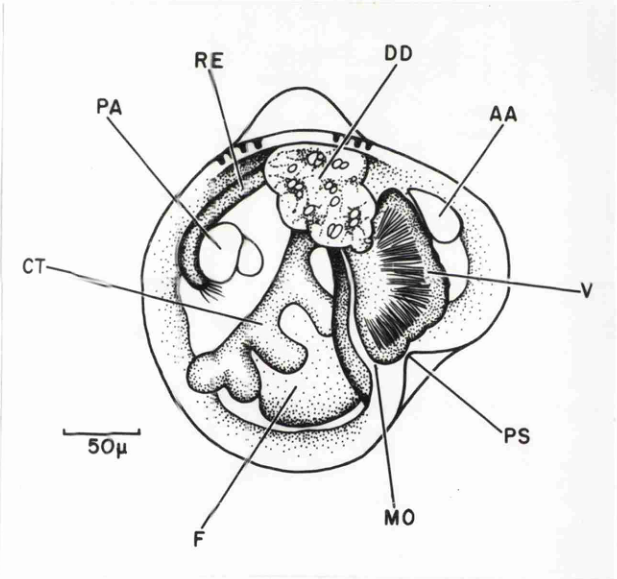


FIGURE 9

FIGURE 10

Heteranomia squamula. Mid post-larva showing alternation of ctenidial filaments in midline as seen in ventral view.

Length - 530 μ. x 130

FIGURE .11

Heteranomia squamula. Ctenidial filaments of post-larva in Figure 10 but photographed with microscope magnification of 450 to show interfilamentary and interctenidial ciliary junctions as seen in ventral view. x 600

FIGURE 12

Heteranomia squamula. Diagrammatic representation of Figure 11 to show interfilamentary (IFJ) and interctenidial (ICJ) ciliary junctions.

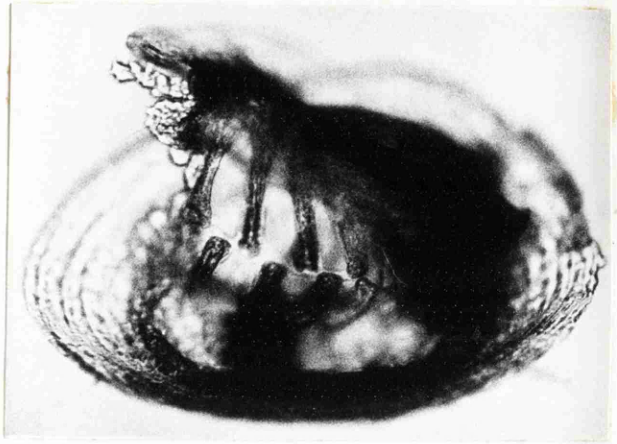


FIGURE 10

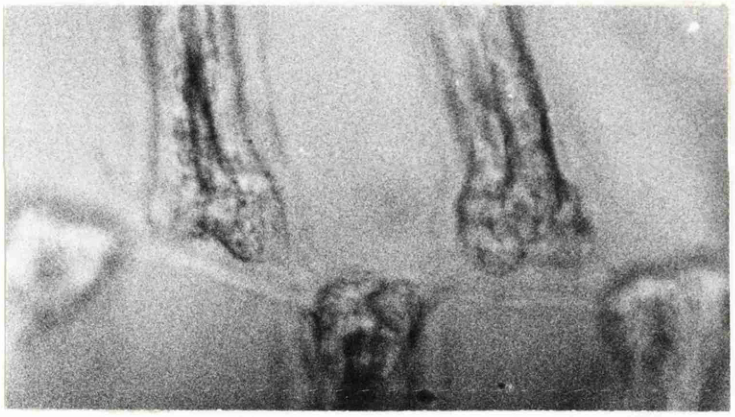


FIGURE 11

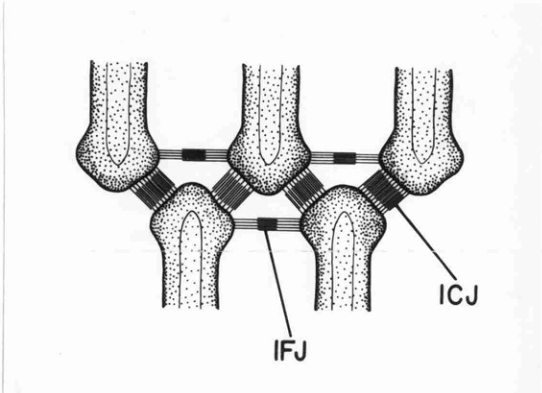


FIGURE 12

The frontal ciliary currents on all filaments are dorsal (Fig. 13). An adoral ciliary current (Fig. 13, AAT) extends along a distinct groove in the ctenidial axis; anteriorly this axial adoral tract curves ventrally to meet the proximal adoral tract (Fig. 13, PAT) leading to the palps. This proximal tract lies on the body wall anterior to filament F_0. Initially, the ctenidial axis remains straight and nearly parallel to the anteroposterior axis of the body (Fig. 13 & 14), but later in development it becomes curved, especially on the right side (Fig. 18). The alternation of filaments in the midline increases the width of the interfilamentary spaces ventrally so that the filaments radiate slightly from the axes.

Medial to the axial adoral groove is a longitudinal muscle whose contraction causes approximation of the gill filaments (Fig. 16, AR). The filaments also appear to have muscles, running along their anterior faces, which usually contract simultaneously with the axial retractor to bend the filaments slightly in the mid-region (Fig. 15). Extension of the axis, and the ctenidium as a whole, is produced by relaxation of these muscles accompanied by the dilation of a longitudinal blood vessel lying dorsal to the axial groove (Fig. 16, AB). Movement of plasma cells in this region was clearly visible in living specimens.

Antagonistic frontal ciliary currents were first detected in specimens approximately 900 μ in length with 9 or 10 filaments in each ctenidium (Fig. 17). At this stage a tract of coarser frontal cilia was apparent along the posterior margin of each filament. The beat of these cilia produced a ventral ciliary current which was

FIGURE 13

Heteranomia squamula. Mid post-larva viewed from right side to show the ciliary and water currents of the mantle cavity. Note particularly the close association between the recurrent path (RP) of the mantle and the ventral edge of the inner demibranch. Length - 740 μ.

Large plain arrows - inhalant and exhalant water currents.

Small plain arrows - frontal and adoral ciliary currents of ctenidium.

Feathered double arrows - recurrent path of mantle.

LEGEND: AAT - axial adoral tract, DD - digestive diverticula, F - foot, F_1L - first filament of left ctenidium, F_1R - first filament of right ctenidium, LM - left mantle margin, LV - left shell valve, ML - pallial lobe, PA - posterior adductor muscle, PAT - proximal adoral tract, PD - prodissoconch, PTR - pallial tentacle of right mantle, RE - rectum, RM - right mantle margin, RP - recurrent path of mantle, RV - right shell valve, RX - rejection point of recurrent path, UP - upper palp.

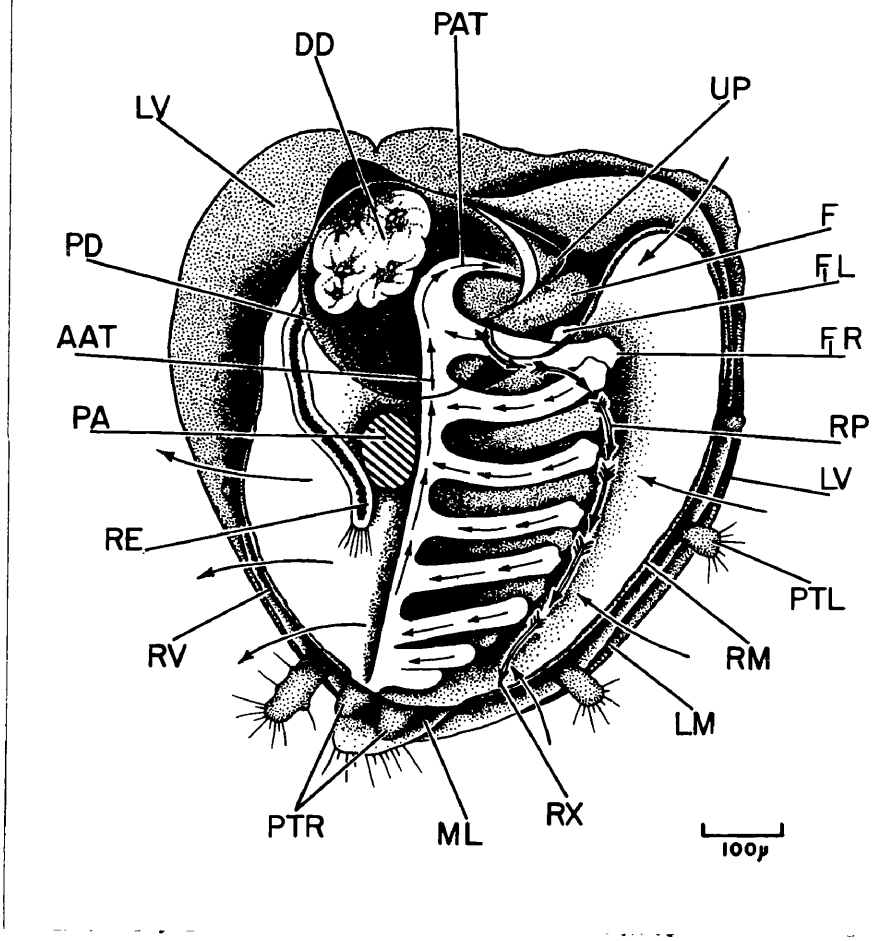


FIGURE 13

FIGURE 14

Monia squama. Mid post-larva with ctenidia fully extended as viewed from right side. This condition is typically adopted during feeding and may be compared with that shown in Figure 15. Note also the prominent red pigment spot just dorsal to the ctenidial axis.

Length - 620 μ x 130

FIGURE 15

Monia squama. Same post-larva as Figure 14 with ctenidia contracted.

Length - 620 μ x 130

FIGURE 14

FIGURE 15

FIGURE 16

Diagram to show typical structure of the ctenidial axis in the Anomiidae and Pectinidae. The ctenidial axis, adjoining section of mantle and dorsal portion of a filament are viewed from the antero-medial aspect. The subaxial tract (SAT), on the medial surface of the mantle, and the accompanying adoral water current (discontinuous arrows), between the subaxial tract and the axial adoral tract (AAT), are found only in the Pectinidae and not in the Anomiidae.

Large plain arrows	-	adoral ciliary currents.
Small plain arrows	-	dorsal frontal ciliary current of filament.
Discontinuous arrows	-	water current produced by combined action of cilia of the axial adoral and subaxial tracts.

LEGEND: AAT - axial adoral tract, AB - axial blood vessel, AR - axial retractor muscle, CA - ctenidial axis, DFC - dorsal frontal ciliary current, F_N - dorsal portion of a filament of the inner demibranch, M - mantle, SAT - subaxial tract of mantle.

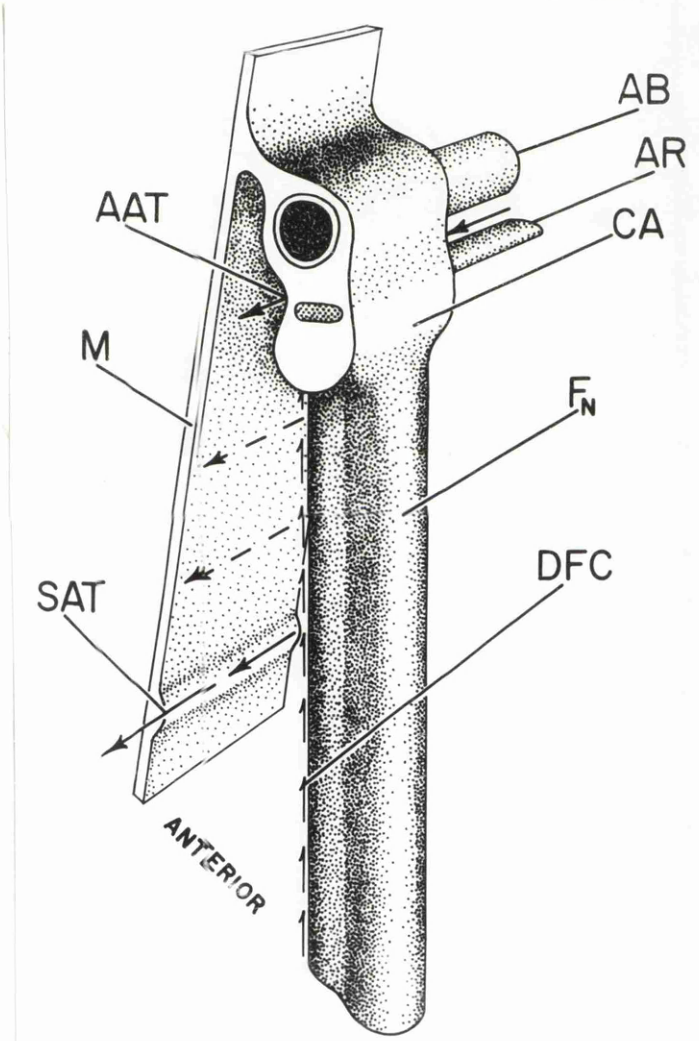


FIGURE 16

evident only when excessive particulate matter entered the inhalant stream. Thus the cilia appeared to be active only on stimulation and in experiments using dilute 'Aquadag' they were active only when a large particle impinged on the frontal surface of the filament. These coarse cilia were never observed on the dorsal portions of the filaments. Coincident with the appearance of the ventral frontal tracts, a rejection tract is developed along the tips of the filaments of the inner demibranchs (Fig. 17, MRT).

The outer demibranch begins to form at the same time. The smallest specimen in which it was observed measured 920 μ in length but already had 6 short filaments representing the outer demibranch (Fig. 17). These filaments grow ventrally from the ctenidial axis to overlie the filaments of the inner demibranch (Fig. 17 & 18). The most anterior filament of the outer demibranch forms at the level of the 5th filament of the inner demibranch and as the ctenidium extends posteriorly both demibranchs acquire new filaments simultaneously. The frontal ciliary currents of the outer demibranch are initally dorsal. As only the early stages in the development of this demibranch were studied, the formation of ventral frontal ciliary tracts was not observed; presumably they appear at a later stage.

Pallial Development

In the young post-larva the mantle edge develops small papillae bearing cirri (Fig. 13, PTL & PTR) which later become the pallial tentacles (Fig. 17, PT). At a point opposite the posterior end of the ctenidial axis the mantle of each side forms a lobe, the two lobes projecting medially to separate the inhalant and exhalant streams

FIGURE 17

Heteranomia squamula. Late post-larva viewed from right side to show the ciliary and water currents of the mantle cavity. Note, in comparison to Figure 13, the altered position of the recurrent path (RP) of the mantle and the presence of ventral frontal ciliary currents (discontinuous arrows) and of the marginal rejection tract (MRT) on the ctenidium.

Length - 920 μ.

Large plain arrows	- inhalant and exhalant water currents.
Small plain arrows	- dorsal frontal and adoral ciliary currents of inner demibranch.*
Discontinuous arrows	- ventral frontal ciliary currents; cilia active only on stimulation.
Double arrows	- ciliary currents leading away from mouth.
Feathered arrows	- ciliary currents of mantle.

* (Frontal ciliary currents on filaments of outer demibranch are dorsal, but are not shown since they are on the medial surface of the filaments.)

LEGEND: AAT - axial adoral tract, B - byssal attachment, FID - filament of inner demibranch, LP - lower palp, LV - left shell valve, MRT - marginal rejection tract, OD - outer demibranch, PAT - proximal adoral tract, PD - prodissoconch, PT - pallial tentacle, RM - right mantle margin, RP - recurrent path of mantle, RV - right shell valve, RX - rejection point of recurrent path, U - umbone, UP - upper palp.

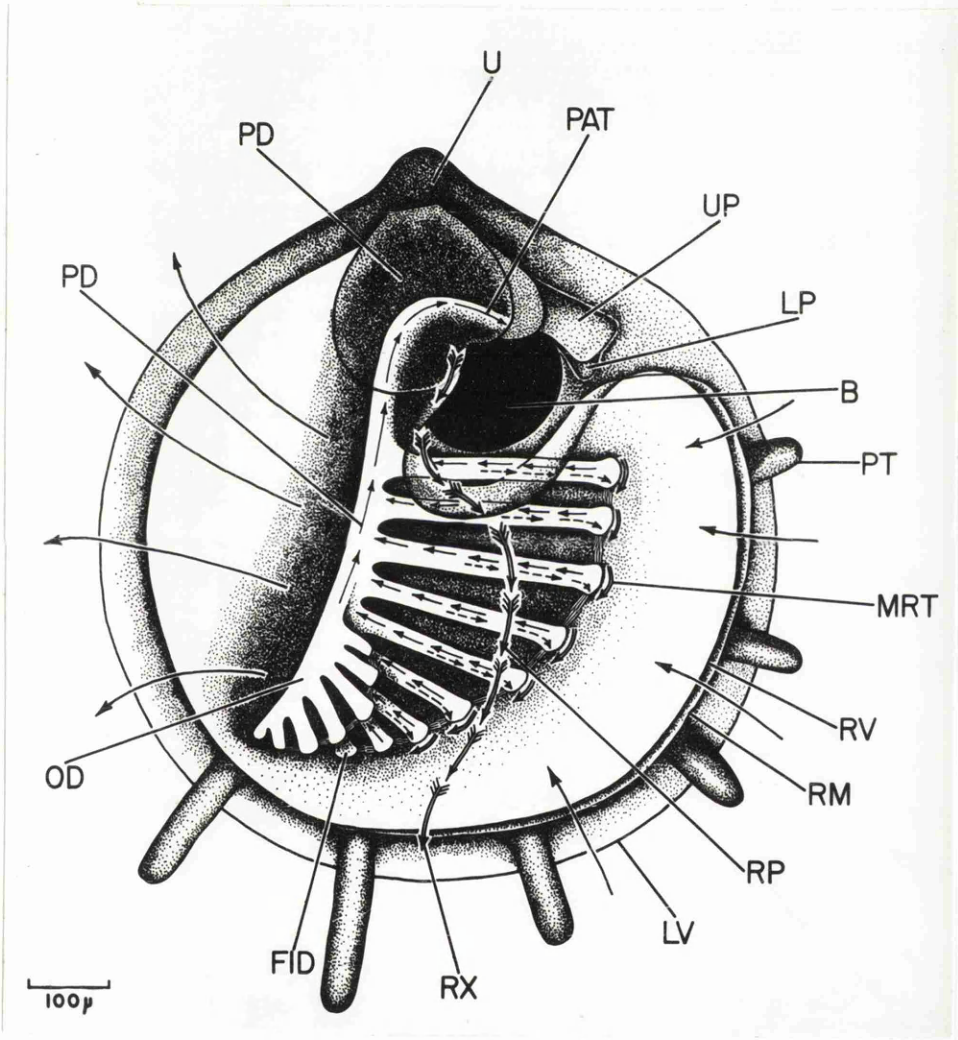


FIGURE 17

(Fig. 13, ML). The mantle margin contracts strongly on stimulation and is extended by the dilation of a marginal blood vessel.

Early in post-larval life, the inner surface of the mantle develops a thickened ridge of tissue bearing a well-defined tract of rather coarse cilia which, by reason of their posteriorly directed beat, form a recurrent path along the mantle. These cilia are easily observed through the transparent right valve. The left valve being thicker and more opaque, obscures the actual tract of cilia on the mantle, but its presence is readily demonstrated by the movement of particles along a well-marked path. Beginning anteriorly near the palps, this recurrent tract extends along the mantle posteriorly and parallel to the margin of the ctenidium before passing to the mantle edge just ventral to the posterior end of the ctenidium (Fig. 13, RP). On the right side the tract circumscribes the dorsal and posterior edges of the pedal sinus before turning posteriorly.

Growth of the mantle is probably restricted almost entirely to the margin so that while the recurrent path maintains its original position, elongation of the filaments changes its location relative to the ctenidium. Thus, when the post-larva reaches a length of 920 u the recurrent path passes over the middle of the anterior filaments (Fig. 17, RP). As the filaments of the outer demibranch increase in length they extend ventrally toward the recurrent path, which in the adult lies along the ventral margin of this demibranch (Atkins, 1936).

Palpal Development

The palps develop early in post-larval life and are

FIGURE 18

Heteranomia squamula. Late post-larva viewed from right side to show curved ctenidial axis. Filaments of the outer demibranch are out of focus but can be seen overlying those of the inner demibranch.

Length - 1.4 mm. x 60

FIGURE 19

Heteranomia squamula. Upper palps seen from posterior aspect to show ciliary currents.

LEGEND: AT - adoral tract, MO - mouth, PAT - proximal adoral tract, RT - rejection tract, RX - points of rejection from palps.

FIGURE 18

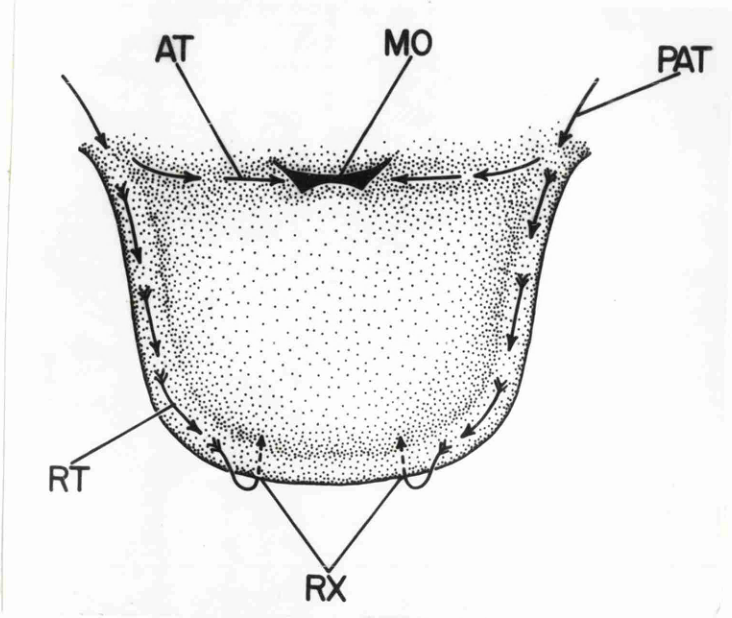


FIGURE 19

represented first by the upper lamellae and later by the lower. The proximal adoral tract leads to the lateral margin of the upper palp lamella dorsally (Fig. 19, PAT), where it bifurcates to form the adoral tract (AT) leading to the mouth, and the rejection tract (RT) leading to the ventral edge of the lamella. Particles are rejected from the upper lamella at 'RX'.

Feeding

During feeding, the ctenidia of the young post-larva are extended and the lateral cilia produce an inhalant water current carrying particles into the mantle cavity. Since the interfilamentary spaces are large and the micro-latero-frontal cilia do not extend across these spaces, many particles pass between the filaments into the supra-branchial cavity and are not utilized in feeding. Those which impinge on the frontal surfaces of the filaments are carried dorsally into the axial adoral groove, anteriorly along the groove to the proximal adoral tract and thence ventrally to the palps (Fig. 13). Some particles are diverted into the adoral tract of the upper palp and reach the mouth, others follow the rejection tract leaving the upper palp at 'RX' (Fig. 19), and fall on the mantle where they travel posteriorly along the recurrent path (Fig. 13, RP).

As already noted the development of adjacent antagonistic frontral tracts has no effect on the feeding mechanism as long as the concentration of particles carried by the inhalant stream is low. However, when the concentration of particles becomes excessive, only the smaller particles are carried dorsally and thus utilized in feeding. All others proceed ventrally to the tips of the filaments

where they are transported posteriorly by the combined action of the cilia of the marginal rejection tract (Fig. 17, MRT), and the recurrent path (RP) on the mantle. As the latter changes its position relative to the ctenidium, such particles are carried by the marginal rejection tract alone until they come in contact with the recurrent path in the posterior region (Fig. 17).

With the formation of the outer demibranch particles also impinge on the frontal surfaces of these filaments whence they are carried dorsally to the axial groove and accompany particles collected by the inner demibranch to the palps. At a later stage in development the recurrent path becomes associated with the outer demibranch (Atkins, 1936) in the same manner that it was originally associated with the inner.

Pectinidae

Scallop larvae were most abundant in the plankton tows in October and November, but were present in small numbers as early as June. With the exception of Chlamys opercularis, the larvae of the other seven species recorded in the Clyde Sea Area by Allen (1953) were not abundant. Moreover, only 50 per cent of the late veligers metamorphosed in laboratory cultures, development of post-larvae was slow and mortality of both veligers and post-larvae was high. Later stages of development were found amongst spat attached to hydroids collected in Fairlie Channel, but here again there were a variety of species and the numbers of each were small.

Ctenidial Development

Since the majority of spat collected were Chlamys opercularis (Linné) and many of these showed critical stages in the development of the ctenidia, the description below applies to this species. Development of Chlamys (varia) (Linné) and Chlamys sp. was comparable to that of C. opercularis although less rapid.

The formation of the inner demibranch in Chlamys is initially similar to that described for Heteranomia (cf. Fig. 7 & 20); the ciliary currents of the ctenidia, prior to the development of the distal lamella of the inner demibranch, are also identical (cf. Fig. 13 & 21). A weak adoral ciliary current is present along the ventral margin of the inner demibranchs (Fig. 21, MAT).

At a length of approximately 850 μ when the post-larva has 18 filaments on either side, reflection of the filaments gives rise to the distal lamella of the inner demibranch. By a process of unequal growth the ventral end of each filament becomes bent inwards and upwards (Fig. 22), carrying with it the interfilamentary and interctenidial junctions which thereby become located at the free dorsal edge of the distal lamella. At the point of flexure a second interfilamentary junction develops (Fig. 22, IFJ_2). The cilia comprising this junction are longer than those of the primary junction (IFJ_1) and permitted positive identification of the two junctions; the width of the primary junction in living specimens was 30 μ, that of the secondary one 70 μ. Measurements of the primary junctions were identical in specimens with unreflected and with reflected filaments. Since post-larvae were never observed with two interfilamentary junctions and unreflected filaments, or with one interfilamentary

FIGURE 20

Chlamys opercularis. Post-larva viewed from right side to show alternation of filaments in mid-ventral line. The general similarity between pectinid and anomid post-larvae may be seen by a comparison of this figure with Figure 7 of Heteranomia.

Length - 480 μ. x 130

FIGURE 20

FIGURE 21

Chlamys opercularis. Post-larva viewed from right side to show the ciliary and water currents of the mantle cavity characteristic of the pectinids. In comparison with the anomids (Figures 13 & 17) three main differences should be noted: the position of the recurrent path (RP) adjacent to the mantle margin, the presence of a subaxial tract (SAT) on the mantle and the marginal adoral tract (MAT) which replaces the marginal rejection tract of the anomids. Length - 690 μ.

Large plain arrows	-	inhalant and exhalant water currents.
Small plain arrows	-	adoral ciliary currents of the ctenidium.
Discontinuous arrows	-	ventral frontal ciliary current; cilia active only on stimulation.
Double arrows	-	ciliated tracts leading away from the mouth.
Feathered arrows	-	ciliated tracts on the mantle.

LEGEND: AAT - axial adoral tract, F - foot, FL & FR - filaments of left and right ctenidia respectively, LP - lower palp, MAT - marginal adoral tract, PA - posterior adductor muscle, PAT - proximal adoral tract, PD - prodissoconch, PS - pedal sinus, PT - pallial tentacle, RP - recurrent path, RX - rejection points of palp and mantle margin, SAT - subaxial adoral tract, UP - upper palp.

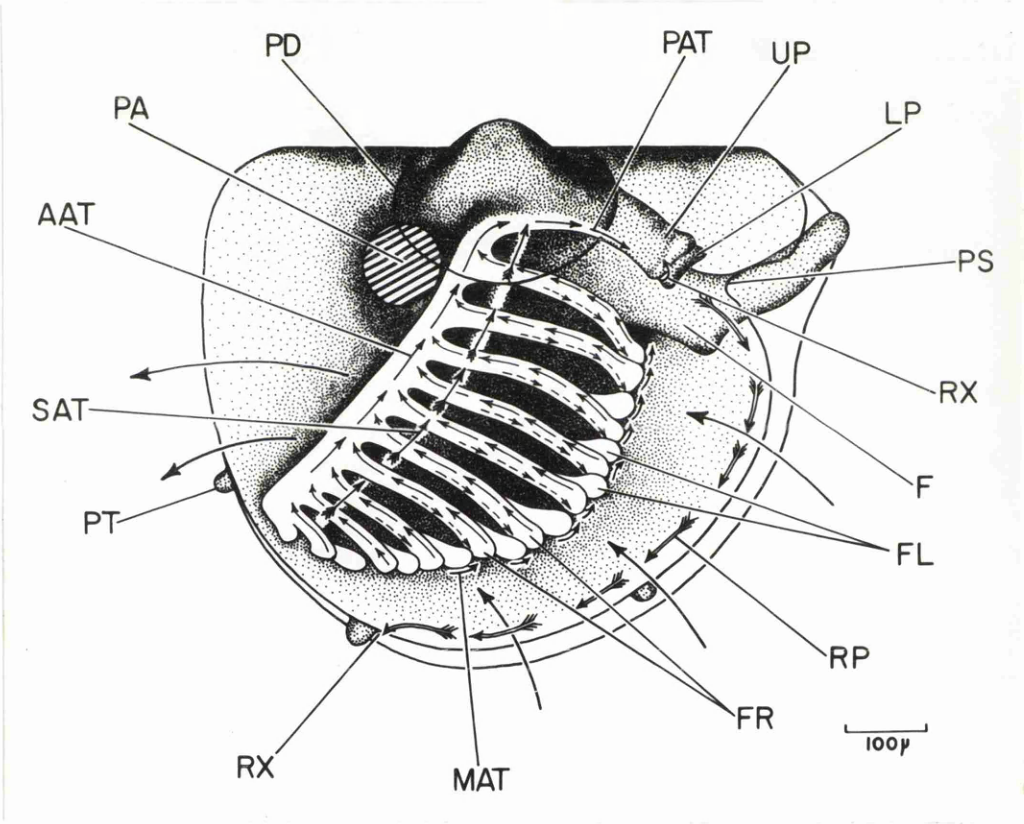


FIGURE 21

FIGURE 22

Chlamys opercularis. Ventral portion of newly reflected filament from lateral aspect; the reflected portion is 70 μ in length. The direction of beat of the coarse (CC) and fine (FC) frontal cilia could not be determined. Note the absence of cilia on the frontal surface at the point of flexure.
From specimen 890 μ in length.

Large arrows - ventral frontal ciliary current (coarse cilia).

Small arrows - dorsal frontal ciliary current (fine cilia).

LEGEND: CC - position of coarse frontal cilia, FC - position of fine frontal cilia, LC - position of lateral cilia, ICJ - inter-ctenidial ciliary junction, IFJ_1 & IFJ_2 - primary and secondary interfilamentary junctions respectively, NC - non-ciliated region of frontal surface.

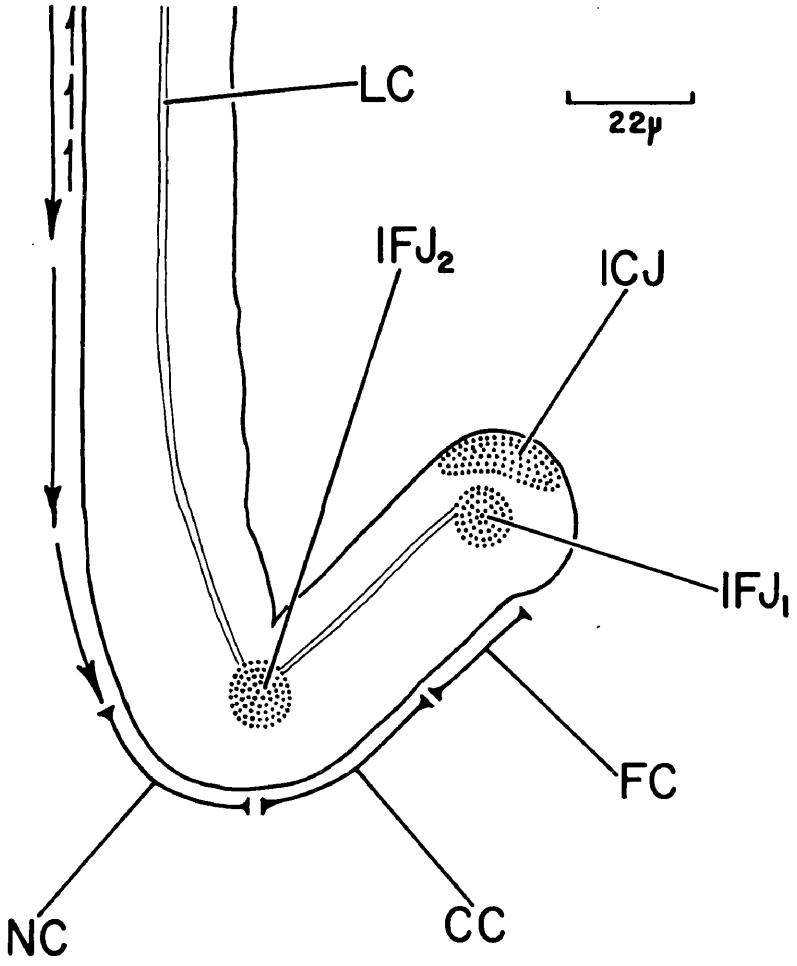


FIGURE 22

junction and reflected filaments, the two processes appear to occur simultaneously. Reflection begins in the anterior portion of the inner demibranch, and proceeds posteriorly as the new filaments elongate and additional filaments are formed from the anlage.

The direction of frontal currents on the distal lamella when first formed could not be determined, but in later stages of development they were seen to be identical to those of the proximal lamella. Although reflection would presumably carry the marginal adoral tract to the dorsal edge of the distal lamella, where it is present in the adult (Atkins, 1937 b), it was never observed. However, these filaments could only be satisfactorily observed in dissections where disruption of the ciliary connections between the alternating filaments of the two demibranchs could have impaired the functioning of such a tract. Shortly after the reflection of the filaments, an adoral current is developed along the ventral margin of the inner demibranch. Initially this ciliary current is weak and the passage of particles anteriorly from one filament to the next is hazardous.

The first indication of the outer demibranch appeared in a specimen 925 μ in length. Papillae are formed about midway along the length of the ctenidial axis and as they elongate into filaments, frontal ciliary currents identical to those of the inner demibranch are developed. One specimen, 1.16 mm. long with 20 filaments in the outer demibranch, showed the filaments reflected with primary and secondary interfilamentary junctions present. Thus, formation of the distal lamella of the outer demibranch follows the pattern as that of the inner. A more detailed study of this type of ctenidial development would be valuable.

Pallial Development

In the early post-larva the mantle develops papillae along its margin (Fig. 21, PT); these papillae elongate to form the pallial tentacles of the adult.

An adoral ciliated tract forms on the inner surface of the mantle parallel to, but 70 μ below, the ctenidial axis (Fig. 16 & 21, SAT). This subaxial tract overlies the dorsal ends of the filaments, and its adoral current is sufficiently strong to cause a water current between it and the axial adoral ciliary tract. Thus, movement of particles, not actually in contact with the cilia of the dorsal frontal tract, is at right angles to the latter tract (Fig. 16).

A recurrent path appears on the mantle (Fig. 21, RP) but its location differs from that in Heteranomia. Originating anteriorly at the palps, it circumscribes the pedal sinus on the right side and passes posteriorly adjacent to the mantle margin to terminate ventral to the posterior end of the ctenidial axis at 'RX'. Its location anteriorly on the left mantle was not determined. In contrast to Heteranomia, the recurrent path in Chlamys is never associated with the ventral edge of either demibranch.

Feeding

As in Heteranomia a large proportion of the particles entering the mantle cavity in the inhalant stream pass between the filaments into the supra-branchial cavity. Particles impinging on the surface of the ctenidium are carried dorsally along the frontal surfaces of the filaments. While a few particles may reach the axial adoral

groove (Fig. 21, AAT), the majority come under the influence of the water current produced by the cilia of the subaxial tract (SAT) and proceed anteriorly between the two adoral tracts. With the development of ventral frontal ciliary currents and marginal adoral tract (MAT), the movement of particles on the surface of the ctenidium becomes more complicated when the concentration of suspended particles is great. Many particles are then carried ventrally along the frontal surface of the filaments and thence proceed anteriorly along the margin of the inner demibranch. However, since the ciliary current here is weak, these particles usually fall on to the mantle surface. The marginal adoral tract has no connection anteriorly with the palps. All particles rejected by the palps, or falling on to the mantle, are carried posteriorly along the recurrent path (RP).

Currents on the frontal surfaces of the filaments of both proximal and distal lamellae of both demibranchs are the same. The fate of particles travelling dorsally on the reflected lamellae was not determined. While, as explained above, there is probably an adoral tract along the dorsal margin of the distal lamella of the inner demibranch, due to the position of the foot between filaments F_0 and F_1, such an adoral tract can have no connection with the palps.

Limidae

Lima hians (Gmelin) is the only species of this Family found in the vicinity of the Isle of Cumbrae. Larvae were never plentiful in the plankton tows and the breeding season is short, August to October, in the Clyde Sea Area. Two-thirds of the veligers collected failed to metamorphose in laboratory cultures, but the 18 which did were reared with moderate success, attaining a length of 750 μ in a little over four months. After several months the nests became clogged with algal and fungal growths which interfered with the feeding currents of the young spat. If removed from their nests, the post-larvae often became unhealthy and died. No young stages were found amongst the nests of the adults. The larva of Lima hians has been described by Odhner (1914), Lebour (1937), Jørgensen (1946) and Rees (1950); Odhner and Lebour also give descriptions of the post-larva.

Ctenidial Development

At metamorphosis the larva is 370 μ in length and has 4 to 5 filaments in each inner demibranch. The ctenidial anlagen are separate. The larval filaments are connected by ciliary interfilamentary junctions similar to those of Heteranomia and Chlamys, the interctenidial junctions being formed after metamorphosis. Initially the filaments of the two inner demibranchs generally alternate and the interctenidial junctions resemble those of the anomids and pectinids. In older post-larvae the filaments are opposite and are connected directly by short interlocking cilia, forming a second interctenidial junction (Fig. 23, ICJ_2). The longer cilia, which formed the primary

FIGURE 23

Lima hians. Diagram to show secondary pairing of ctenidial filaments as seen in ventral view. Note the positions of the primary and secondary interctenidial ciliary junctions (ICJ_1 & ICJ_2) and compare with Figure 12 which shows their positions immediately following metamorphosis when the filaments are alternate.

FIGURE 24

Lima hians. Upper palp and anterior filaments of early post-larva viewed from right side to show ciliary currents. Note that, due to the proximity of the first filament and palp, the marginal adoral tract (MAT) of the ctenidium is almost continuous with the adoral tract (AT) of the palp, whereas the proximal adoral tract (PAT) is continuous with the palpal rejection tract (RT). (Ciliary tracts of palp are on the inner or medial surface.)

LEGEND: AAT - axial adoral tract, AT - adoral tract of upper palp, ICJ_1 & ICJ_2 - primary and secondary interctenidial ciliary junctions, IFJ - interfilamentary ciliary junction, MAT - marginal adoral tract, PAT - proximal adoral tract, RT - rejection tract of upper palp, RX - rejection point of upper palp, UP - upper palp, VFC - ventral frontal ciliary current.

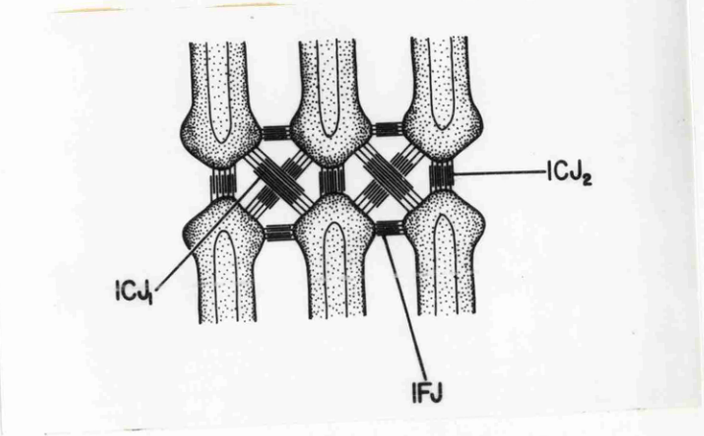


FIGURE 23

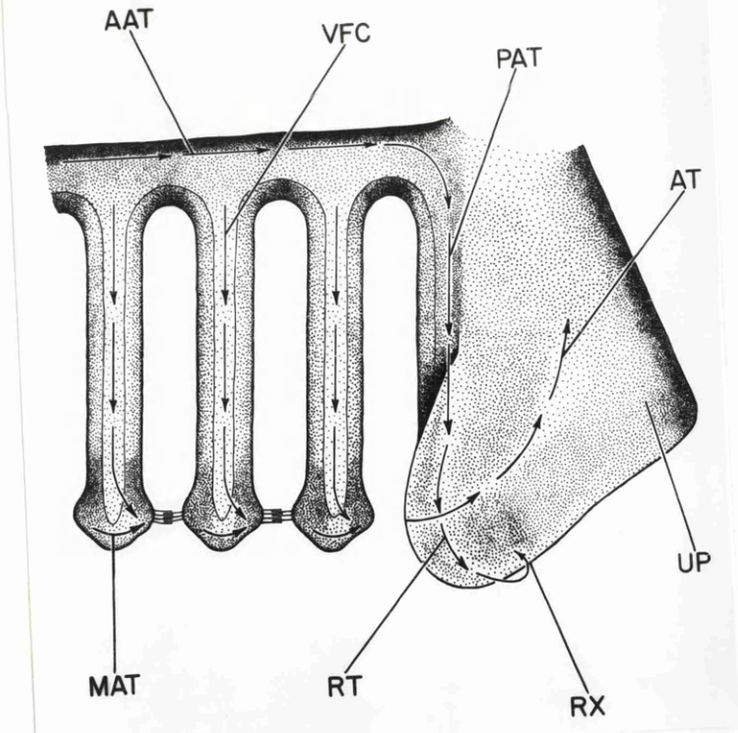


FIGURE 24

interctenidial junctions (ICJ_1), on the anterior and posterior faces of the tip of each filament, interlock with the cilia of the filaments of the opposite demibranch immediately anterior and posterior to it. These primary junctions now cross over one another in the midline. Thus, each filament has three groups of cilia comprising the interctenidial junctions, one of which, the secondary junction, is formed after the transition from alternate to opposite positions. Comparison of Figure 12 with Figure 23 shows that this change necessitates the disruption of some of the primary junctions which are later reformed between different pairs of filaments. New filaments added posteriorly frequently alternate, but later they too become arranged in pairs. Anteriorly the filaments lie on either side of the foot but do not appear to be attached to the foot in any way. Thus, the first filament lies adjacent to the upper palp (Fig. 24) rather than being separated from the latter by the intervening foot as in the anomids and pectinids.

Frontal currents on all filaments are ventral. There were also indications of a dorsal frontal current whose presence was masked by the stronger ventral one. In Heteranomia and Chlamys dorsal frontal currents were obscured by the coarse ventrally beating cilia when the latter were active, but since in Lima the coarse frontal cilia are continuously active it was impossible to determine with certainty the presence of dorsal tracts in this genus. Both axial and proximal adoral tracts are present together with a marginal adoral tract which develops along the ventral margin of the demibranch at an early stage (Fig. 24, MAT).

Development of the ctenidium is more rapid than in Heteranomia and Chlamys. When 9 filaments are present in each inner demibranch (post-larva 750 μ in length) reflection has already taken place (Fig. 25), and the marginal adoral tract is now located at the dorsal edge of the distal lamella (DDL). Unfortunately the number of post-larvae reaching this stage of development was insufficient to permit a study of the process of reflection. The similarity of the post-larval ctenidium to that of Chlamys makesit reasonable to assume that formation of the distal lamella is similar to reflection in the Pectinidae.

Pallial Development

Several small rounded papillae are present along the mantle edge of the late larva. Following metamorphosis they rapidly elongate into tentacles which are so prominent in the post-larva (Fig. 25). They have a distinctly segmented appearance and are provided with cirri. At a later stage small red pigment spots develop between the tentacles.

In the late veliger a pair of small triangular lobes project from the mantle margin near the posterior end of the ctenidial axes. These enlarge during post-larval life and become thin membraneous pallial lobes overlapping one another medially when the shell valves are open (Fig. 25 & 26, ML).

A recurrent path (Fig. 25, RP) originates on the mantle overlying the palps and leads to the mantle margin directly opposite its origin (Fig. 25 & 27, RX).

FIGURE 25

Lima hians. Mid post-larva viewed from right side to show ciliary and water currents of mantle cavity characteristic during development of the distal lamella of inner demibranch. Note the short anterior recurrent path (RP) and the new position of the marginal adoral tract (Fig. 24, MAT) which now runs along the dorsal edge of the distal lamella (DDL).

Length - 750 μ.

Large plain arrows - inhalant and exhalant water currents

Small plain arrows - ciliary currents of ctenidium.

Feathered double arrow - recurrent path of mantle.

LEGEND: AAT - axial adoral tract, DDL - dorsal edge of distal lamella of inner demibranch, F - foot, ML - pallial lobe, PD - prodissoconch, PAT - proximal adoral tract, PT - pallial tentacle, RP - recurrent path, RX - rejection point of recurrent path, UP - upper palp.

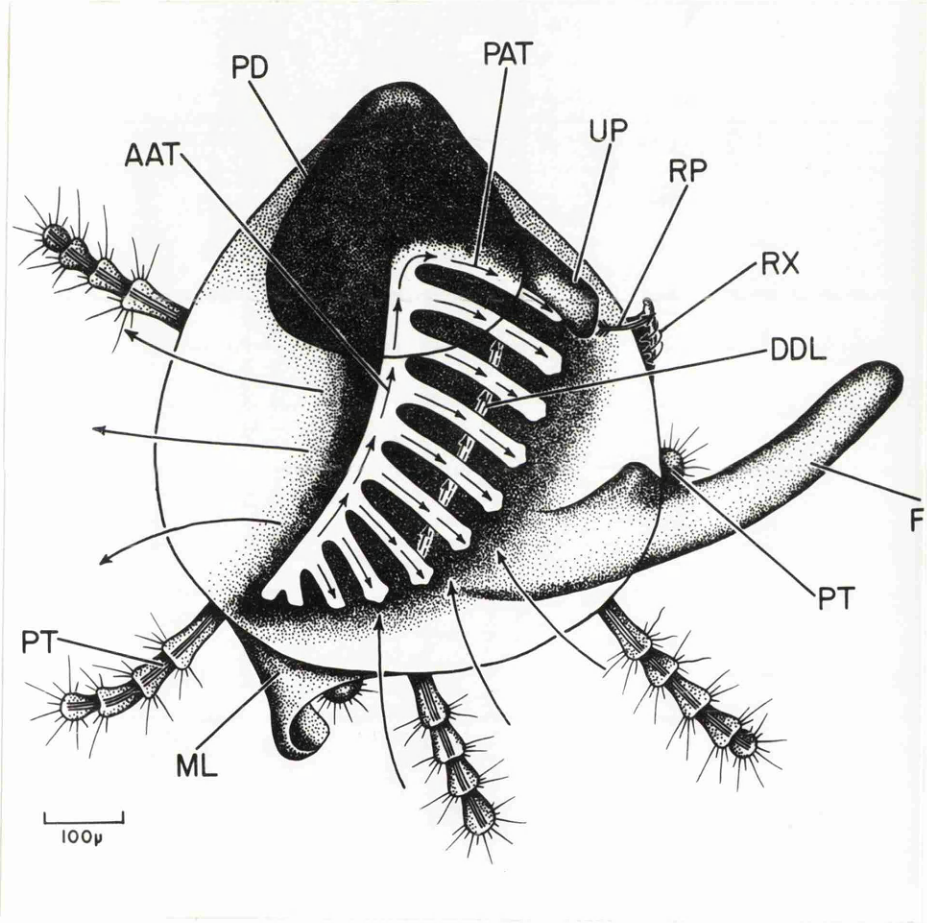


FIGURE 25

FIGURE 26

Lima hians. Postero-dorsal view of same post-larva as Figure 25 to show medial overlapping of pallial lobes (ML) to separate inhalant (IN) and exhalant (EX) areas.

FIGURE 27

Lima hians. Antero-ventral view of same post-larva as Figure 25 to show rejection points (RX) of recurrent paths of mantle.

LEGEND: BG - byssal groove of foot, DS - dissoconch, EX - exhalant area, H - heel of foot, IMM - inner and middle mantle folds, IN - inhalant area, LCT - left ctenidium, ML - pallial lobe, MPT - median pallial tentacle, OM - outer mantle fold, PT - pallial tentacle, RCT - right ctenidium, RX - rejection point of recurrent path.

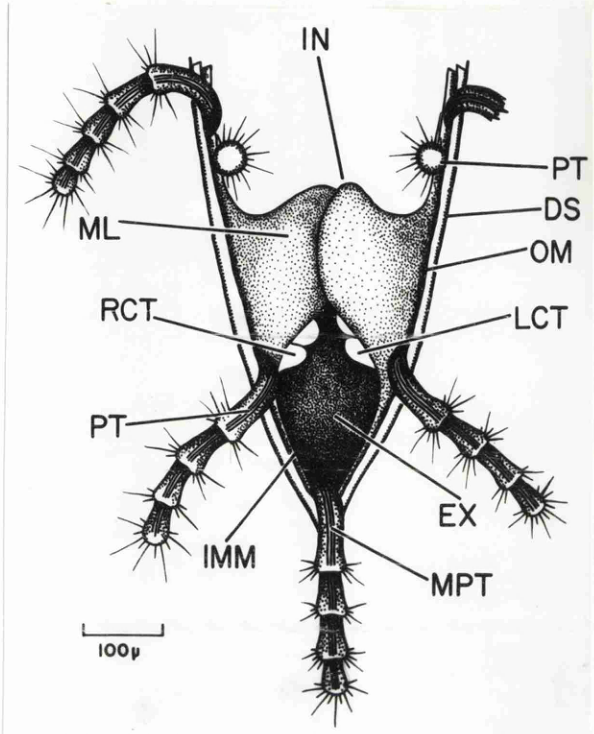


FIGURE 26

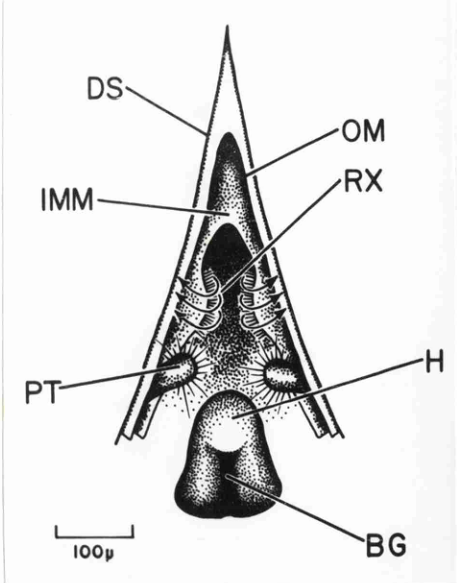


FIGURE 27

Palpal Development

Both palps develop early in post-larval life, the upper ones appearing first. Two distinct pairs of ciliary tracts traverse the inner surface of the upper palps (Fig. 28); from the latero-ventral margins adoral tracts (AT) lead to the mouth, while rejection tracts (RT) running parallel to the lateral margins, pass from the dorsal to the ventral margin and carry particles over the edge of the palps at 'RX'. These rejection tracts terminate near the origins of the recurrent paths of the mantle (Fig. 25).

Pedal Development

Prior to metamorphosis the foot of Lima is directed forwards as in other lamellibranch larvae and post-larvae, but shortly after the velum is shed the foot is rotated through 180° to face posteriorly as in the adult (Fig. 25). The young post-larvae frequently became byssally attached to the side of the culture dish at the water level, and sometimes hung from the surface film as described by Nelson (1928) for Mytilus. Later they returned to the bottom of the dish and constructed nests from the grains of sand.

Feeding

Since the pairing of the filaments of the two demibranchs in the midline reduces the size of the interfilamentary spaces, most of the particles entering in the inhalant stream are retained by the ctenidia. Such particles are carried ventrally to the margin of the demibranch and thence along the marginal adoral tract

FIGURE 28

Lima hians. Upper palps seen from posterior aspect to show ciliary currents.

LEGEND: AT - adoral tract, MO - mouth, PAT - terminal portion of proximal adoral tract, RT - rejection tract, RX - points of rejection from upper palps.

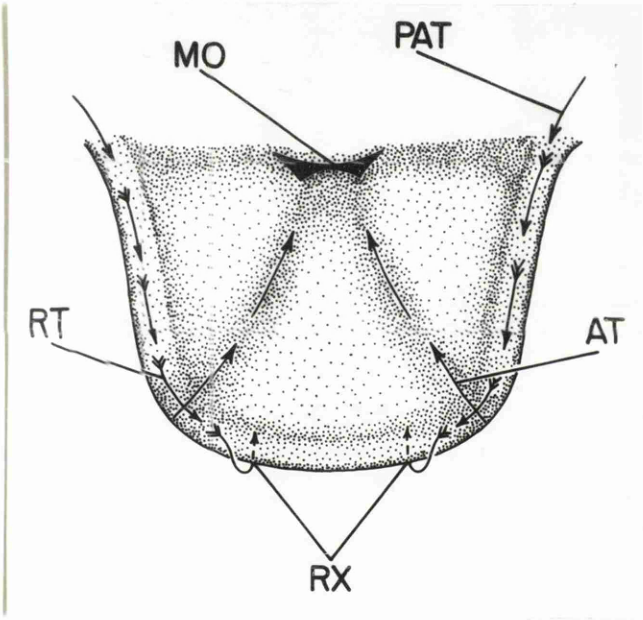


FIGURE 28

(Fig. 24, MAT) to the palps where they usually pass directly into the adoral tract (Fig. 24 & 28, AT) of the upper palp. However, some particles appear to be carried by the inhalant stream directly to the axial adoral tract (Fig. 24 & 25, AAT) --- although they may be influenced by the dorsal frontal tracts whose presence was suggested above --- travel anteriorly to the proximal adoral tract (PAT) and so ventrally to the palps. These particles appear to enter the rejection tract (Fig. 24 & 28, RT) of the upper palp and are transferred to the recurrent path (Fig. 25, RP) of the mantle to be ejected from the mantle cavity (Fig. 25 & 27, RX). The pallial lobes (Fig. 25 & 26, ML) overlap medially during feeding, thus separating the inhalant and exhalant streams.

Ostreidae

Post-larval development was observed in two species of oysters belonging to different genera: Ostrea edulis Linné, which metamorphoses at an average length of 300 μ (Cole, 1937), and Crassostrea virginica Gmelin, in which metamorphosis occurs at 350 μ (Sullivan, 1948). Preliminary examination of living post-larvae (Ostrea edulis) were made at Conway, Wales in 1955 and a more detailed study of post-larvae (Crassostrea virginica), 500 μ to 1.3 mm. in length, was conducted at Ellerslie, Prince Edward Island, Canada in 1957. Both visits were of brief duration and observations were limited to the developmental stages available at the time.

Ctenidial Development

Examination of living, newly metamorphosed Ostrea spat revealed little concerning the initial phases of ctenidial development. The opacity of the larval shell makes it impossible to observe the ctenidia in whole spat, while dissections were hampered by the convexity of the prodissoconch. Thus it is necessary to recount the few details of ctenidial development recorded in the literature. Erdmann (1935) states that the ctenidial anlagen of Ostrea edulis are fused and he figures 6 filaments on the left side of the 'ansatzreifen' larva. Cole (1937) found 7 filaments on the same side of the youngest spat which he examined. With regard to Crassostrea virginica a little more is known. Stafford (1913) reports that the anlagen are fused and that on either side of the mature larva there are 8 filaments "with their lower ends free." Following

metamorphosis, the filaments of the left side become divided proximally into two parts to form the proximal and distal lamellae of the inner demibranch. This process, as described by Stafford, resembles that recorded by Rice (1908) for other lamellibranchs at a much later stage of development (Fig. 5). Proximal division of the filaments is already apparent in spat 460 μ in length but the two lamellae are more clearly separated in spat 760 μ in length (Stafford, 1913). The fact that this process is complete "within 6 hours after attachment" led Nelson and Yonge (1947) to describe the 8 filaments on the left side of the mature larva as "a potentially functional demibranch ready to unfold." Interfilamentary junctions, described by Nelson and Yonge as originating from the fusion of outgrowths at the tips of adjacent filaments, are present along the ventral edge of the left inner demibranch in spat measuring 420 μ (Stafford, 1913). Although the marginal bridge was present in both inner demibranchs of all spat exceeding 500 μ in length (Ostrea and Crassostrea) examined during the present investigation, no mention of such a structure is made in the literature. Its origin thus remains to be determined. Stafford says that in both larvae and newly metamorphosed spat the anterior filaments lie on either side of the foot, but he gives no indication of any attachment, or lack of it, between these filaments and the foot. He merely records that anteriorly the distal lamellae of the two inner demibranchs of the spat "approach each other, towards the median ventral line of the abdomen, where they are attached, but behind this they unite." The present investigation shows that the attachment of the inner demibranchs to one another is effected by fusion of their marginal bridges.

While ctenidial development is extremely rapid during the early post-larval stages, it occurs almost exclusively in the left ctenidium. Development of the right ctenidium is retarded until the post-larva attains a length of approximately 500 μ (Fig. 29). At this stage there are only 3 or 4 filaments present in the right inner demibranch (Fig. 29 & 30) so that, while elongation of the filaments has occurred, differentiation has scarcely advanced beyond that of the late larval stage. Fortunately, this delayed development of the right ctenidium provides an opportunity to study the early genesis of the ctenidium with greater ease and confidence.

The right inner demibranch of spat 500 μ in length is located dorsal to the left inner demibranch (Fig. 29). The two demibranchs are united by the fusion of their marginal bridges, that of the left inner demibranch now lying at the dorsal edge of the distal lamella. Coarse frontal cilia on the ventral half of the filaments of the right inner demibranch produce a conspicuous ventral ciliary current (Fig. 30) which connects with the combined marginal adoral tracts of the two inner demibranchs (Fig. 29 & 30, MAT). While the presence of fine cilia in the dorsal region of the filaments was suspected it could not be verified. Along the axis of the right ctenidium an adoral tract (AAT) leads to the proximal adoral tract (PAT) and thence to the palps.

Subsequent differentiation of filaments from the right anlage proceeds by the fold method described by Wasserloos (1911) for Cyclas cornea (cf. Fig. 3 & 31). The anlage thickens into vertical ridges (Fig. 31, R) while a groove (G), which is later perforated,

FIGURE 29

Ostrea edulis. Ctenidia and palps of mid post-larva viewed from right side to show the ciliary currents and also the relationship of the right and left ctenidia to one another. From specimen approximately 500 μ in length.

FIGURE 30

Crassostrea virginica. Right ctenidium of mid post-larva viewed from right side to show the ciliary currents. The left ctenidium of this specimen had 12 filaments in the inner demibranch. From specimen 625 μ in length.

LEGEND: AAT - axial adoral tract, FDL & FPL - distal and proximal portions of filament of left inner demibranch, IAT - intermediary adoral tract, IFB - interfilamentary bridge, LA - anlage of left ctenidium, LP - lower palp, MAT - marginal adoral tract, O_1 to O_4 - first to fourth ostia or interfilamentary spaces, OE - oesophagus, PAT - proximal adoral tract, RA - anlage of right ctenidium, RX - rejection point of upper palp, UP - upper palp or its posterior margin.

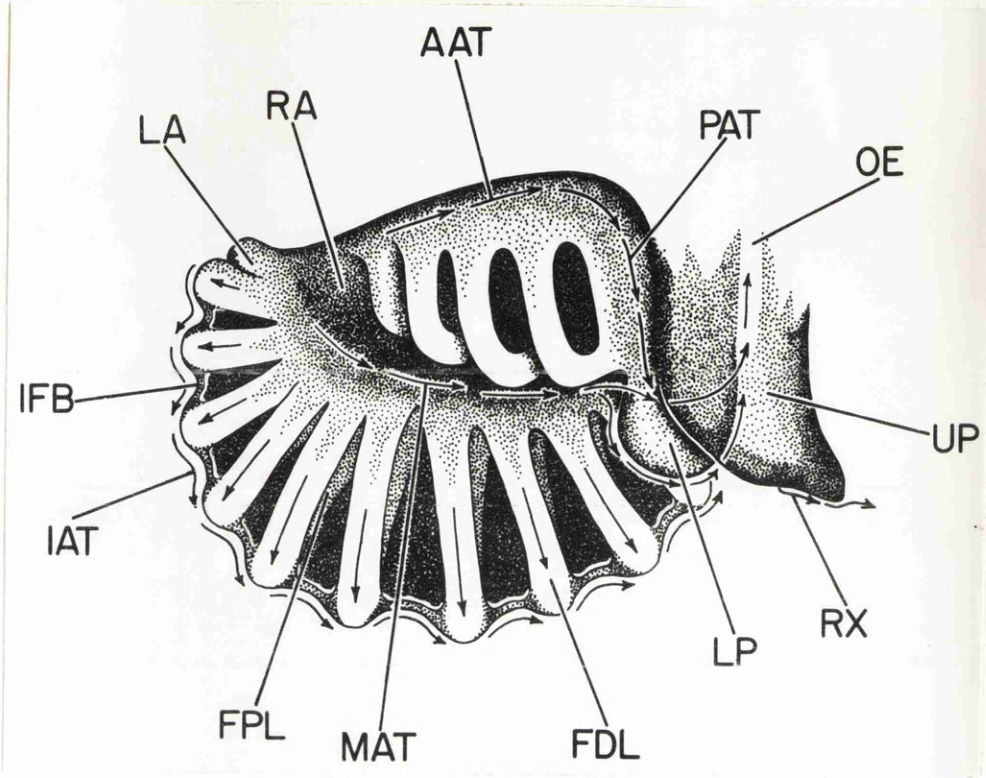


FIGURE 29

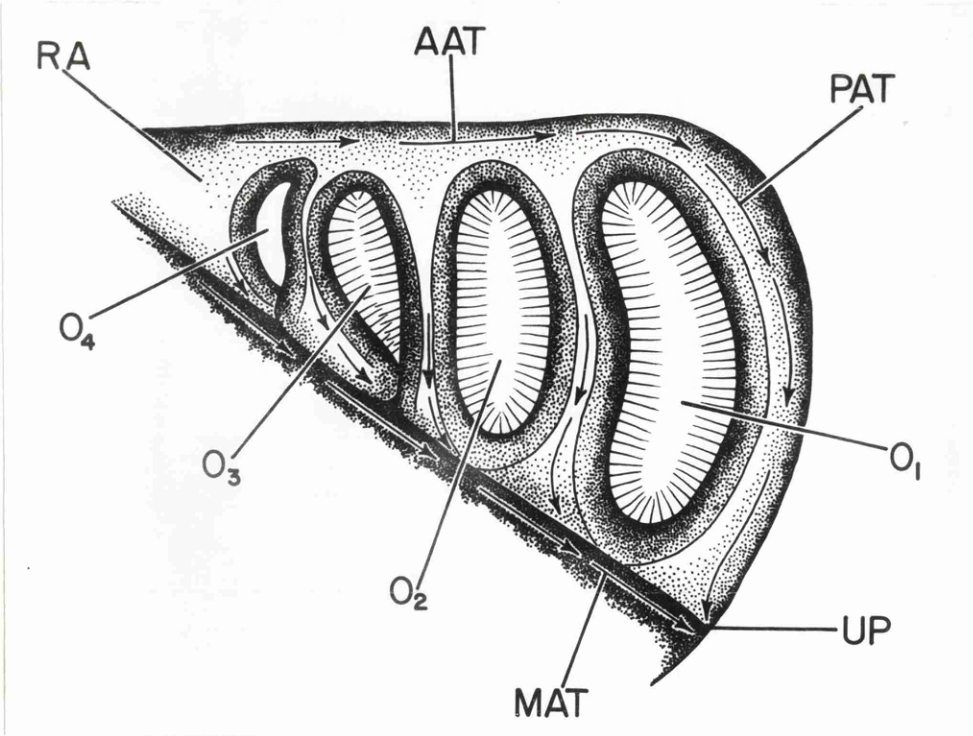


FIGURE 30

forms between the ridges. While the first 4 ostia are perforated by one continuous slit (e.g. O_4), the 5th is pierced by a long slit dorsally and a short one ventrally, the two being separated by an interfilamentary bridge (IFB). In perforation of ostia posterior to the 5th the interfilamentary bridges come to lie progressively nearer the centre of the ostia (e.g. O_8). These bridges mark the division between proximal and distal lamellae; portions of the filaments dorsal to the bridges become the proximal lamella while those ventral to the bridges become the distal lamella. Interfilamentary bridges across ostia 2, 3 and 4 are secondary structures formed by the fusion of outgrowths from adjacent filaments and do not make their appearance until much later. Ostium 1 is never divided by an interfilamentary bridge.

Prior to perforation, groups of coarse cilia are evident on the ridges adjacent to the points where interfilamentary bridges will be formed (Fig. 31, IAT). As differentiation proceeds such cilia also develop along the bridges so that a continuous line of cilia, the intermediary adoral tract (Fig. 32, IAT and also Fig. 29, IAT on the left inner demibranch), is formed. Subsequently, coarse cilia (Fig. 31, CC) also appear dorsal and ventral to the intermediary tract to form the frontal tracts of the proximal and distal lamellae respectively. The cilia of these frontal tracts beat toward the intermediary adoral tract and eventually become the ventral frontal tracts of the inner demibranch (Fig. 32 and also Fig. 29 on the left inner demibranch). Lateral cilia develop shortly after perforation (Fig. 31, OL) but the appearance of anomalous latero-frontals

FIGURE 31

Crassostrea virginica. Posterior portion of right ctenidium of late post-larva viewed from right side to show the method of differentiation of filaments of the inner demibranch from the anlage and the formation of the interfilamentary bridges. The cilia shown around ostia 4 and 5 are the anomalous latero-frontals; lateral cilia were present around ostia 4 to 7. Large dots show the distribution of coarse cilia. The left ctenidium of this specimen had 20 filaments in the inner demibranch.

From specimen 950 μ in length.

FIGURE 32

Crassostrea virginica. Right ctenidium of late post-larva viewed from right side to show the differentiation of the inner demibranch into proximal and distal lamellae. Note the position of the marginal adoral tract (MAT) along the marginal bridge (MB) located at the dorsal edge of the distal lamella. The filaments are numbered. The left ctenidium of this specimen had approximately 25 filaments in the inner demibranch.

From specimen 1.3 mm. in length.

LEGEND: AAT - axial adoral tract, CC - coarse cilia, FDR - distal portion of filament of right inner demibranch, FPR - proximal portion of filament of right inner demibranch, G - groove representing initial stage in formation of ostium, IAT - intermediary adoral tract, IFB - interfilamentary bridge, MAT - marginal adoral tract, MB - marginal bridge, O_5 & O_8 - fifth and eighth ostia, OL - most posterior ostia having lateral cilia, PAT - proximal adoral tract, R - ridge representing initial stage in formation of filament, RA - anlage of right ctenidium.

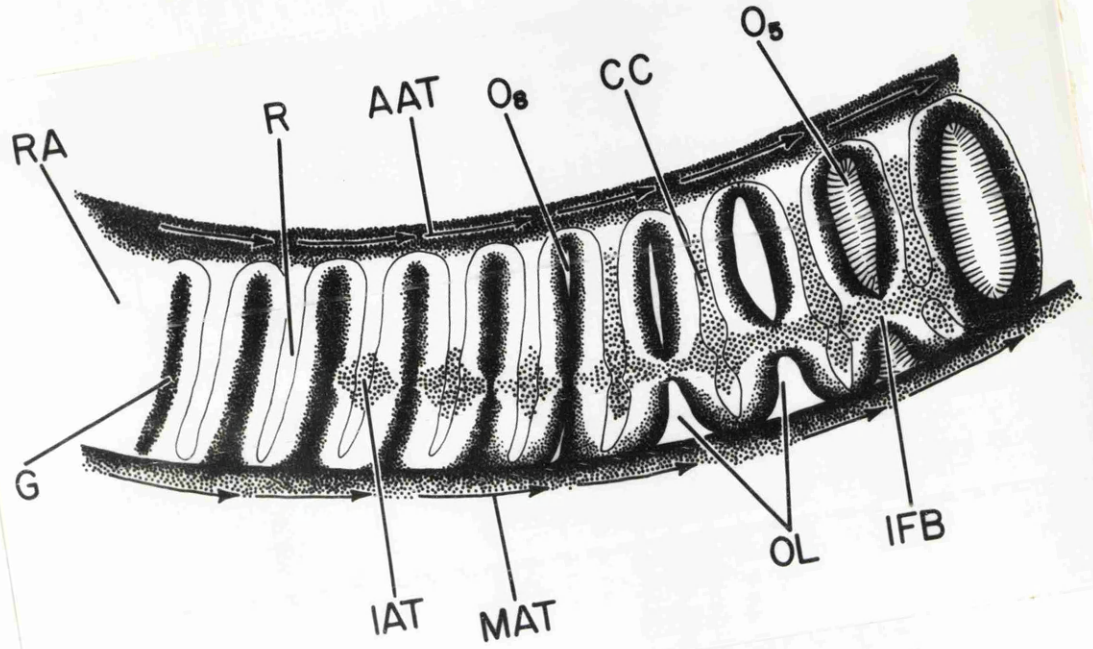


FIGURE 31

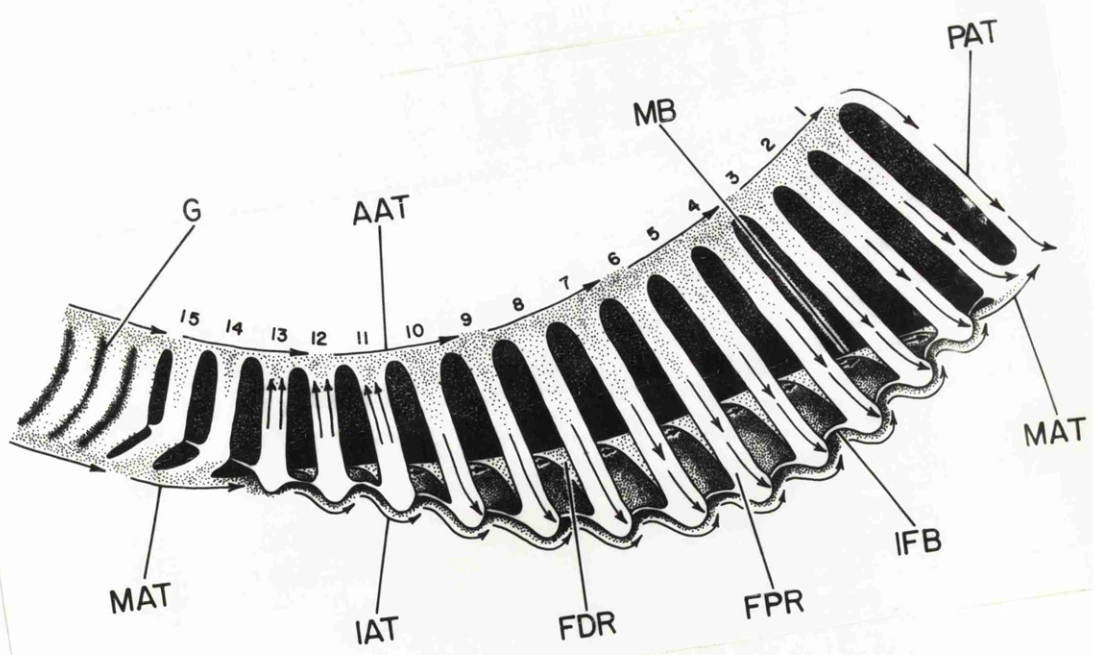


FIGURE 32

is somewhat delayed (O_5). The point and time of origin of the fine frontal cilia could not be determined except in one specimen of Crassostrea, 1.3 mm. in length (Fig. 32), where the 11th to 13th filaments had dorsal frontal tracts but no ventral ones. Dorsal frontal tracts were also evident in later stages of development as described below.

Since the ventral ends of the filaments are fixed in position by the fusion of the marginal bridge to the dorsal edge (marginal bridge) of the distal lamella of the left inner demibranch, elongation of the filaments causes them to bend outwards in the region of the interfilamentary bridges. (Fig. 32, F_{14} & F_{15}). Thus, when approximately 12 ostia are present in the right inner demibranch, it projects laterally into the mantle cavity as a longitudinal ridge. Subsequently, as elongation of the proximal portions of the filaments slightly exceeds that of the distal portions, the demibranch begins to extend ventrally (Fig. 32), overlying the left inner demibranch. This process begins anteriorly at the 4th filament and progresses both posteriorly and anteriorly. Progress in the latter direction is slow so that the 2nd filament is not bent until 13 ostia are present. The 1st filament always remains straight. The intermediary adoral tract (Fig. 32, IAT) proceeds along what is now the ventral edge of the inner demibranch, and anterior to the 2nd filament it merges with the marginal adoral tract (MAT) before leading to the palps. The outward, and later downward, growth of the right inner demibranch changes its orientation relative to the left inner demibranch from the early dorsal location to that typical of the adult where the two

demibranchs occupy approximately corresponding positions on the right and left sides.

The frontal ciliation was only clearly discerned in later stages of development when it was seen to correspond to that on the ordinary filaments of the adult (Atkins, 1937 b). The conspicuous coarse cilia, noted above, occupy the centre of the frontal surface and are flanked on either side by tracts of fine cilia beating dorsally (Fig. 33). Ventrally, the presence of fine cilia could not be verified with absolute certainty due to the stronger beat of the coarse cilia. Whereas, the dorsal frontal tracts probably occupy almost the full length of the filament, the ventral tracts (coarse cilia) are restricted to the ventral portion of the filament.

Development of the outer demibranch was not examined in either ctenidium but is said by Stafford (1913) to be similar to that of the inner demibranch.

Pallial Development

Serial sections of young spat of Ostrea showed a tract of cilia on the right mantle extending from the palps to the edge of the mantle posteriorly. This tract, presumably the recurrent path of the mantle, was not observed in living specimens since the right mantle was removed in all dissections, and the tract was not visible through the shell in whole specimens. No evidence of a similar tract could be found on the left mantle.

FIGURE 33

Crassostrea virginica. Fourteenth filament from distal lamella of left inner demibranch to show adjacent antagonistic frontal ciliary currents. The dots show the distribution of the coarse frontal cilia whose beat is directed ventrally.

From specimen 950 μ in length.

FIGURE 34

Ostrea edulis. Upper palps seen from posterior aspect to show ciliary currents.

From specimen approximately 500 μ in length.

Plain arrows - adoral ciliary currents.

Feathered arrows - rejection ciliary currents.

LEGEND: AT_1 - first adoral tract, AT_2 - second adoral tract, IAT - intermediary adoral tract, IFB - interfilamentary bridge, MAT - marginal adoral tract, MB - marginal bridge, MO - mouth, PAT - proximal adoral tract, RT - rejection tract, RX - points of rejection of particles from upper palps.

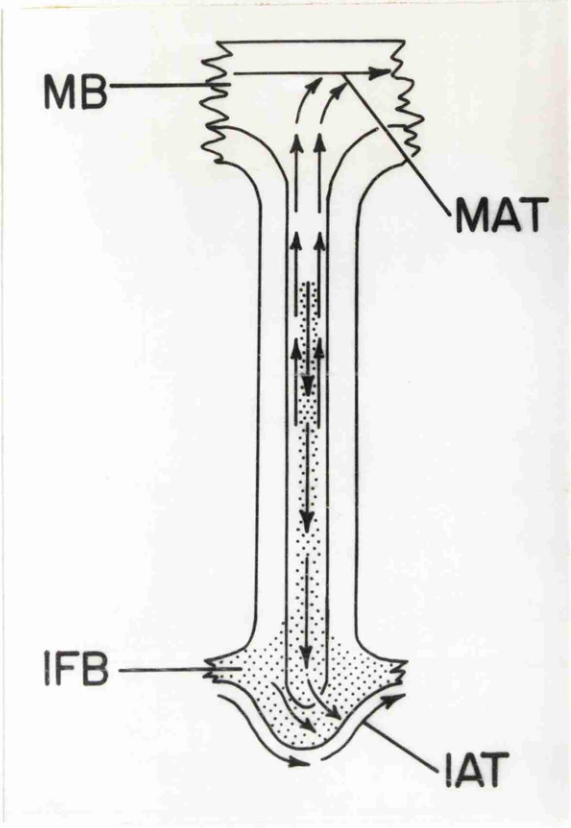


FIGURE 33

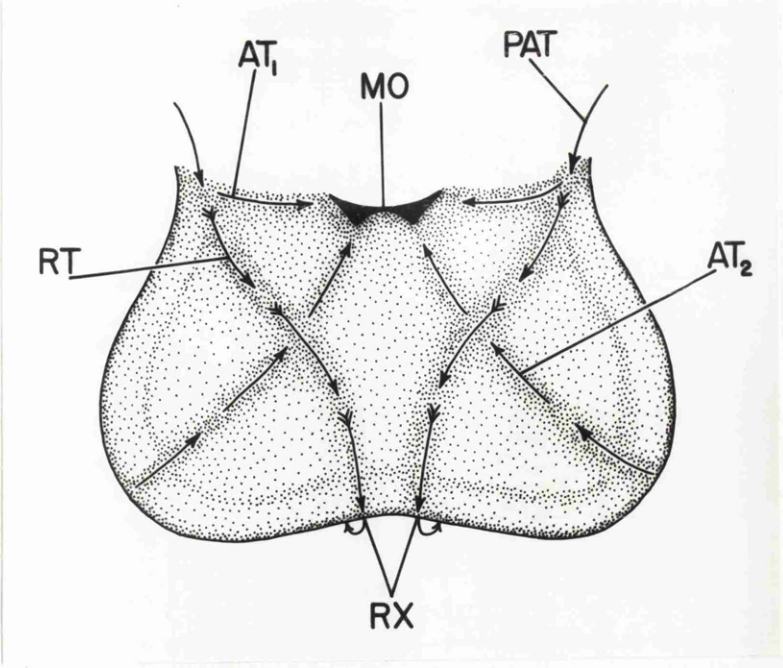


FIGURE 34

Palpal Development

In Ostrea edulis the upper palps are formed during the first 3 to 4 days after settlement (Cole, 1938). The upper palps bear three pairs of ciliary tracts, two pairs of adoral tracts (Fig. 34, AT_1 and AT_2) and a single pair of rejection tracts (RT). The first pair of adoral tracts (AT_1) resembles those of Heteranomia (Fig. 19, AT) and lead to the mouth from the dorso-lateral margins of the palps, while the second pair (Fig. 34, AT_2) resembles those of Lima (Fig. 28, AT) and traverses the palps diagonally from the ventro-lateral margins to the mouth. The rejection tracts (Fig. 34, RT) originate at the same points as the first pair of adoral tracts and pass diagonally, intersecting the second pair of adoral tracts at right angles, and terminate near the centre of the antero-ventral margin of the palps.

Feeding

The inhalant area is of the same magnitude as that in the Anomiidae and Pectinidae and extends along the ventral mantle margins from an anterior position opposite the palps to a postero-dorsal point adjacent to the fused ctenidial anlagen. Since the ctenidial axes are curved, the filaments radiate slightly from the axes and the width of the interfilamentary spaces near the ventral margin of the inner demibranch (Fig. 29, left inner demibranch; Fig. 32, right inner demibranch) is too great to be completely bridged by the anomalous-latero-frontal cilia (Atkins, 1938). Consequently some of the particles carried in the inhalant stream are not retained by

the ctenidia but pass through into the supra-branchial cavity. Nevertheless, filtration is more efficient than in the Anomiidae and Pectinidae.

In spat approximately 500 μ in length the majority of particles fall on the left inner demibranch, the larger ones impinging on the ventral portions of the demibranch where they are carried ventrally to the intermediary adoral tract (Fig. 29, IAT). Small particles are carried dorsally and enter the marginal adoral tract (MAT). A few particles reach the right ctenidium and most of these are transported ventrally to the marginal adoral tract (Fig. 30, MAT). Only a small number reaches the dorsal region of the right ctenidium where they enter the axial adoral tract (AAT) and travel to the palps along the proximal adoral tract (PAT). When development of the right inner demibranch is more advanced (Fig. 32) the large particles impinging on it travel to the ventral edge of the demibranch where they enter the intermediary adoral tract (IAT) while small particles are carried dorsally, those on the proximal lamella entering the axial adoral tract (AAT) while those on the distal lamella are conveyed to the marginal adoral tract (MAT). The intermediary and marginal adoral tracts merge anteriorly (Fig. 32).

All particles collected in the adoral tracts converge anteriorly near the palps. Those from the intermediary adoral tract of the left inner demibranch (Fig. 29, IAT) pass directly into the second adoral tract of the upper palp (Fig. 34, AT_2). Particles arriving at the palps along the marginal adoral tract (Fig. 29, MAT) may either pass over the lower palp to enter the second adoral

tract of the upper palp, or they may pass directly onto the upper palp at its dorso-lateral margin as do particles from the proximal adoral tract (PAT). Such particles are sorted according to size, the larger ones passing into rejection tract (Fig. 34, RT) while the smaller ones travel along the first adoral tract (AT_1) to the mouth.

Mytilidae

Mytilid larvae appeared in the plankton tows as early as March, reaching their peak during the summer months, while in autumn their numbers dwindled and only occasional larvae were encountered during the winter months. The late larvae of all species are eyed and the velar cilia have a dexioplectic metachronal wave. Since larvae and spat of Mytilus edulis Linné were most abundant the account below applies to this species. However, post-larvae of Modiolus modiolus (Linné), Modiolus barbatus (Linné), Modiolus phaseolinus (Philippi), and Musculus marmoratus (Forbes) were also examined and followed the same developmental pattern. The larvae of Mytilus edulis, Modiolus modiolus and Musculus marmoratus have been described by Rees (1950) while 'Mytilid A' (Rees, 1950) has been identified as Modiolus phaseolinus in a later paper (Rees, 1954). Post-larvae of 'Mytilid G' (Rees, 1954) were identified as Modiolus barbatus in the present investigation.

Ctenidial Development

On either side of the body, the mature veliger of Mytilus, approximately 290 μ in length, has 3 to 4 ctenidial filaments connected to one another by ciliary interfilamentary junctions. Immediately after metamorphosis, the 2nd and 3rd filaments of each side pair in the midline posterior to the foot (Fig. 35) where they are united to one another by ciliary interctenidial junctions located on the medial surface of the filaments (Fig. 36, ICJ). Anteriorly the 1st filament of each side forms a ciliary junction with the pedal wall.

FIGURE 35

Mytilus edulis. Early post-larva viewed from right side to show ciliary and water currents of the mantle cavity.

Length - 340 μ.

Large plain arrows	-	inhalant and exhalant water currents.
Small plain arrows	-	frontal and adoral ciliary currents of ctenidium.
Double arrows	-	ciliary currents of mantle.
Feathered arrows	-	ciliary currents leading away from mouth.

FIGURE 36

Mytilus edulis. Cross sections of the inner demibranch during successive stages in its differentiation. This method of ctenidial development was seen only in the Mytilidae where it was characteristic of all species examined. For explanation of this figure see pages 43 to 45.

LEGEND: AA - anterior adductor muscle, AB - axial blood vessel, CA - ctenidial axis, CF - cuticular fusion of marginal bridge with foot, DEZ - distal embryonic zone, E - eye spot, EX - exhalant aperture, F - foot, IAT - intermediary adoral tract, ICJ - interctenidial ciliary junction, IFJ - interfilamentary ciliary junction, IN - inhalant aperture, LC - position of lateral cilia, LP - lower palp, MAT - marginal adoral tract, MB - marginal bridge, MO - mouth, PA - posterior adductor muscle, PAT - proximal adoral tract, PEZ - proximal embryonic zone, PD - prodissoconch, P_1 - median papilla, RP - recurrent path of mantle, RX - rejection point of recurrent path, S - septum, UP - upper palp.

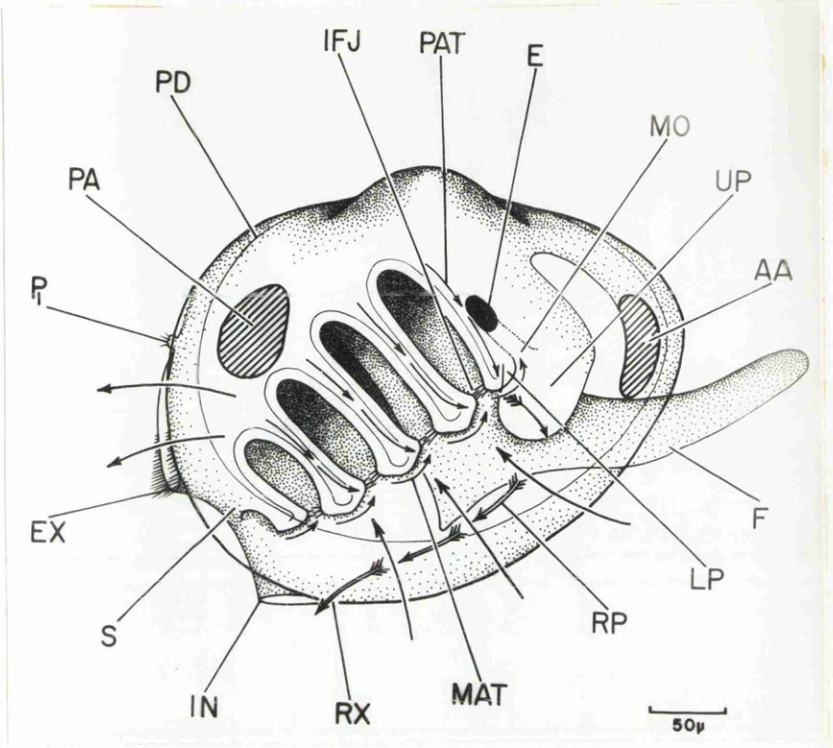


FIGURE 35

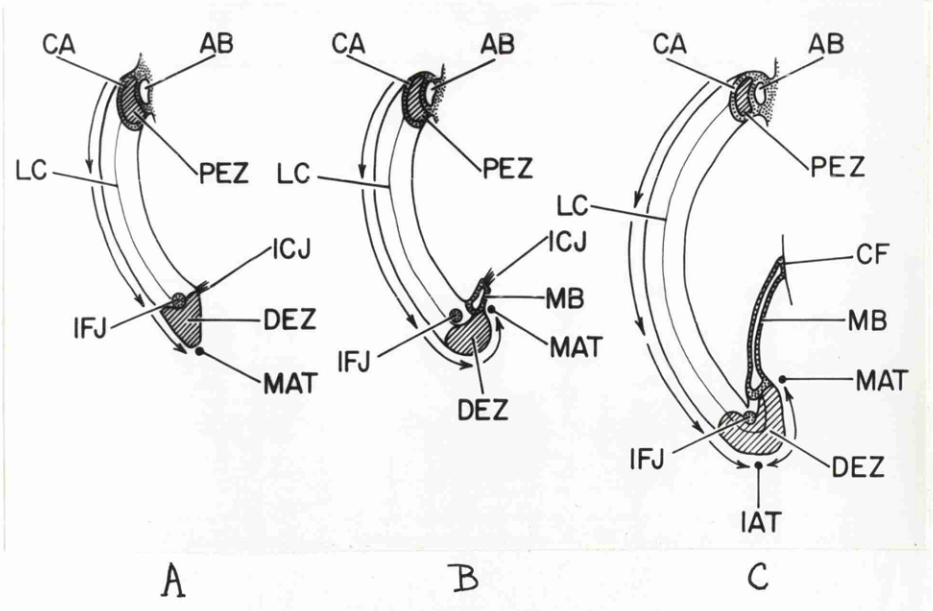


FIGURE 36

New filaments are formed from the fused anlagen by the papilla method (Fig. 2) as described by Lacaze-Duthiers (1856). Lateral cilia arise concurrently on both the anterior face of the newly formed papilla and the posterior face of the preceding one; the posterior face of the new papilla does not acquire cilia until another papilla is formed. As each papilla elongates its ventral end becomes enlarged into a capitulum (Fig. 2, CP) and it forms a ciliary interfilamentary junction (Fig. 35, IFJ) with the preceding filament. Eu-latero-frontal cilia and frontal cilia, beating ventrally, then appear, while two long cirrus-like cilia develop on the capitulum. Cilia on the capitulum beat anteriorly forming the marginal adoral tract (MAT). Transverse free-hand sections one filament in thickness show a concentration of nuclei, the distal embryonic zone (Fig. 36 A, DEZ), in the capitulum. In the remainder of the filament the nuclei are dispersed and the cells differentiated into the various components of the filament. However, a similar concentration of nuclei, the proximal embryonic zone (PEZ), is located in the ctenidial axis.

At an early stage the anterior filaments of each inner demibranch fuse with one another to form a marginal bridge (Fig. 36 B, MB). This bridge is formed by outgrowths from the medial surface of the filaments at the dorsal edge of the capitula in such a way that the original ciliary interctenidial junctions (Fig. 36 A, ICJ) are now located along the dorsal edge of the marginal bridge (Fig. 36 B, ICJ). The ciliary interfilamentary junctions (IFJ) persist and retain their original positions throughout post-larval development (cf. Fig. 36 A, B & C, IFJ). Anteriorly the ciliary junctions with the foot are replaced by a cuticular fusion (Fig. 36 C, CF). Thus when the

post-larva has reached a length of 600 μ the marginal bridge unites the first 6 filaments, while the 6th to 8th are united only by ciliary interfilamentary junctions and the 9th filament is without any junction.

Soon after the differentiation of the 10th filament, it becomes apparent that, anteriorly, the marginal adoral tract is no longer located at the extreme ventral edge of the demibranch, but occupies a position on the medial surface of the filaments between the ventral margin and the marginal bridge (Fig. 36 B, MAT). The frontal ciliary currents continue around the ventral edge of the demibranch to merge, as before, with the marginal adoral tract. The distal embryonic zone (Fig. 36 C, DEZ) produces ventral growth so that the filaments assume a J-shape and eventually the typical V-shape. Thus, the demibranch is differentiated into proximal and distal lamellae. The evidence in favour of this method of formation of the distal lamella, as opposed to that described by Lacaze-Duthiers (1856) for the same species, lies in three important facts.

1. The marginal adoral tract (Fig. 36 B & C, MAT) is located at the dorsal edge of the distal lamella there being, initially, no adoral tract along the ventral margin of the demibranch (Fig. 36 B). Only when 13 filaments are present is the intermediary adoral tract (Fig. 36 C, IAT) formed in this position.
2. The frontal ciliary currents of the distal lamella are initially dorsal (Fig. 36 B). After the appearance of the intermediary adoral tract, ventral frontal tracts are formed on the distal (Fig. 36 C), as on the proximal, portions of the filaments as they elongate.

3. The ciliary interfilamentary junctions (Fig. 36 A, B & C, IFJ) remain at the ventral edge of the demibranch throughout the differentiation of the distal lamella.

Thus, once a permanent connection has been established between the anterior filaments and the walls of the foot, the distal ends of the filaments are fixed and elongation can only occur ventrally so that the filaments assume the characteristic V-shape. As the marginal bridge is fused anteriorly to filament F_0, the growth of the distal portion of the 1st filament is retarded. Consequently, although formation of the distal lamella begins anteriorly, the depth of this lamella is greatest at the level of the 2nd filament. When approximately 19 filaments are present, the distal lamella is more than half the depth of the proximal lamella and a second row of ciliary interfilamentary junctions has formed in the proximal lamella. This row lies parallel to the ctenidial axis and at a distance of two-thirds the height of the anterior filaments from it.

Development of the outer demibranch begins in spat approximately 1.6 mm. in length and is similar to that of the inner.

Pallial Development

After metamorphosis, the mantle margins fuse with one another and with the ctenidial anlagen to form a septum (Fig. 35, S). Dorsal to the septum a trough-like protrusion of the mantle bearing conspicuous cirri marks the ventral limit of the exhalant aperture (EX), and a short median papilla (P_1) with terminal cirri marks its dorsal limit. A similar trough-like protrusion ventral to the septum forms

the posterior limit of the inhalant aperture (IN) and here the mantle edge is densely covered by cilia which beat out of the mantle cavity (RX). This point marks the end of the recurrent path (RP) which begins anteriorly near the palps and extends posteriorly near the mantle edge.

Palpal Development

Dissections of young spat show the upper palps to be somewhat kidney-shaped, the lateral portions extending further ventrally than the medial portions (Fig. 37). On the inner surface, medial and lateral portions are sharply delimited from one another by their ciliation. The former is densely covered by fine cilia beating adorally, while the lateral portions of each palp is raised into two ridges (R) separated by a groove along which runs a rejection tract (RT). The cilia on the ridges are stouter than those of the medial portion and their beat is directed toward the groove. Between the insertion lines of the upper and lower palps is a groove bearing an adoral tract (AT).

The lower palps form a deep flange posterior to the mouth which is apposed to the medial portion of the upper palps (Fig. 37), and extend laterally on either side as a narrow ridge continuous with the distal end of filament F_0 (Fig. 35, LP). The ciliary currents on the lateral portions lead anteriorly to the adoral tract (Fig. 37, AT).

Feeding

The posterior flanges of the mantle above and below the septum separate the inhalant and exhalant water currents

FIGURE 37

Mytilus edulis. Upper and lower palps with adjacent portions of filaments F_0 and F_1 viewed from posterior aspect to show ciliary currents of the palps and their relationship to the adoral tracts of the ctenidia.

Plain arrows - ciliary currents on exposed surface of palps and ctenidial filaments.

Discontinuous arrows - ciliary currents seen through lower palps.

Feathered arrows - rejection ciliary current of upper palps.

LEGEND: AT - adoral tract, F_0 & F_1 - filaments, LP - lower palp, MAT - marginal adoral tract, MO - mouth, PAT - proximal adoral tract, R - ridges of upper palp, RT - rejection tract, RX - point of rejection from upper palp, VFC - ventral frontal ciliary current.

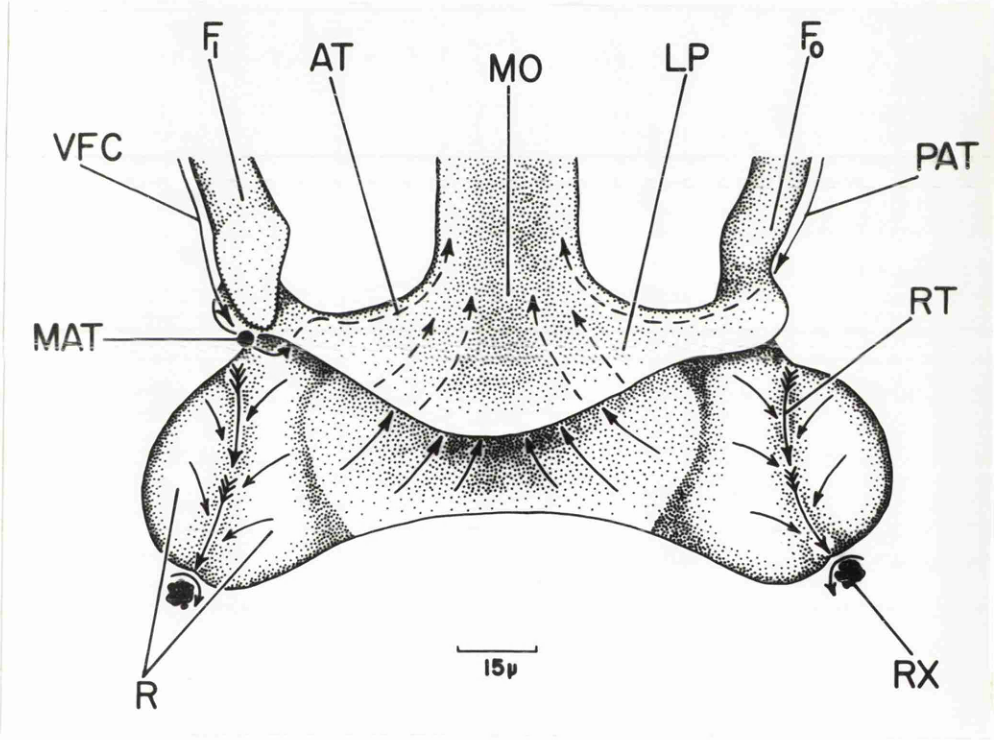


FIGURE 37

(Fig. 35). As the eu-latero-frontal cilia bridge the interfilamentary spaces, filtration of particles from the inhalant stream is almost complete. During feeding the shell valves are less widely open than in Heteranomia and Chlamys so that the majority of particles impinge on the ventral portions of the filaments. Here they are transported ventrally to the marginal adoral tract (MAT) and anteriorly to the lower palps (LP). Crossing the lateral portions of the lower palps they may either enter directly into the adoral grooves (Fig. 37, AT) or be diverted into the rejection tracts (RT) of the upper palps. The route taken seems to depend on the number of particles reaching the palps at one time. When this is excessive the mucous laded mass passes into the rejection tract but when the concentration of particles is low the smaller ones are carried into the adoral groove and only the larger ones enter the rejection tract. The proximal adoral tract (Fig. 35 & 37, PAT) leads directly to the adoral groove (Fig. 37, AT) between the upper and lower palps.

With the formation of the intermediary adoral tract (Fig. 36 C, IAT) the majority of particles collected by distal and proximal lamellae travel anteriorly along this tract to the point where it merges with the marginal adoral tract at the tip of filament F_0. The marginal adoral tract along the dorsal edge of the distal lamella plays a minor role, transporting only particles impinging directly on the dorsal portion of the distal lamella.

All particles rejected by the palps are rotated by cilia at the end of the rejection tract (Fig. 37, RX) until the mass is so large that it falls onto the mantle. It then passes posteriorly along the recurrent path (Fig. 35, RP) of the mantle and leaves the mantle cavity near the posterior limit of the inhalant aperture (RX).

Eulamellibranchia

Post-larval development was studied in 15 different species of Eulamellibranchia and these, together with the source of identification of the late larvae, are listed in Table I. Cursory observations were also made on a number of other species but post-larval development of these did not proceed far enough to enable them to be identified with any certainty. The velar cilia of all eulamellibranch larvae exhibit laeoplectic metachronal waves and the larvae are never eyed. It was seldom possible to rear post-larvae in laboratory cultures to the conclusion of ctenidial development, but spat of Tellina, Abra, Spisula, Mya, Thracia, Mysella and Hiatella collected in the field supplied later stages of development.

Ctenidial Development

Ctenidial development in the Eulamellibranchia follows the pattern described in such detail by Wasserloos (1911) for Cyclas cornea. With the exception of minor variations, the ciliary currents and genesis of the ctenidia are similar in all the genera examined and they may, therefore, be described concurrently.

Since the filaments are differentiated by the fold method (Fig. 3) the marginal bridge (MB) is a primary structure, but in other respects the ctenidia of eulamellibranch late larvae and early post-larvae show a marked resemblance to those of Mytilus (cf. Fig. 35 & 36). Generally there are 3 to 4 filaments on either side of the late larva and the ctenidial anlagen are fused to one another and to the siphonal septum. Following metamorphosis the 3rd and 4th

FIGURE 38

Lutraria lutraria. Early post-larva viewed from left side to show ciliary and water currents of mantle cavity which are characteristic of most Eulamellibranchia.

Length - 370 μ.

Large plain arrows - inhalant and exhalant water currents.

Small plain arrows - adoral ciliary currents of ctenidia and palps.

Double arrows - ciliary currents of mantle.

Feathered arrows - ciliary currents leading away from mouth.

FIGURE 39

Cross sections of a eulamellibranch ctenidium during successive stages in its differentiation. For explanation of this figure see pages 50 to 54 and also pages 79 to 81. Compare with Figures 58 and 59.

Embryonic zones are shown cross-hatched.

Ctenidial axis is shown as solid black area.

Regions of continuity between adjacent filaments are shown stippled.

LEGEND: AA - anterior adductor muscle, AAT - axial adoral tract, CA - ctenidial axis, DEZ - distal embryonic zone, F - foot, INS - inhalant siphon, LP - lower palp, MAT - marginal adoral tract, MB - marginal bridge, MO - mouth, O_1 - first ostium of left ctenidium, P_1 - median primary siphonal tentacle, $\overline{IP}_1$ - paired primary siphonal tentacle, $\overline{IP}_2$ - paired secondary siphonal tentacle, PA - posterior adductor muscle, PD - prodissoconch, PES - primary exhalant siphon, PEZ - proximal embryonic zone, RE - rectum, RP - recurrent path of mantle, YUP - Y-shaped groove of upper palp.

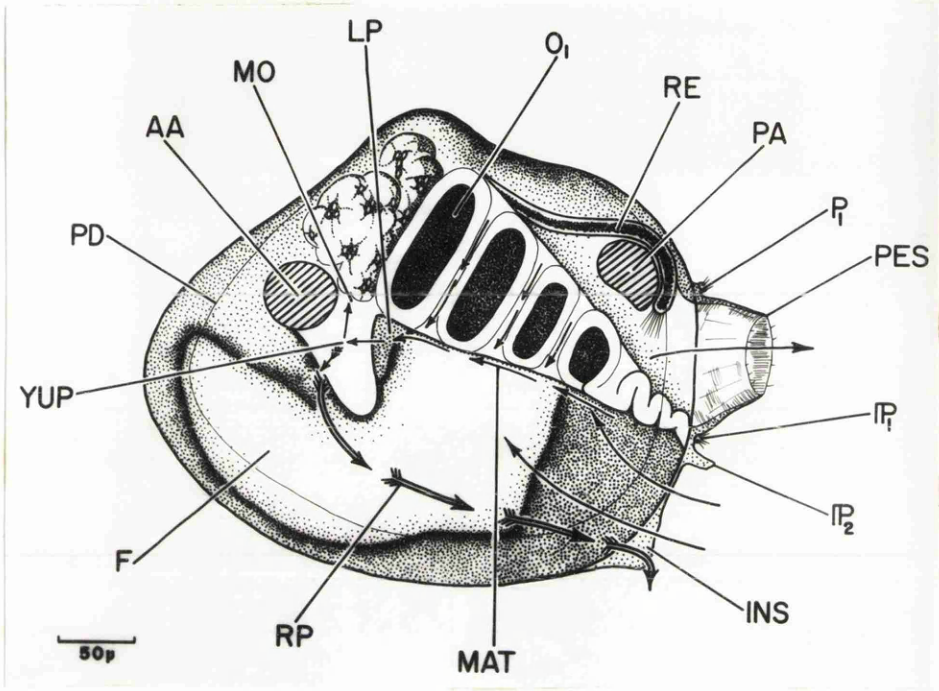


FIGURE 38

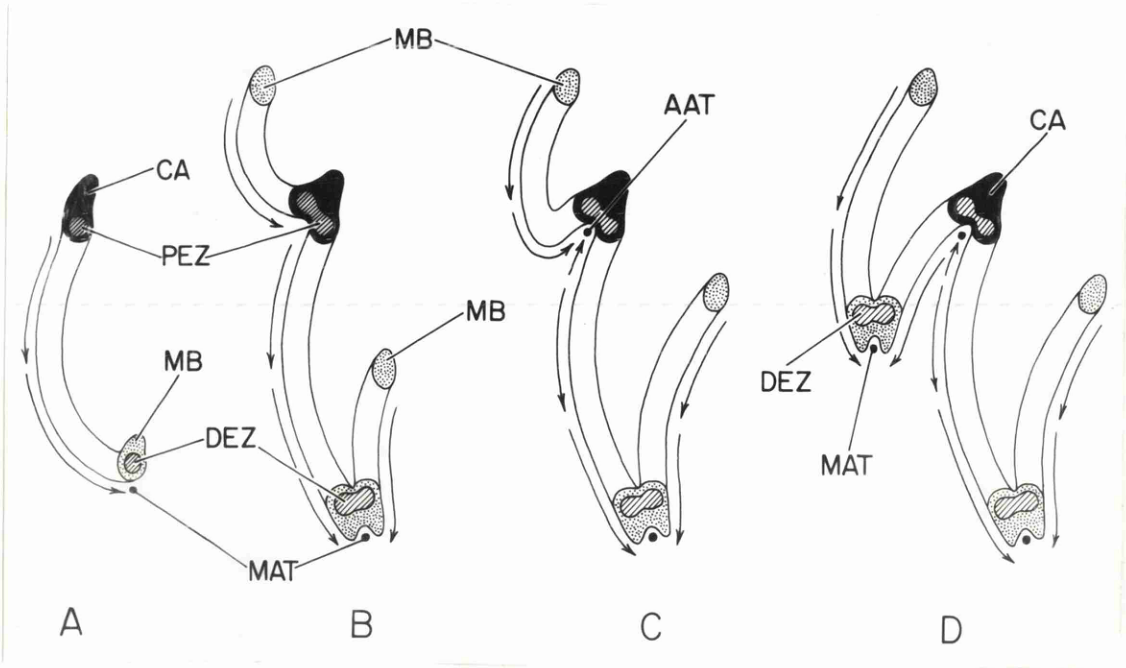


FIGURE 39

TABLE I

	Larval Identification
Family Erycinidae	
Kellia suborbicularis (Montagu)	*Glycymeris glycymeris* (Rees, 1950)
Family Montacutidae	
Mysella bidentata (Montagu)	*Mysella bidentata* (Rees, 1950)
Family Tellinidae	
Tellina spp.	**Tellina* (Rees, 1950)
Family Scrobiculariidae	
Abra spp.	**Abra* (Rees, 1950)
Family Solenidae	
Cultellus pelucidus (Pennant)	*Cultellus pelucidus* (Rees, 1950)
Ensis siliqua (Linné)	*Ensis siliqua* (Rees, 1950)
Family Mactridae	
Spisula subtruncata (da Costa)	*Spisula subtruncata* (Rees, 1950)
Spisula solidissima Dillwyn	*Spisula solidissima* (Sullivan, 1948)
Family Lutrariidae	
Lutraria lutraria (Linné)	Mactrid G (Rees, 1954)
Family Myidae	
Mya arenaria Linné	(*Lyonsia*) (Rees, 1950) *Mya arenaria* (Sullivan, 1948)
Family Hiatellidae	
Hiatella arctica (Linné)	*Hiatella arctica* (Rees, 1950)
Family Veneridae	
Venus spp.	**Venus* (Rees, 1950)
Venerupis pullastra	*Venerupis pullastra* (Quayle, 1952)
Family Pholadidae	
Zirfaea crispata (Linné)	*Zirfaea* (Rees, 1950)
Family Thraciidae	
Thracia sp.	Only spat collected in field.

* Prodissoconch had general shape and hinge structure of this genus, but the various species could not be distinguished or identified.

filaments pair in the midline behind the foot where the marginal bridges are united by ciliary or organic interctenidial junctions. Anteriorly the marginal bridges may form either ciliary or organic junctions with the pedal wall. The ciliary currents of the ctenidia are identical to those of Mytilus (cf. Fig. 35 & 38).

Transverse serial sections of Mya spat revealed two concentrations of nuclei, the proximal and distal embryonic zones, similar to those of Mytilus except that the distal embryonic zone is located within the marginal bridge rather than adjacent to it (cf. Fig. 36 A & 39 A, DEZ). An early post-larva of Ensis stained with neutral red showed the stain, after several weeks, to be concentrated in the distal regions of the filaments indicating maximum elongation in the proximal regions. Further evidence for the activity of the proximal embryonic zone comes from the mode of formation of antagonistic frontal tracts in late post-larvae of Ensis. In spat approximately 650 μ in length the subaxial regions of the filaments clearly exhibit dorsal frontal ciliary currents. Unfortunately, the number of post-larvae reared to this size were insufficient to permit a thorough investigation of the frontal tracts and it is not known whether the subaxial regions of the filaments bear ventral frontal tracts in addition to the dorsal ones. Atkins (1936), in describing the adjacent antagonistic frontal tracts in Ensis, suggests that the coarse, ventrally beating cilia "may normally be motionless and only active on stimulation." This would explain the apparent lack of ventral frontal tracts adjacent to the dorsal ones. As elongation of the filaments continues, the dorsal frontal tracts occupy an increasing proportion of their frontal surfaces, but are never present

in the distal regions. In spat 700 μ in length the dorsal half of the anterior filaments exhibit dorsal frontal currents. In Mysella dorsal frontal tracts --- but not adjacent antagonistic tracts --- in the subaxial region, together with an axial adoral tract, are present in spat 580 μ in length. Unlike Ensis, these dorsal frontal tracts remain restricted to a short subaxial region. In other genera tracts similar to those of Mysella are formed but not until after differentiation of the distal lamella. No such tracts are ever developed in Tellina and Abra.

Evidence for elongation from the distal embryonic zone is lacking until after the formation of the first row of organic interfilamentary junctions. This row of junctions lies parallel to the ctenidial axis and serves as a reference point for determining elongation from the distal embryonic zones. Following elongation of the filaments between the first row of junctions and the ventral margin of the demibranch, a second row of junctions develop parallel, but ventral to the first. This was observed in both Lutraria and Ensis. Thus it appears that both embryonic zones contribute to the elongation of the filaments, but the relative time and extent of their activity probably varies considerably in different genera and would merit further investigation.

While the filaments increase in length, the marginal bridge shows a comparable increase and may attain a depth equal to two-thirds the length of the filaments. Immediately posterior to the foot a tissue bridge, the post-pedal bridge, is formed by the fusion of outgrowths from the dorsal edge of each marginal bridge. The post-pedal bridge is particularly prominent in genera in which

the junctions between the foot and marginal bridges are ciliary. Its position varies with the size and location of the foot relative to the inner demibranchs, being at the level of the 9th or 10th filaments in Mysella and Mya. The ventral edge of each demibranch, bearing the marginal adoral tract, becomes broad and flat while guarding cilia (Atkins, 1937 a) appear on the outer, but not the inner, side of this tract in Tellina and on the inner, but not the outer, side in Mysella.

Differentiation of the distal lamella usually commences in spat approximately 1.2 mm. in length with 14 filaments in each demibranch, but not in Tellina until the spat reaches a length of 1.8 mm. and has 19 filaments in each demibranch. The first indication of the distal lamella is a series of thickenings (Fig. 40 R) of the marginal bridge (MB), adjacent to its ventral margin, caused by proliferation from the dorsal side of the distal embryonic zones. Between these thickenings, invaginations (I) appear which are later perforated to form ostia (CDL). Perforation commences opposite the 8th or 9th interfilamentary space of the proximal lamella in Mya and Tellina and proceeds both anteriorly and posteriorly. Frontal and eu-latero-frontal cilia appear prior to perforation, while lateral cilia are not present until after perforation is complete. The frontal currents on the distal lamella are ventral and toward the marginal adoral tract (MAT) at the ventral edge of the demibranch. In Tellina a second row of guarding cilia appear on the inner side of the marginal adoral tract, while in other genera this tract becomes enclosed in a groove (MG) formed by the ventral enlargements of the filaments.

FIGURE 40

Thracia sp. Inner demibranch during formation of distal lamella by perforation of the marginal bridge. Portion shown is of the left inner demibranch, seen from the medial aspect, and includes filaments 3 to 9 as indicated by numbers on the proximal lamella.

LEGEND: I - invagination representing incipient ostium, IFB - interfilamentary bridge of proximal lamella, MAT - marginal adoral tract, MB - marginal bridge, MG - marginal food groove, ODL - ostium of distal lamella, PL - proximal lamella, R - ridge representing incipient filament of distal lamella.

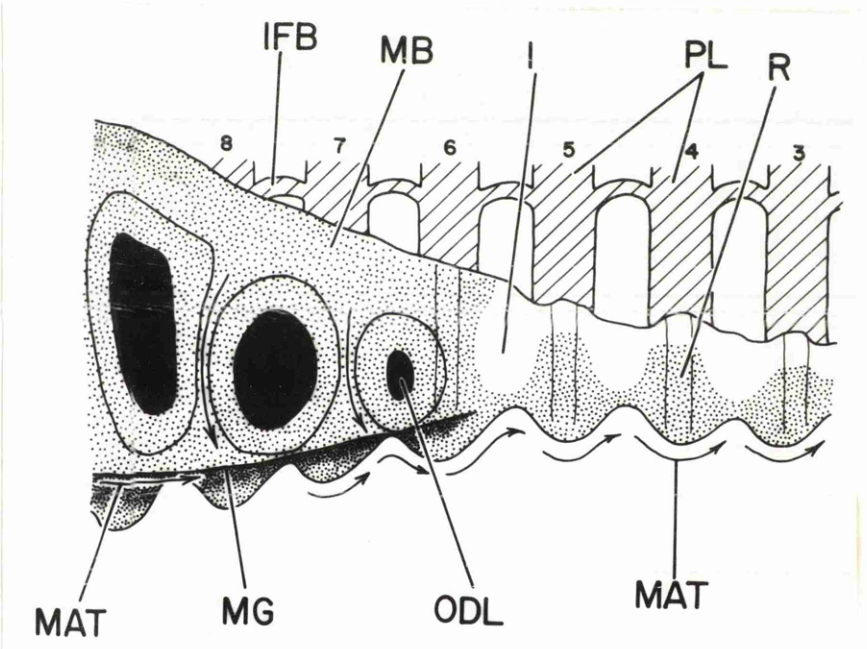


FIGURE 40

None of the post-larvae reared in the laboratory from late larvae reached the stage at which development of the outer demibranch begins and consequently observations were limited to occasional spat, at appropriate stages of development, collected in the field. The outer demibranch forms by perforation of a fold extending dorsally from the ctenidial axis as described by Wasserloos (1911) and thus differs from the outer demibranch of Heteranomia, Chlamys and Mytilus in that the filaments are directed dorsally (Fig. 39 B). The frontal tracts are ventral and lead to the axial adoral tract (Fig. 39 C, AAT). Attachment of the marginal bridge (MB) to the mantle causes elongation of the filaments to occur ventrally, and results in the formation of J-shaped and later V-shaped filaments (Fig. 39 C & D). Stages corresponding to Figure 39 C were observed in both Hiatella and Mya. In Hiatella further development of the outer demibranch consists only of continued ventral elongation of the filaments, there being no fusion of the filaments at the ventral margin of the demibranch, nor an adoral tract along this margin in the adult (Atkins, 1937 b). However, in Mya elongation and differentiation continues from the axial region (proximal embryonic zones) producing proximal portions of the filaments bearing ventral frontal tracts (Fig. 39 D). A marginal adoral tract (MAT) is formed along the ventral margin of the demibranch where the filaments are broadly fused to one another in such a way that the tracts of lateral and eu-latero-frontal cilia are interrupted. The origin of this fusion was not determined, but the interruption of the tracts of lateral and eu-latero-frontal cilia at this point suggests that the

proximal lamella may be formed by perforation of a previously undifferentiated portion of the original fold, lying between the filaments of the distal lamella and the axis.

Pallial Development

All eulamellibranch post-larvae studied, with the exception of Kellia, developed a recurrent path on the mantle originating anteriorly near the palps and passing posteriorly to the mantle margin below the extremity of the ctenidial axis (Fig. 38, RP). In Mysella, Tellina and Abra the tract is not continuous anteriorly but consists of small groups of long cirrus-like cilia located near the palps. In Kellia the recurrent path commences adjacent to the palps and continues anteriorly to the margin of a large projection of the mantle forming the inhalant region. Fusion of the mantle folds and the development of the siphons will be described separately below.

Palpal Development

The upper palps of eulamellibranch post-larvae closely resemble those of Nucula (Part I, Fig. 9). Each palp bears a Y-shaped groove (Fig. 38,YUP), the stem and one arm of the 'Y' bearing an adoral tract leading from the posterior margin of the palp lamella to the mouth, while the second arm diverges from the adoral tract and leads to the antero-ventral margin as the rejection tract. In Tellina and Abra palpal development is extremely rapid, the palps being as large as the ctenidia in young post-larvae. In spat 800 μ in length the palps are already miniature replicas of those of the adult (Yonge, 1949).

Siphonal Development

The initial stages of siphonal development are fairly uniform in all siphonate eulamellibranchs, with the exception of Tellina and Abra, but in later development variations occur which are correlated with the degree of mantle fusion exhibited in the adult (Yonge, 1948, 1949 & 1957). Siphon development in Tellina and Abra bears no relation to that of other eulamellibranchs and will not be described here.

A. Siphonal Septum

The siphonal septum, formed by the fusion of the mantle margins at the posterior extremity of the ctenidial axes, is invariably present in the late larvae of all eulamellibranchs and is fused with the ctenidial anlagen.

B. Primary Exhalant Siphon

The primary exhalant siphon, which represents the siphonal membrane typically terminating the exhalant siphon of the adult, may be present in the late larva, as in Cultellus (Fig. 41) and Zirfaea, but is more usually formed immediately after metamorphosis. Situated dorsal to the siphonal septum, it consists of a delicate membraneous tube (Fig. 38, PES) formed from the inner mantle fold (Yonge, 1957), the wall of which contains both circular and longitudinal muscles. Whereas, in the post-larvae of all siphonate genera examined, the structure of the primary exhalant siphon is constant, the form varies considerably (cf. Fig. 49 & 53). It is generally curved or

FIGURE 41

Cultellus pellucidus. Mature veliger showing primary exhalant siphon (arrow).

Length - 330 μ. x 130

FIGURE 42

Unidentified species. Primary exhalant siphon partially withdrawn and aperture completely closed due to contraction of circular muscles.

Length - 830 μ. x 130

FIGURE 43

Ensis siliqua. Primary exhalant siphon during extension showing distal constriction of aperture due to contraction of circular muscles and proximal dilation due to water current produced by lateral cilia of ctenidia.

Length - 1.1 mm. x 130

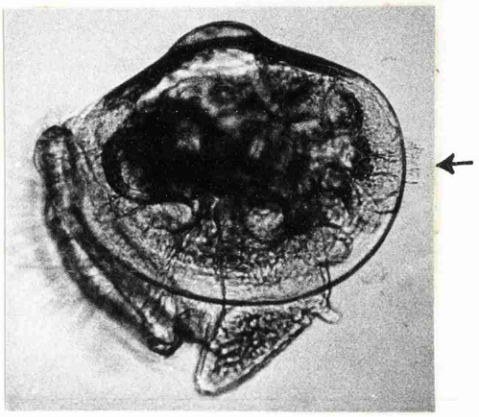


FIGURE 41

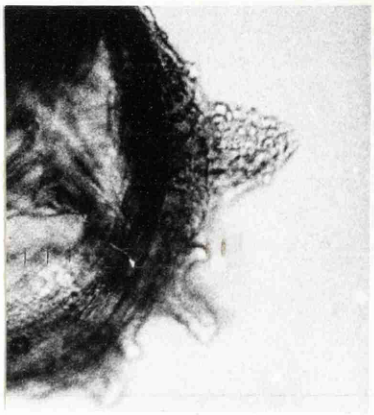


FIGURE 42

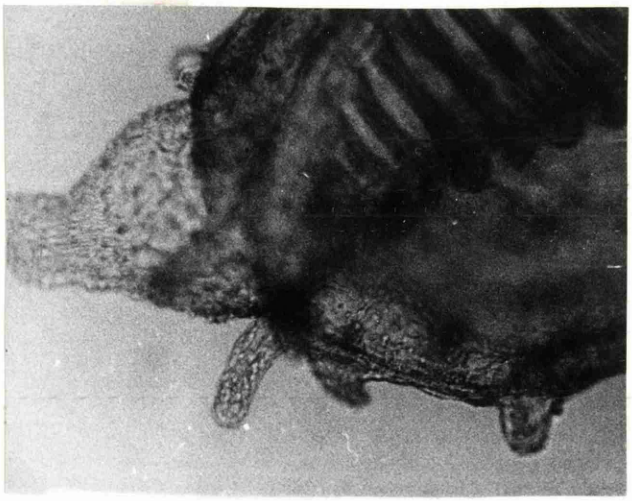


FIGURE 43

directed slightly upward so that the exhalant current exits dorsally rather than posteriorly.

Careful observation demonstrates most convincingly that extension of the primary exhalant siphon is not due to dilation of blood sinuses. In young spat movement of plasma cells in the mantle margins is clearly visible and undoubtedly would be even more obvious in the transparent siphon, but no such movement was ever correlated with siphonal extension. The latter is also entirely independent of the sudden variations in water pressure within the mantle cavity produced by the action of the adductor muscles. Extension is unimpaired by the removal of both shell valves --- provided the mantle is not torn in the region of the supra-branchial cavity --- and occurs when the lateral cilia commence to beat strongly. Clearly, pressure in the supra-branchial cavity, created by the activity of the lateral cilia of the ctenidia, is solely responsible for the extension of the primary exhalant siphon. A similar method of extension of the siphons in adult Mya arenaria has been described by Chapman and Newell (1956). Frequently the primary exhalant siphon was observed to be closed by the rapid contraction of the circular muscles and then more slowly inflated, the distal circular muscles constricting the aperture (Fig. 42) while the dilation progressed from the proximal portion (Fig. 43) to the tip. When withdrawn the primary exhalant siphon is introverted (Fig. 44 & 45) and its extension from this position by the same process is seen in Figures 46 to 49. The diameter and length of the siphon are controlled by the interaction of pressure within the supra-branchial cavity and the tension exerted by the circular and longitudinal muscles.

FIGURE 44

Lutraria lutraria. Primary exhalant siphon almost completely withdrawn and introverted.

Length - 530 μ. x 130

FIGURE 45

Lutraria lutraria. Drawing to clarify siphonal structure depicted in Figure 44. Note introversion of retracted primary exhalant siphon (PES).

x 130

LEGEND: CT - ctendium, INB - infra-branchial cavity, ML - mantle lobes forming ventral limit of inhalant area, P_1 - median primary siphonal tentacle, IP_1 - paired primary siphonal tentacles, IP_2 - paired secondary siphonal tentacles, PES - primary exhalant siphon, SB - supra-branchial cavity.

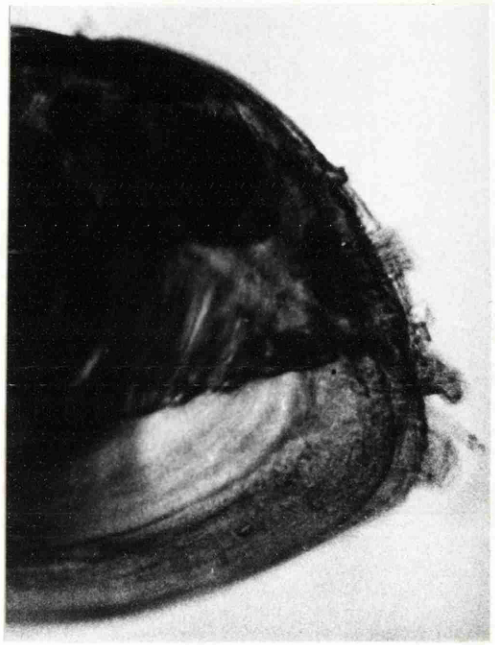


FIGURE 44

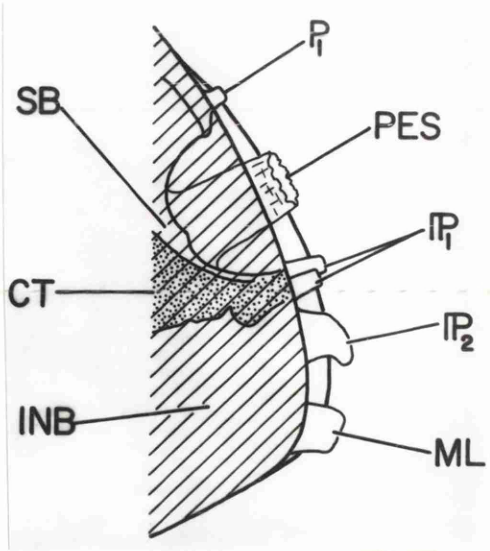


FIGURE 45

FIGURE 46

Spisula subtruncata. Introverted primary exhalant siphon with extension just beginning. x 80

FIGURE 47

Spisula subtruncata. Primary exhalant siphon half extended. Length of specimen - 1.0 mm. x 80

FIGURE 48

Lutraria lutraria. Primary exhalant siphon almost fully extended but with aperture still closed by contraction of distal circular muscles. x 80

FIGURE 49

Spisula subtruncata. Primary exhalant siphon fully extended. Same specimen as Figures 47 and 54.

Length of specimen - 1.0 mm. x 80

FIGURE 46

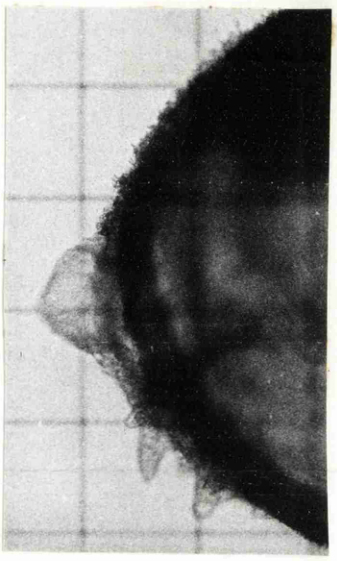


FIGURE 47

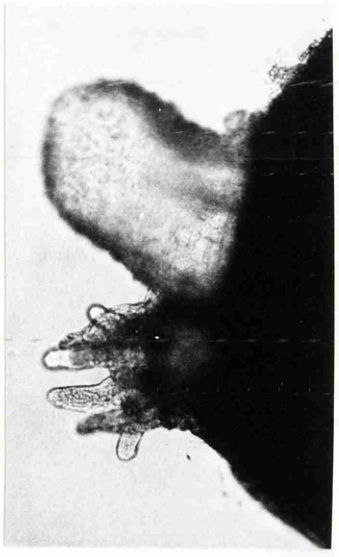


FIGURE 48

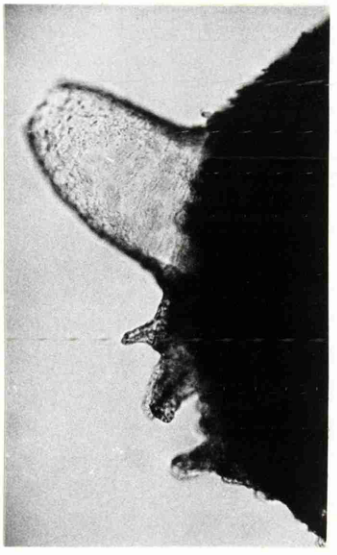


FIGURE 49

While the primary exhalant siphon is inflated passively and rather slowly, its withdrawal is extremely rapid. For a long time, it had been observed that this rapid withdrawal, together with the peculiar habit of introverting the siphon on retraction (Fig. 44 & 45), was characteristic of all siphonate spat, but the mechanism by which this was achieved remained elusive. While studying the ciliary currents on the ctenidia of a young post-larva of Spisula, from which the shell valves had been removed, it was unexpectedly found that the behaviour of the siphon was quite normal. Upon closer examination, using a microscope magnification of 675 diameters, the delicate retractor mechanism was seen in action. Later dissections of Spisula post-larvae verified the initial observations.

Along the mid-dorsal line of the inner surface of the primary exhalant siphon, there is attached a membrane (Fig. 50 & 51, SM) which projects slightly into the siphonal lumen. A retractor muscle (SR) lies along the free ventral edge of this membrane. The muscle fibres vary in length and are inserted along the edge of the membrane, the longest reaching approximately two-thirds the length of the siphon where they attach directly. The retractor fibres originate along the dorsal side of the wall of the rectum where it passes over the posterior adductor muscle (Fig. 52, SR). This was verified in sectioned material of Spisula spat. Contraction of this muscle causes simultaneous withdrawal (Fig. 53 & 54) and introversion of the siphon (Fig. 44 & 45), bringing it within the confines of the mantle cavity. In view of the striking similarity in the behaviour of the siphon in all genera, and the

FIGURE 50

Lutraria lutraria. Siphons showing siphonal retractor muscle and siphonal membrane within lumen of the primary exhalant siphon.

x 80

FIGURE 51

Lutraria lutraria. Drawing to clarify the siphonal structure depicted in Figure 50. At the base of the primary exhalant siphon note the demarcation line representing incorporation of the middle mantle fold (MM) while proximally there is a second demarcation representing the inner surface of the outer fold (IOM). Proximal to the second demarcation both siphons are enclosed in a thin sheet of periostracum (PE). x 80

LEGEND: CT - ctenidium, D - edge of dissoconch, IOM - inner surface of outer mantle fold, MM - middle mantle fold, P_1 - median primary siphonal tentacle, IP_1 - paired primary siphonal tentacles, IP_2 - paired secondary siphonal tentacles, PE - periostracum, PES - primary exhalant siphon, PS - pallial sinus, SM - siphonal membrane within lumen of primary exhalant siphon, SR - siphonal retractor muscle at free margin of siphonal membrane, SS - siphonal septum.

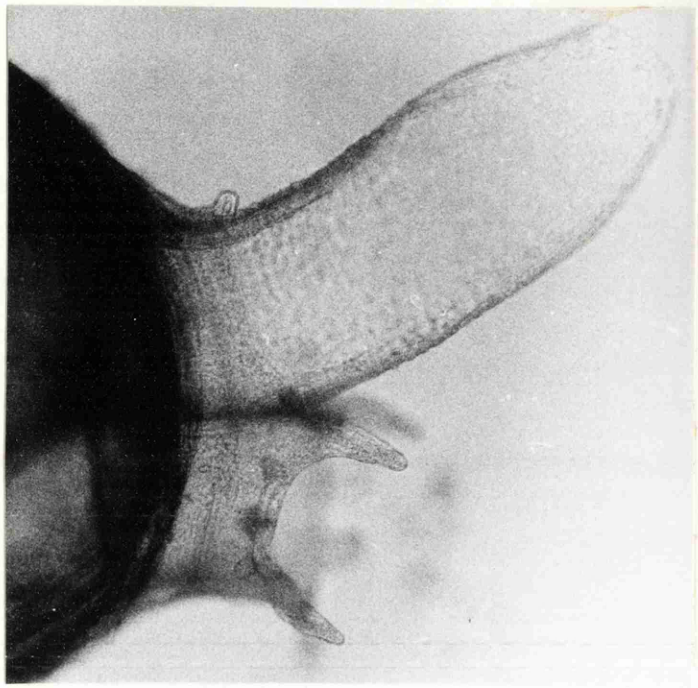


FIGURE 50

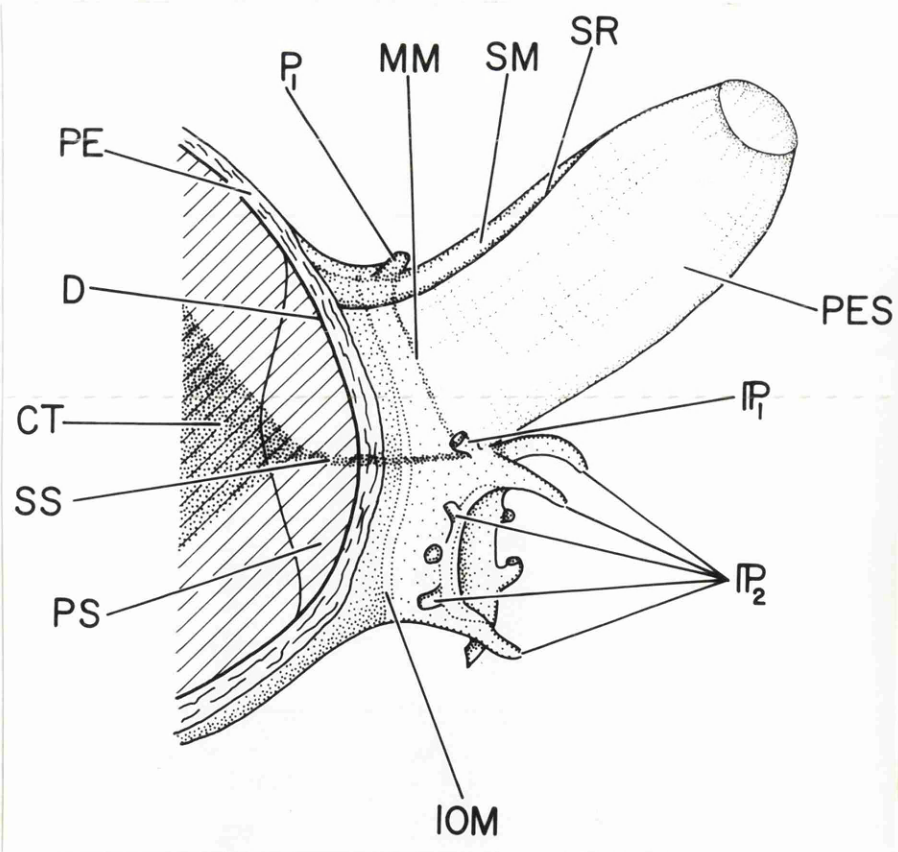


FIGURE 51

FIGURE 52

Ensis siliqua. Late post-larva showing siphonal retractor muscle (SR) near the postero-dorsal margin of the shell where it can be traced to its origin on the wall of the rectum (RE). The siphons are completely withdrawn. x 80

FIGURE 53

Venerupis pullastra. Withdrawal of primary exhalant siphon began during the 1 second exposure of this photograph giving a double image of the siphon. Note the evidence of contraction of the siphonal retractor(s?) in the proximal region.

Length of specimen - 660 μ. x 130

FIGURE 54

Spisula subtruncata. Withdrawal of primary exhalant siphon commencing and showing contraction of siphonal retractor (s?). Same specimen as in Figures 47 and 49.

Length of specimen - 1.0 mm. x 80

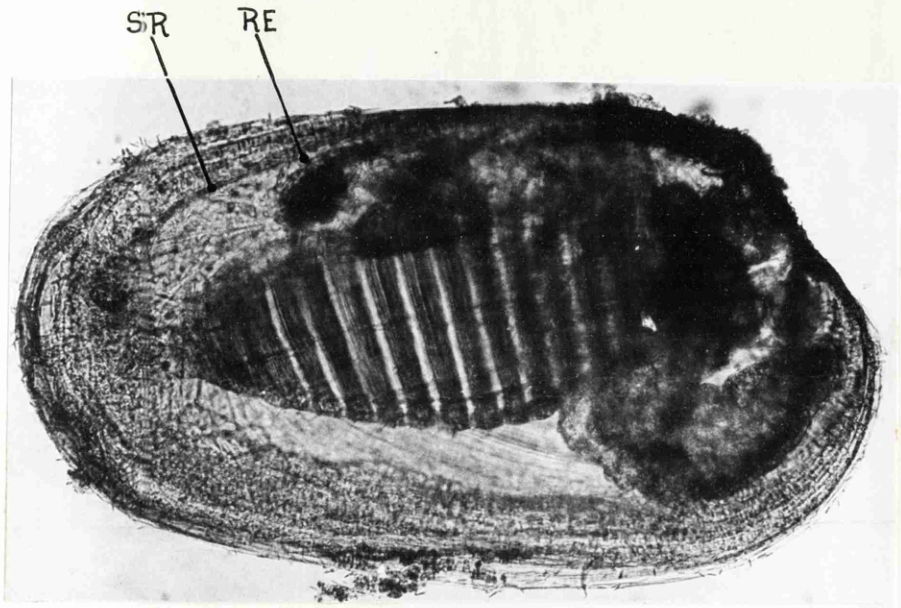


FIGURE 52

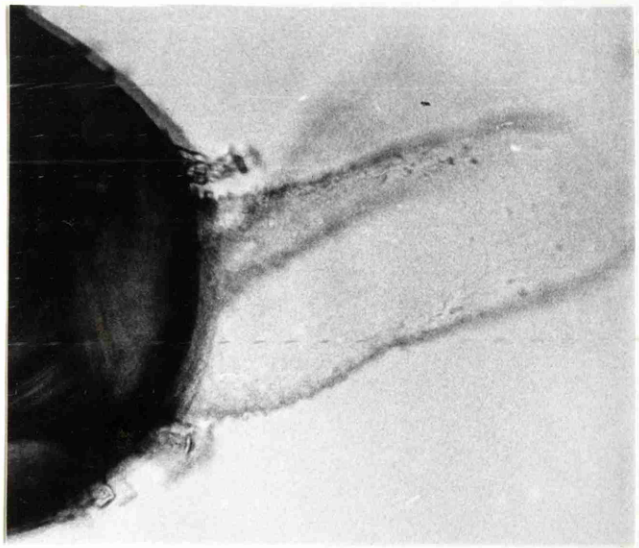


FIGURE 53

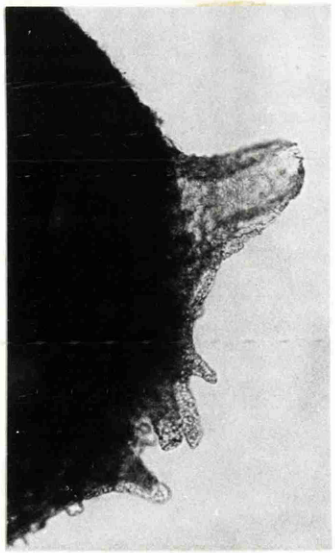


FIGURE 54

presence of the retractor muscle in photographs of Ensis, Lutraria and Spisula, it is almost certain that this retractor mechanism is invariably associated with the primary exhalant siphon of all eulamellibranch post-larvae. Photographs of Spisula (Fig. 54) and Lutraria (Fig. 55) suggest the presence of a similar ventral retractor originating at the siphonal septum.

As far as could be determined there is but one mention of a siphonal retractor of this type described in the literature. Yonge (1946) in his description of adult Aloidis gibba gives a brief account of two retractor muscles, one mid-dorsal, the other mid-ventral, of the primary exhalant siphon. These extend along the proximal half of the primary exhalant siphon and cause closure but not the retraction and introversion described here. From Yonge's account it appears that the retractor muscles constitute a part of the siphonal wall rather than being located along the edge of a membrane, but it is probable that they represent a modification of the retractor mechanism in the spat.

C. Siphonal Tentacles

Shortly after the formation of the primary exhalant siphon, a single median papilla (Fig. 38, P_1) arises dorsal to it and a pair of papillae ($\mathbb{P}_1$) appear at the base of the siphonal septum. These primary siphonal tentacles become incorporated into the outer, common ring of tentacles in the adult and are formed from the middle mantle fold (Yonge, 1957). Initially the tentacles are short and blunt, their tips being enlarged into disc-like structures bearing

FIGURE 55

Lutraria lutraria. Primary exhalant siphon with suggestion of a ventral siphonal retractor similar to the dorsal one.

x 80

FIGURE 56

Zirfaea crispata. Early post-larva showing the distinctive curvature of the inhalant siphon.

Length - 490 μ. x 130

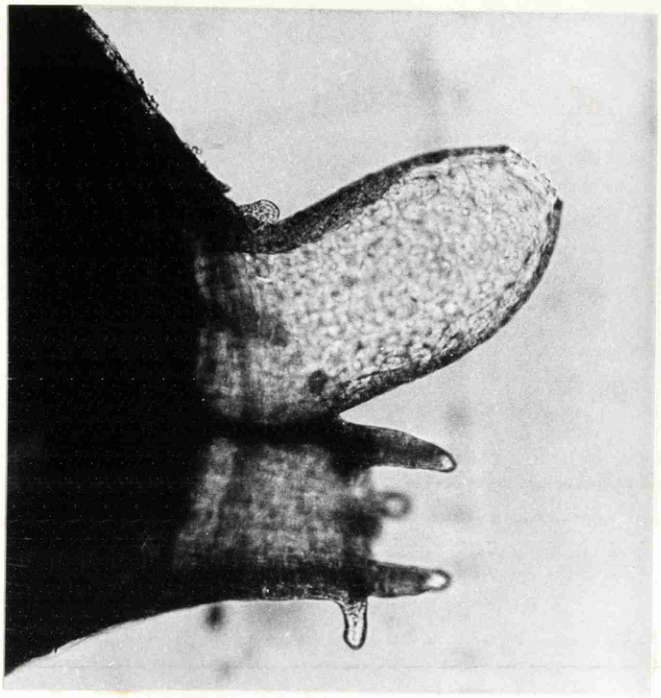


FIGURE 55

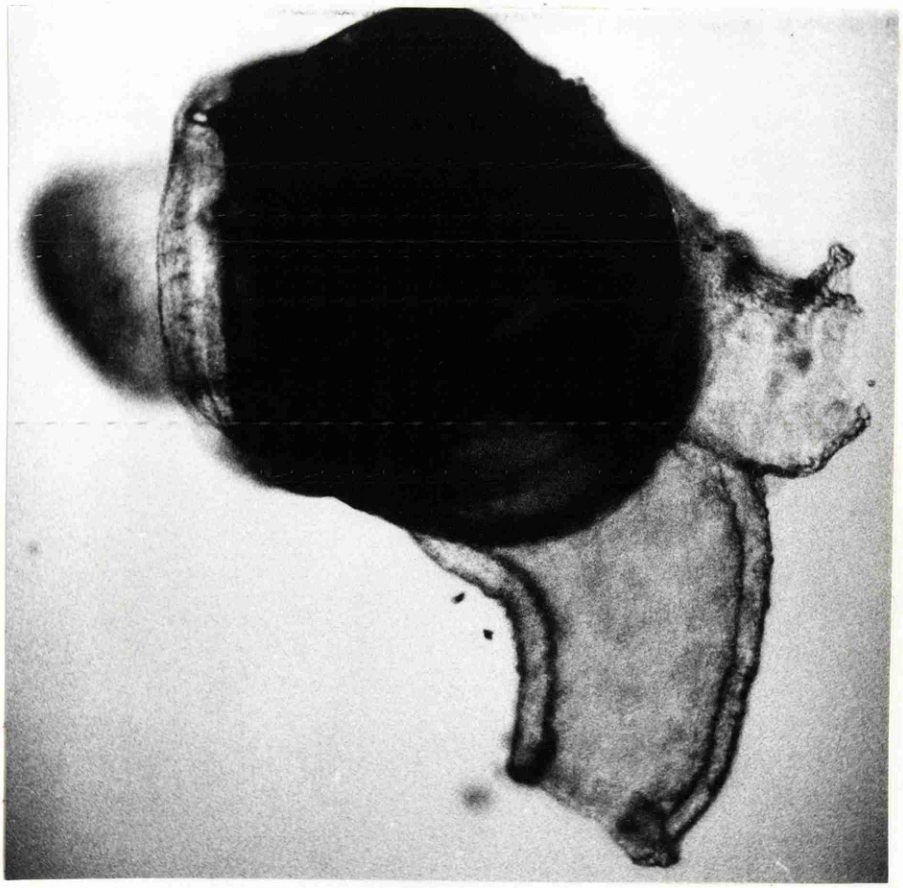


FIGURE 56

rather conspicuous stiff cirri. Occasionally, the rudiments of these tentacles are present prior to setting, but more usually they are formed shortly after metamorphosis.

A little later a pair of secondary papillae (Fig. 38, P_2) appear ventral to the primary ones (P_1) at the base of the siphonal septum. The secondary papillae differ markedly from the primary ones in appearance, being of stouter form and rounded terminally, while cirri, if present, are short. These differences are significant for the secondary papillae represent the first of the inner ring of tentacles encircling the inhalant siphon of the adult and are formed from the inner mantle fold (Yonge, 1957).

At the ventral limit of the presumptive inhalant aperture the inner mantle fold on each side enlarges to form a projecting lobe (Fig. 44 & 45, ML). When the foot is withdrawn and the animal quiescent, the mantle margins on each side, anterior to the projecting lobes, are closely applied to one another, so that the functional inhalant opening (Fig. 38, INS) is confined to the posterior region. The projecting lobes then form a flange at the ventral limit of the restricted inhalant aperture. Along the ventral edge of the projecting lobes, on the inner surface of the mantle is located a small area densely covered with cilia beating posteriorly and over the mantle edge. This marks the end of the recurrent path (Fig. 38, RP) of the mantle.

D. Fusion of Mantle Folds and Elongation of Siphons

Fusion of the inner mantle folds mid-ventrally, establishing a permanent separation of inhalant and pedal apertures,

may occur at any time during post-larval development; in Mya and Zirfaea it occurs immediately after metamorphosis, but in the venerids at a much later stage. From the mid-ventral point, fusion of the inner mantle folds proceeds posteriorly to the extremity of the projecting lobes (Fig. 44 & 45, ML) and the inhalant siphon begins to elongate from its proximal end. This elongation is quite extensive in Venerupis and Zirfaea, and is rather unique in the latter genus in that the dorsal side of the inhalant siphon grows more rapidly than the ventral side and results in a curved structure pointing ventrally. Thus the two siphons of Zirfaea (Fig. 56) diverge from one another like the arms of a 'T'.

Further fusion of the mantle, incorporating the middle mantle fold, is accompanied by elongation of both siphons (Fig. 50 & 51). As they extend beyond the shell margin a distinct line of demarcation, which appears as a slightly thickened ridge (MM), encircles the base of the primary exhalant siphon. Meanwhile, secondary papillae (P_2) arising in pairs between the first pair and the projecting lobes (Fig. 45, ML) have formed around the aperture of the inhalant siphon. Later primary papillae develop at the margin of the middle mantle fold to encircle both siphons and form the outer common ring of tentacles. Siphon development in the Veneridae, Cardiidae and Solenidae, where the siphons of the adult are of Type B (Yonge, 1957), stops at this point.

In other families, where the siphons of the adult are of Type C (Yonge, 1957), another less distinct demarcation line appears relatively late in post-larval development. This line (Fig. 50, 51 & 57, IOM) marks the incorporation of the inner surface of

FIGURE 57

Spisula subtruncata. Siphons of juvenile showing incorporation of various mantle folds and the mid-dorsal and mid-ventral fusion lines marked by rows of papillae.

LEGEND: D - dissoconch, DF - dorsal fusion line, INS - inhalant siphon, IOM - inner surface of outer mantle fold, MML - middle mantle fold, P_1 - median primary siphonal tentacle, IP_1 - paired primary siphonal tentacle, IP_2 - paired secondary siphonal tentacle, PE - periostracum, PES - primary exhalant siphon, VF - ventral fusion line.

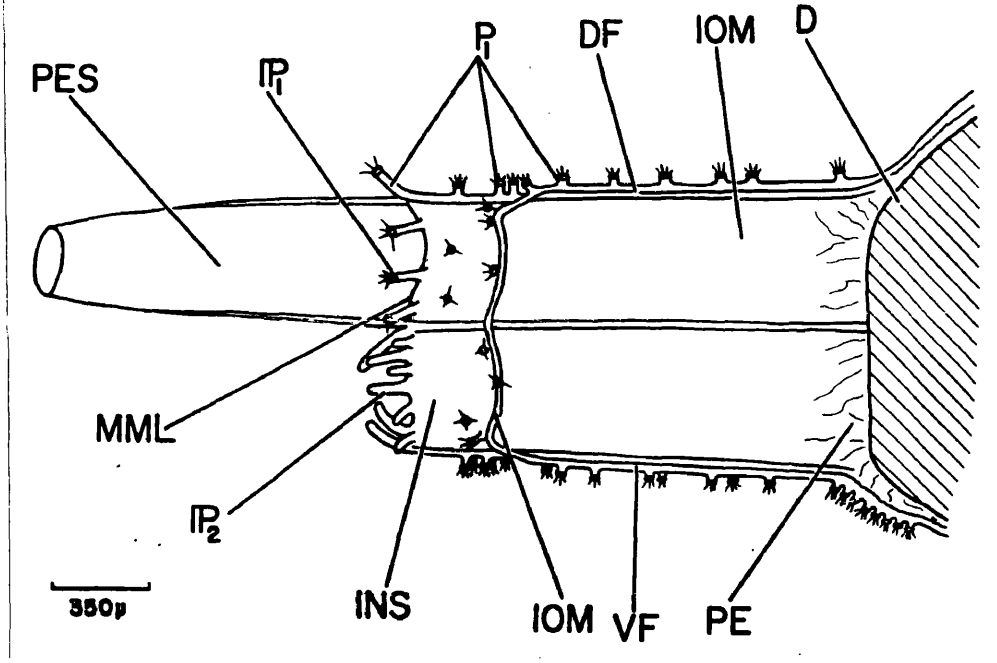


FIGURE 57

the outer mantle folds into the siphonal structure and a thin sheet of periostracum (PE) extends from this ridge to the shell margin. Frequently, the mid-dorsal and mid-ventral walls of the siphonal structure are marked externally by a distinct fusion line. In Spisula a row of primary papillae appear along these two lines of junction (Fig. 57, DF & VF).

Feeding

The differences in the ciliary tracts of the ctenidia and palps between the Mytilidae and Eulamellibranchia have little effect on feeding, which remains essentially similar in the post-larvae of the two groups. However, the fusion of the mantle lobes ventrally in many eulamellibranch post-larvae means that the inhalant stream enters posteriorly rather than ventrally, while the formation of siphons ensures a more effective separation of inhalant and exhalant streams.

DISCUSSION

Metamorphosis

In marine lamellibranchs the second larval stage is, with the exception of a few species which incubate their young throughout the larval period, a free swimming veliger. The velum functions in both locomotion and food collection and initially occupies the whole mantle cavity. In the late larva it retains its prominence and is independent of the developing foot and ctenidia.

In the post-larva food collection is performed by the ctenidia and the mechanism of collection, while of necessity much simpler than that of the adult, involves the same basic principles. Lateral cilia draw a current of water into the mantle cavity; latero-frontals strain the particles from the inhalant current and transfer them to the frontal surfaces of the filaments; frontal and adoral tracts of cilia collect the particles and transport them anteriorly to the palps. With respect to these ciliary components the ctenidia of the late larva are potentially functional. Each ctenidium generally has 3 or 4 filaments in the inner demibranch, and lateral and latero-frontal cilia are present. While frontal and adoral tracts of cilia could not be detected until shortly after metamorphosis, they are probably present earlier. Quayle (1952) shows frontal cilia on the larval filaments of Venerupis pullastra.

However, the position of the ctenidia in the mantle cavity must undergo subsequent modification before feeding commences. In order to serve as efficient filtering organs, the ctenidia must partition the mantle cavity; in the late larva the

filaments lie in the vertical plane overlying the lateral portions of the foot. Secondly, a connection must be established between the ctenidia and the mouth, which in the late larva is widely separated from the latter and opens to the posterior distal edge of the velum.

Reorganization of the body at metamorphosis in Ostrea edulis has been described by Cole (1938). Within 48 hours from the time of settlement, the body of the spat has rotated forward carrying the mouth and oesophagus anteriorly, while the components of the velum, with the exception of the apical plate, have dissociated. The apical plate comes to lie astride the oesophagus anteriorly and contributes to the formation of the upper palps. The lower lips of the mouth are now immediately adjacent to the ventral ends of filaments F_0.

This process is characteristic of the metamorphosis of all lamellibranch larvae and, as far as could be determined, is of approximately the same duration. The forward rotation of the body carries the foot to a median position so that the ctenidia now extend into the posterior region of the mantle cavity where the filaments are connected to one another in the midline. This partitioning of the mantle cavity is maintained throughout the subsequent development of the inner demibranch, being undisturbed by the formation of the distal lamella. Similarly, with the formation of the outer demibranch a junction is established between the ends of these filaments and the mantle in the eulamellibranchs; while such a connection was not detected in the Heteranomia and Chlamys, it was probably overlooked.

Thus, the interval of reorganization at metamorphosis is short and feeding is not interrupted for more than two or three days.

Comparison of Post-larval Feeding and Sorting Mechanisms

Generally speaking, the function of the lamellibranch ctenidium is to collect the particles carried in with the inhalant stream, and that of the palps is to sort the particles conveyed to them by the ctenidia. However, in certain lamellibranchs the ctenidia also have a selective action (Atkins, 1936 & 1937 a) and are designed to reject large particles or large concentrations of particles, while collecting and conveying to the palps the small particles. Selection by the ctenidium is characteristic of the Pectinidae, Limidae and Ostreidae where the ctenidia are heterorhabdic and sorting occurs on the plicae (Atkins, 1937 a), and also, although the method is different, of the Anomiidae where the ctenidia are homorhabdic and flat. Sorting in the Anomiidae is effected by the adjacent antagonistic frontal tracts, rejected particles being carried posteriorly along the ventral margins of the demibranchs (Atkins, 1936). The similarity of the ctenidial selection mechanisms described by Atkins in the adults of the Pectinidae, Limidae and Ostreidae is not nearly so marked in the post-larvae. In order to appreciate the similarities and differences it is necessary to distinguish between selection mechanisms where the ciliary currents concerned with rejection have no access to the palps, and those where the ciliary currents may function in rejection but do have access to the palps. The former will be termed cleansing mechanisms and are similar to the selection shown in adult Anomiidae, while the latter will be referred to as selective feeding mechanisms and are similar to the type of

selection shown in adult Pectinidae, Limidae and Ostreidae.

The period immediately following metamorphosis is no doubt a critical one in the life of lamellibranchs, for the ctenidia, whose efficiency in food collection depends on a large surface area, are small. Thus, while ctenidial selection mechanisms are of adaptive value in adult lamellibranchs living in habitats where silting is heavy, it is doubtful that they are of much advantage in young spat. Rather it would appear to be more advantageous to make the most efficient use of the small surface area of the ctenidia for purposes of food collection. While not indicative of a phylogenetic sequence the families of the Anisomyaria can be arranged in a series illustrating a progressive increase in the efficiency of the post-larval feeding mechanism. The culmination of such a series is represented by the Mytilidae, a position which is only surpassed by those families of the Eulamellibranchia in which fusion of the mantle lobes ventrally, and development of siphons has enhanced the efficiency of food collection.

Anomiidae

Due to the rapid degeneration of the anterior adductor muscle, the posterior adductor assumes a somewhat central position which, together with the freedom of the ctenidial axes posteriorly, allows the latter to curve dorsally. While this provides for greater elongation of the ctenidia by addition of filaments posteriorly, it also produces a large inhalant area. Consequently, the inhalant water current is dispersed and relatively weak.

The alternate arrangement of the filaments of the inner demibranchs in the midline creates large interfilamentary spaces which cannot be bridged by the micro-latero-frontal cilia. As a result, many particles pass between the filaments into the supra-branchial cavity. During feeding the ctenidia are fully extended; the axial retractors are not utilized to reduce the interfilamentary spaces but contract only when the animal is disturbed or the shell valves closed.

Food collection by the ctenidia is essentially simple, particles being carried by the dorsal frontal, axial and proximal adoral tracts to the palps. All other ciliary tracts of the ctenidia, i.e. the ventral frontal and marginal rejection tracts, are concerned with cleansing. These tracts are associated with the reccurrent path of the mantle which, prior to the formation of the marginal rejection tract, lies adjacent to the margin of the inner demibranch and is later associated with the margin of the outer demibranch. Thus, a considerable portion of the ctenidial mechanism is devoted to cleansing activities. However, the cilia of the ventral frontal tracts, while producing a stronger ciliary current than those of the dorsal tracts, are active only when stimulated by large or excessive particulate matter in the inhalant stream. Moreover, since the shell valves are widely open during feeding, the majority of particles --- particularly smaller ones --- are carried dorsally by the inhalant stream to impinge on the subaxial portions of the filaments where coarse frontal cilia are absent and the interfilamentary spaces are narrower.

Pectinidae

The feeding and cleansing mechanisms of Chlamys are similar in effect, although not in method, to those of Heteranomia. While there is an adoral tract along the ventral margin of the inner demibranch, interruption of the latter between filaments F_0 and F_1 by the foot, means that particles carried ventrally by the coarse frontal cilia and thence along the marginal adoral tract never reach the palps. The same is true of particles collected by the intermediary adoral tract, formed at the ventral margin of the demibranch after reflection of the filaments to form the distal lamella. Thus, the ventral frontal tracts of both lamellae and, as far as could be determined, the dorsal frontal tracts of the distal lamella have no connection with adoral tracts which reach the palps. Since only the dorsal frontal tracts of the proximal lamella of the inner demibranch, together with the axial and proximal adoral tracts, function in food collection, the presence of the subaxial tract of the mantle whose cilia produce a strong adoral water current adjacent to the axial adoral tract is of considerable significance.

The recurrent path of the mantle is never associated with the ctenidia as it is in Heteranomia, but it carries all particles originally collected in the marginal and intermediary adoral tracts since these must eventually fall onto the mantle. It is interesting to note that although in the adult both marginal and intermediary adoral tracts lead to the palps, only the former (located at the dorsal edge of the distal lamella) generally functions in food collection since passage along the ventral margin of the demibranch is

hazardous and particles usually fall onto the mantle (Atkins, 1937 a).

Limidae

The acquisition, in Lima, of two features characteristic of the Mytilidae and Eulamellibranchia has a profound effect on the feeding mechanism. The filaments of the two inner demibranchs, although initially alternate, become paired in the midline early in post-larval life. This reduces the size of the interfilamentary spaces at the ventral margins of the demibranchs so that filtration is more effective. Also the filaments overlie the lateral walls of the foot, so that the marginal adoral tract, now leading directly to the palps, becomes an integral part of the feeding mechanism. This means that the coarse cilia of the ventral frontal tracts, which are no longer active only on stimulation, are also utilized in food collection.

Particles collected by the ventral frontal and marginal adoral tracts pass directly into an adoral tract of the upper palps which was not present in the Anomiidae and Pectinidae. The dorsal frontal tracts, whose presence is inferred, and the axial and proximal adoral tracts appear to play a much smaller role in food collection. Although particles collected by these tracts --- presumably the smaller particles --- appeared to pass directly into the rejection tract of the upper palps, it is probably that an adoral tract of the type found in the Anomiidae and Pectinidae is present but was overlooked. In the Limidae all the ciliary currents of the ctenidia are integrated into a selective feeding mechanism which is more flexible than the ctenidial mechanism of the Pectinidae

and Anomiidae. When the concentration of particles entering in the inhalant stream is low, those collected by the ventral frontal and marginal adoral tracts may be used as food, ~~whereas in the Pectinidae and Anomiidae such particles are always rejected~~. Should the concentration of particles become excessive those collected by the ventral frontal tracts --- presumably the larger ones --- and accumulating along the ventral margin of the demibranch would probably fall onto the mantle before reaching the palps as in adult Pectinidae (Atkins, 1937 a). The ctenidia of post-larval Lima are clearly designed to achieve the most efficient use of particles entering in the inhalant stream.

The large pallial lobes produce a more effective separation of the inhalant and exhalant streams than that found in the Anomiidae and Pectinidae.

Ostreidae

Although as in the Anomiidae and Pectinidae the filaments radiate from the markedly curved ctenidial axes, creating large interfilamentary spaces, the presence of anomalous latero-frontal cilia in the Ostreidae enhances the efficiency of filtration. Both ventral frontal, and marginal and intermediary adoral tracts appear shortly after metamorphosis and are completely integrated into the selective feeding mechanism which shows the same characteristics as that of Lima. The most remarkable feature of post-larval development, however, is the extreme rapidity of ctenidial development which allows the early stages, when the filaments are few in number

and the ctenidium at its lowest feeding efficiency, to be of minimum duration.

Mytilidae and Eulamellibranchia

The anlagen are fused to the siphonal septum thus completing the internal separation of the inhalant and exhalant streams. The development of flanges above and below the septum in the Mytilidae, and of siphons in many Eulamellibranchia, ensures separation of the two streams externally. The shell valves are only slightly parted during feeding thus limiting the inhalant aperture and permitting a greater regulation of the size of the aperture by the inner mantle folds. Ventral fusion of the mantle lobes in many Eulamellibranchia and formation of the inhalant siphon even further reduces the aperture, increasing the strength and range of the inhalant current.

Due to the retention of both adductor muscles, the ctenidial axes are straight and the filaments lie parallel to one another. This together with the pairing of the filaments in the midline produces small interfilamentary spaces across which the long eu-latero-frontal cilia extend completely, even overlapping with one another.

Due to the restriction of the inhalant aperture, the majority of particles impinge either on the ventral portions of the filaments or directly on the marginal adoral tract. There is no selection of particles by the ctenidia, except in Ensis, and sorting occurs only on the palps.

Analysis of Ctenidial Development

In the preceding section some of the variations in ctenidial development which affect the efficiency of feeding in the post-larval have been outlined. The significance of these and other variations can only be evaluated by a complete analysis of the component factors.

Monomyarian Condition

It has been clearly shown that the rapid degeneration of the anterior adductor following metamorphosis in the Anomiidae, Pectinidae, Limidae and Ostreidae has a pronounced effect on the form of the ctenidia which is reflected in the efficiency of the post-larval feeding mechanism. The disadvantages of a wide inhalant aperture and large interfilamentary spaces are partly overcome in the Limidae by the opposite arrangement of filaments, but more fully solved in the Ostreidae by an acceleration of ctenidial development and the presence of anomalous latero-frontal cilia.

Progressive Alterations in Ctenidial Development

Certain variations in the development of these monomyarians appear to involve changes which are of adaptive value to the post-larva and do not seem to be related to corresponding differences in the structure or function of the ctenidia in the adult.

1. Integration of the ciliary currents of the cleansing mechanism of the Pectinidae into the selective feeding mechanism in the Limidae and Ostreidae. (In the Anomiidae

the use of the ventral frontal and marginal rejection tracts in cleansing during post-larval development is related to the corresponding condition in the adult).

2. Change from alternate (Pectinidae) to opposite (Limidae) arrangement of the filaments of the inner demibranch in the midline.
3. Change in position of the anterior filaments of the inner demibranch from their location posterior to the foot in the Pectinidae to overlie the lateral walls of the foot in the Limidae, and the consequent linking of the marginal adoral tract, and later the intermediary adoral tract, with the palps in the Limidae. (The connection of these adoral tracts with the palps in the Ostreidae is related to the degeneration of the foot).

Modifications in Rate and Sequence of Development

Ctenidial development can be considered as following a basic 'blue print' which may be secondarily altered by the factors listed below.

A. Rate of Development

In different species the rate of development of the ctenidia may vary considerably, with all processes occurring in the original or basic sequence. Development in the Anomiidae and Pectinidae is less rapid than in the Limidae.

B. Heterochrony

Certain structural features may appear earlier in some species than in others; that is their development is precocious and hence deviates from the time sequence of the basic plan. Thus, in the Limidae and Ostreidae development of ventral frontal tracts and the marginal adoral tract is precocious when compared with the developmental sequence in the Anomiidae and Pectinidae.

C. Tachygenesis

Certain processes of ctenidial differentiation may be condensed, eliminating many of the intermediate steps and may thus appear as an entirely different method of differentiation. Condensation has been demonstrated in the later development of the ctenidia in several lamellibranchs by Rice (1908) and is believed by him to be characteristic of late post-larval development of all Lamellibranchia. Wasserloos (1911) has suggested that the fold method of anlage differentiation represents a condensation of the papilla method.

The post-larval development of the ctenidia in the Ostreidae can only be considered as condensed. Filaments of the right inner demibranch posterior to the 5th are differentiated with both proximal and distal components present. This process must be compared with the later method of differentiation described by Rice (1908) and not with early post-larval development in other lamellibranchs. Only during the larval period are

filaments formed according to the basic plan: that is by the papilla method (Erdmann, 1935; Stafford, 1913).

D. Suppression

Certain phases of ctenidial development may be suppressed. This has already been discussed by Lacaze-Duthiers (1856) and illustrated by the absence of distal lamellae in both demibranchs of Heteranomia and of the outer demibranch in Mysella and Teredo.

Elongation of Filaments and Differentiation of Secondary Lamellae

Before proceeding to an analysis of the method of differentiation of the demibranchs into proximal and distal lamellae in ontogeny, it is necessary to consider the phylogenetic origin of these lamellae.

> The molluscan ctenidium, exhibited in its most primitive condition in the zygobranch Archaeogastropoda (Yonge, 1947), consists of an axis containing afferent and efferent blood vessels, nerves and muscles, with on either side alternating series of elongated triangular filaments. An upward water flow is created by lateral cilia on the opposed faces of the filaments, flow of blood within them being in the opposite direction. Skeletal rods beneath the zone of lateral cilia give rigidity to the filaments; cilia on the frontal and abfrontal faces of the filaments and on the upper surface of the axis are cleansing. This structure is virtually unchanged in the protobranchiate Nuculacea except that attachment is now by an upper, afferent membrane instead of by a lower, efferent one; there is also some attachment of the more numerous filaments by ciliary junctions. In the lamellibranchiate Bivalvia the still more numerous filaments are elongated and bent back on themselves. [1]

---

[1] Yonge, C.M., 1961. Personal communication.

Typically these V-shaped filaments bear at their ventral edge a food groove. Yonge (1947) has shown that during the evolution of the Bivalvia, the V-shaped filaments must have been derived from a condition in which the filaments were "horizontal structures (as in Nucula) which with both ends fixed, bent ventrally in the middle forming a downward-projecting V." Only thus would "the area occupied by the food groove ... remain as a fixed point throughout development and the filaments could function as soon as the requisite cilia appeared."

A. Anomiidae, Pectinidae and Limidae

In the Pectinidae, and probably also in the Limidae and Anomiidae exclusive of Heteranomia, the distal ends of the filaments of the inner demibranch are reflected to form the primordia of the distal lamella. Reflection is incontestable in view of the distinctiveness of the primary and secondary ciliary interfilamentary junctions, the primary ones being incorporated into the distal lamella. Reflection may be explained by postulating an embryonic zone, situated dorsal to the primary interfilamentary junction (Fig. 58 A), which provides for elongation of the filament. Proliferation from this zone on or near the frontal surface of the filament produces a flexure of the filament so that its distal portion is directed toward the midline. Simultaneously, the original embryonic zone divides into two parts (Fig. 58 B) so that subsequent elongation from the

FIGURE 58

Cross sections of a pectinid ctenidium during successive stages in its differentiation. With minor variations this type of development is also typical of the Anomiidae and Limidae, while the condensed form of ctenidial development in the Ostreidae is clearly derived from this type as well. For explanation of this figure see pages 75 to 77.

FIGURE 59

Cross sections of a mytilid ctenidium during successive stages in its differentiation. For explanation of this figure see pages 77 to 79. Compare these two figures with Figure 32 of a eulamellibranch ctenidium.

Embryonic zones are shown cross-hatched.

Ctenidial axis is shown as solid black area.

Regions of continuity between adjacent filaments are shown stippled.

Ciliary interfilamentary junctions (IFJ, IFJ_1 & IFJ_2) are shown as small stippled circles.

LEGEND: AAT - axial adoral tract, CA - ctenidial axis, DEZ - distal embryonic zone, IAT - intermediary adoral tract, IFJ, IFJ_1 & IFJ_2 - interfilamentary ciliary junctions, primary and secondary respectively, MAT - marginal adoral tract, MB - marginal bridge, PEZ - proximal embryonic zone.

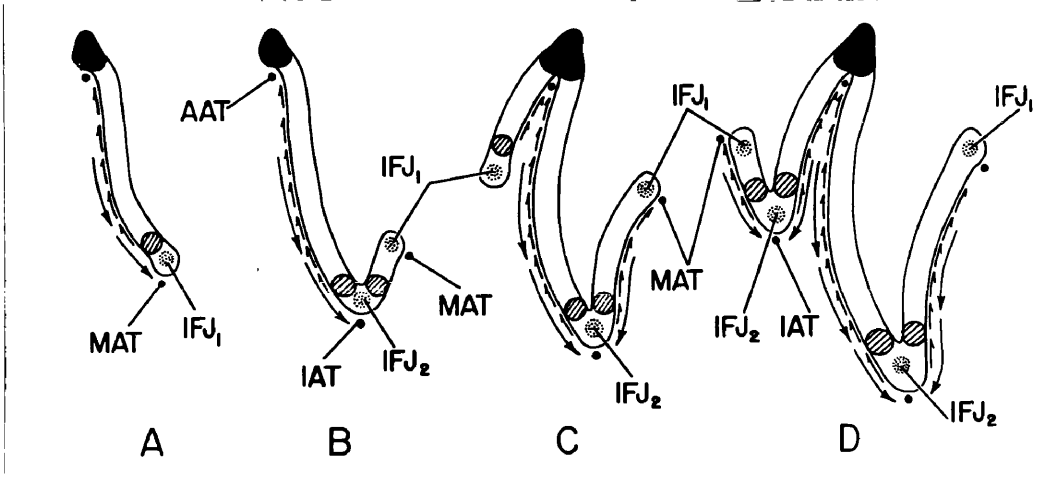


FIGURE 58

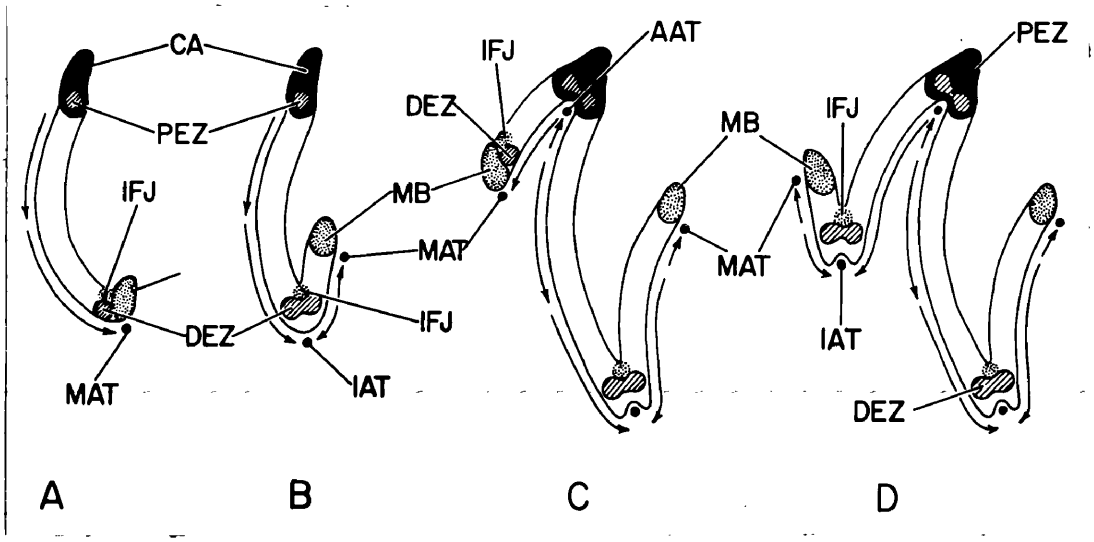


FIGURE 59

two embryonic zones produces ventral growth of both proximal and distal portions of the filaments (Fig. 58 C).[1]

While sections of post-larvae were not examined to determine the presence and location of concentrations of nuclei, or embryonic zones, similar to those found in Mytilus and Mya, the above assumption is supported by the genesis of adjacent antagonistic frontal tracts. In the Pectinidae and Anomiidae the dorsal frontal tracts appear first, development of ventral frontal tracts occurring later and then only in the distal regions of the unreflected filaments (Fig. 58 A). Since the proportion of the frontal surfaces bearing ventral frontal tracts increases during growth of the filaments, elongation must occur near the tips of the filaments. Drew (1906) reports that in Pecten tenuicostatus, which has organic interfilamentary junctions, ciliary interfilamentary junctions occur adjacent to the ventral margins of the demibranchs, which "are growing and consequently the youngest portions." Atkins (1938) found "vestiges of ciliated discs" in the same regions in Lima.

Although the filaments can hardly be considered as fixed at both ends, the distal ends of the filaments do behave as fixed points in development. Flexure occurs adjacent to the 'fixed' end of the filament due to unequal growth in the embryonic zone and subsequent growth is ventralward between the axial fixed point and the distal 'fixed' point.

---

[1] While division of the embryonic zone is shown in Figure 58, the growth of the filaments could also be explained by a single embryonic zone at the ventral margin of the demibranch as shown in Figure 59 for Mytilus.

Development of the outer demibranch (Fig. 58 C & D) is a repetition of the same processes which form the inner demibranch. In Heteranomia the formation of the distal lamella is suppressed and the embryonic zones remain entire.

B. Ostreidae

While post-larval development of the ctenidia must be considered as a condensed form of development, it is clearly related to that of the Anomiidae, Pectinidae and Limidae. The assumption of embryonic zones at the ventral edge of the demibranch, i.e. in the same position as in the above families, also explains the observed processes of development. In the differentiation of filaments of the right inner demibranch posterior to the 5th, the embryonic zone must be located at the point where the interfilamentary bridges are formed, thereby providing for elongation of both proximal and distal portions of the filaments. As in the Anomiidae and Pectinidae the dorsal frontal tracts extend to the axis (and to the dorsal edge of the distal lamella), but the ventral frontal tracts are absent in the subaxial region of the proximal lamella (and at the dorsal edge of the distal lamella). In the Ostreidae the filaments of the right inner demibranch are fixed at their distal ends by the fusion of the marginal bridge to that of the left inner demibranch.

C. Mytilidae

Differentiation of the distal lamella in the Mytilidae is ~~essentially~~ in some ways similar to that in the ~~Anomiidae~~,

Pectinidae ~~and Limidae~~. The marginal bridge (Fig. 59, MB) takes the place of the primary interfilamentary junction of Chlamys, while after reflection the ciliary interfilamentary junction (IFJ) remains at the ventral edge of the demibranch, i.e. the position where the secondary interfilamentary junction is formed in Chlamys. The difference between the reflection processes in Chlamys and Mytilus is that in Chlamys the distal end of the filament is reflected, whereas in Mytilus it is only the frontal surface of the filament which is reflected. This is due to the different locations of the embryonic zones. The embryonic zone of Chlamys occupies a position somewhat distal to the tip of the filament so that proliferation from the frontal side of the embryonic zone produces flexure of the distal tip of the filament, whereas in Mytilus the embryonic zone (Fig. 59 A, DEZ) lies immediately adjacent to the marginal bridge at the tip of the filament. Therefore, proliferation from the frontal side of the embryonic zone produces only flexure of the frontal surface of the filament.

The ends of the anterior filaments are fixed by their ciliary junctions --- later replaced by cuticular fusion --- with the lateral walls of the foot and growth of the filaments occurs ventrally to produce V-shaped filaments (Fig. 59 B & C). Development of the outer demibranch (Fig. 59 C & D) is similar to that of the inner. In addition to the distal embryonic zones, proximal embryonic zones (Fig. 59, PEZ) are located within the ctenidial axis. Whether or not these are continuously active

during post-larval development was not determined, but they are no doubt responsible for the formation of the dorsal frontal tracts described by Atkins (1937 b) in the subaxial regions of the proximal lamellae of both demibranchs.

D. Eulamellibranchia

In eulamellibranchs the distal embryonic zone (Fig. 39 A, DEZ) is located within, rather than adjacent to, the marginal bridge (MB) of the inner demibranch. Consequently, proliferation from the dorsal side of this zone produces thickenings in the marginal bridge, while perforation of the bridge between these thickenings form the ostia of the distal lamella. There is no reflection and the marginal adoral tract remains at the ventral edge of the demibranch (Fig. 39 B, MAT). As in the Mytilidae the distal ends of the filaments are fixed by their attachment to the lateral walls of the foot. Thus while elongation of the filaments is produced by proliferation from the dorsal side of the distal embryonic zone, such proliferation results in ventral growth of the filaments. A second embryonic zone (Fig. 39, PEZ) is located within the axis and there is evidence that elongation of the proximal portions of the filaments occurs both from the proximal and distal embryonic zones.

Formation of the outer demibranch in eulamellibranchs is not the same as that of the inner. Initially the filaments are directed dorsally (Fig. 39 B) where they become attached to the mantle by the marginal bridge (MB). Elongation of the filaments

occurs ventrally to produce J-shaped filaments (Fig. 39 C). The position of the embryonic zones was not determined, but the proximal embryonic zones in the axis are sufficient to account for the growth of the filaments to the stage represented in Figure 39 C. Development of the outer demibranch does not progress past this point in eulamellibranchs belonging to Atkins' Type C (1) and E such as Hiatella and Tellina. (Atkins, 1937 b).

In eulamellibranchs of Type C (2) of which Mya is an example, proliferation from the axial region is responsible for the production of the proximal lamella whose frontal currents lead to the ventral margin of the demibranch (Fig. 39 D) where a marginal adoral tract (MAT) is formed. Since subsequent elongation occurs independently in the two lamellae, there must be embryonic zones in the distal portions of the filaments. These may possibly be formed by splitting of the proximal embryonic zones, to form the distal embryonic zones (DEZ) at the time of differentiation of the proximal lamella. The distal embryonic zones become located at the ventral marginal of the demibranch and are responsible for the formation of the marginal adoral tract.

Eulamellibranchs of Type C (1) and E differ from those of Type C (2) in that the proximal embryonic zones remain entire throughout the development of the outer demibranch, so that the frontal tracts continue around the ventral margin of the demibranch and lead to the axis (Fig. 39 C). While direct evidence for the location of the embryonic zones in the outer demibranch is lacking, the assumptions outlined above do account

for the variability in the frontal tracts of this demibranch noted by Atkins (1937 b).

Differentiation of the outer demibranch in eulamellibranchs is unique in that the filaments are initially directed dorsally and the distal lamella is differentiated first, the proximal one being a secondary lamella. The supra-axial extension of the distal lamella of most eulamellibranchs must be attributable to the original dorsal direction of the filaments of this demibranch; this condition is never found in lamellibranchs in which the outer demibranch is initially directed ventrally.

Siphonal Development

The planktonic veliger is provided with a velum serving both locomotory and feeding functions. Since it operates only when extended beyond the shell margins and not within the mantle cavity, there is little chance of fouling. The latter is further prevented by the fact that swimming and feeding are generally carried on simultaneously. When the velum is shed and the adult feeding mechanism adopted, one of the first requirements to be met by the young spat, as it begins life on the bottom, is the separation of the inhalant and exhalant streams.

The propensity to partition the mantle cavity, exhibited by the ctenidia, is extended to the mantle margins. In post-larvae of the Anomiidae and Limidae pallial lobes, overlapping one another medially, are developed (most evident in Lima) to separate inhalant and exhalant streams externally. In the Mytilidae the mantle margins are fused to form a septum, above and below which are pallial

flanges diverting the two streams from one another externally. In the Eulamellibranchia this tendency culminates in the development of siphons.

Secondary fusion of the mantle margins ventrally in the Eulamellibranchia reduces the size of the inhalant aperture while separating it from the strength and range of the inhalant current, thereby greatly improving its effectiveness in conveying food to the animal.

Ontogeny and Comparative Anatomy

Yonge (1957) has pointed out that siphons are to be considered simply as extensions of the mantle margins, and as such they may be classified into four groups depending on the degree of fusion of the mantle folds. The account of siphonal development given in a preceding section is a somewhat generalized one, but is best exemplified by members of the Mactracea and Myacea, both having siphons of Type C in which the inner, middle and outer surface of the outer mantle folds are involved. However, members of the Cardidae and Veneridae, having siphons in which only the inner and middle mantle folds are involved (Type B), showed an identical developmental sequence to that in members of the Mactracea and Myacea up to the point where the inner surface of the outer fold is included in the siphonal structure in the latter. Thus, in a sense the process of siphonal formation is never completed in the Cardidae and Veneridae. Therefore, in the course of their development, siphons of Type C pass through a stage representing Type B.

The two primary characteristics of siphonal development are: first, progressive fusion of the mantle folds; and second, the subsequent extension of these folds into siphons by a process of elongation from a proximal 'growing point'.

SUMMARY

1. Careful examination of the post-larval feeding mechanisms in the five families of Anisomyaria, the Anomiidae, Pectinidae, Limidae, Ostreidae and Mytilidae, revealed distinctive features in each family.

2. A more general study of the post-larval feeding mechanisms in twelve families of the Eulamellibranchia revealed a marked uniformity with few --- and usually minor --- variations in the different families. Also, the post-larval feeding mechanism of the Eulamellibranchia showed a striking resemblance to that of the Mytilidae, but not to the other Anisomyaria.

3. An analysis of ctenidial development showed that the distinctive features of the anisomyarian families could be attributed to one or more of the following factors:

   i. the effect of the monomyarian condition,

   ii. progressive alterations in developmental pattern and

   iii. modifications in the rate and sequence of development.

Three factors were recognized as effecting the sequence of ctenidial development:

   i. heterochrony,

   ii. tachygenesis and

   iii. suppression (also seen in the Eulamellibranchia).

4. An analysis of the underlying pattern of ctenidial development revealed evidence of localized regions of growth or 'embryonic zones' in the filaments. The number, location and period of

activity of these zones was found to differ in each of the three groups:

i. Anomiidae, Pectinidae, Limidae and Ostreidae,

ii. Mytilidae and

iii. Eulamellibranchia.

5. The presence of such embryonic zones also provided an insight into the mode of differentiation of the filaments into the typical V-shape which is distinctive in each of the three groups listed above.

6. Siphonal development was observed in the post-larvae of the eulamellibranchs and was found to involve a progressive fusion of the mantle folds. Thus, adults having siphons of Type C (Yonge, 1957) --- in which the inner, middle, and inner surface of the outer, mantle folds are fused --- passed through developmental stages corresponding to Type B --- in which only the inner and middle mantle folds are involved.

7. Siphonal development was also characterized by a localized region of growth located at the base of the siphons, the proximal 'growing point'.

8. Siphonal development in the Tellinacea in no way resembled that of the other eulamellibranchs but is not described here.

BIBLIOGRAPHY

Allen, J.A. 1953. Observations on the epifauna of the deep-water muds of the Clyde Sea Area, with special reference to Chlamys septemradiata (Müller).
J. anim. Ecol., 22: 240-260.

Atkins, D. 1936. On the ciliary mechanisms and interrelationships of lamellibranchs. Part I. Some new observations on sorting mechanisms in certain Lamellibranchia.
Quart. J. micr. Sci., 79: 181-308.

_____ 1937a. On the ciliary mechanisms and interrelationships of lamellibranchs. Part II. Sorting devices on the gills.
Quart. J. micr. Sci., 79: 339-373.

_____ 1937b. On the ciliary mechanisms and interrelationships of lamellibranchs. Part III. Types of lamellibranch gills and their food currents.
Quart. J. micr. Sci., 79: 375-421.

_____ 1937c. On the ciliary mechanisms and interrelationships of lamellibrancha. Part IV. Cuticular fusion, with special reference to the fourth aperture in certain lamellibranchs.
Quart. J. micr. Sci., 79: 423-445.

_____ 1938. On the ciliary mechanisms and interrelationships of lamellibranchs. Part VII. Latero-frontal cilia of the gill filaments and their phylogenetic value.
Quart. J. micr. Sci., 80: 345-436.

Bernard, F. 1895. Scioberetia australis, type nouveau de Lamellibranche.
Bull. Sci. Fr. Belg., 27: 364-395

Bourne, G.G. 1906. On Jousseaumia, a new genus of Eulamellibranch commensal with the corals Heterocyathus and Heteropsammia.
Report to the Government of Ceylon on the Pearl Oyster Fisheries of the Gulf of Manaar.
Roy. Soc. Lond., Pt. 5: 246-266.

Bruce, J.R., M. Knight and M.W. Parke. 1940. The rearing of oyster larvae on an algal diet.
J. mar. biol. Ass. U.K., 24: 337-374.

Chapman, G. and G.E. Newell. 1956. The rôle of the body fluid in the movement of soft-bodied invertebrates. II. The extension of the siphons of Mya arenaria L. and Scrobicularia plana (da Costa).
Proc. roy. Soc. B, 145: 564-580.

Cole, H.A. 1937. Metamorphosis of the larva of Ostrea edulis.
Nature, 139: 413-414.

Cole, H.A. 1938. The fate of the larval organs in the metamorphosis of Ostrea edulis.
J. mar. biol. Ass. U.K., 22: 469-484.

Davis, H.C. and V.L. Loosanoff. 1953. Utilization of different food organisms by clam larvae.
Anat. Rec., 117: 646.

Drew, G.A. 1899a. Yoldia limatula.
Mem. biol. Lab. Johns Hopk. Univ., 4: no. 3.

_____ 1899b. Some observations on the habits, anatomy and embryology of members of the Protobranchia.
Anat. Anz., 15: 493-518.

_____ 1901. The life history of Nucula delphinodonta (Mighels).
Quart. J. micr. Sci., 44: 313-391.

_____ 1906. The habits, anatomy and embryology of the giant scallop (Pecten tenuicostatus Mighels).
Univ. Maine Studies, 6: 1-71.

Erdmann, W. 1935. Untersuchungen über die Lebensgeschichte der Auster. Nr. 5. Uber die Entwicklung und die Anatomie der "ansatzreifen" Larve von Ostrea edulis.
Wiss. Meeres. Helgoland, 19: 1-25.

Field, I.A. 1922. The biology and economic value of the sea mussel Mytilus edulis.
Bull. Bur. Fish., Wash., 38: 1-259.

Harms, W. 1909. Postembryonale Entwicklungsgeschichte der Unioniden.
Zool. Jb., abt. Anat., 28: 325-386.

Hatschek, B. 1880. Uber die Entwicklung von Teredo.
Arb. zool. Inst. Wien, 3: 1-44.

Herbers, K. 1913. Entwicklungsgeschichte von Anodonta cellensis, Schröt.
Z. wiss. Zool., 108: 1-174.

Jackson, R.T. 1890. Phylogeny of the Pelecypoda, the Aviculidae and their allies.
Mem. Boston Soc. nat. Hist., 4: 277-394.

Jørgensen, C.B. 1946. Reproduction and larval development of Danish marine bottom invertebrates. 9. Lamellibranchia.
Medd. Komm. Danmarks Fisk. Havunders., Ser. Plankton, 4: 277-311.

Kellogg, J.L. 1915. Ciliary mechanisms of Lamellibranchia with descriptions of anatomy.
J. Morph., 26: 625-701.

Lacaze-Duthiers, H. de. 1856. Memoire sur le développement des branchies des Mollusques Acéphales Lamellibranches. Ann. Sci. nat., Zool., 5: 5-47

Lebour, M.V. 1937. Larval and post-larval Lima from Plymouth. J. mar. biol. Ass. U.K., 21: 705-710.

Loosanoff, V.L. 1954. New advances in the study of bivalve larvae. Amer. Sci., 42: 607-624.

_____, H.C. Davis and P.E. Chanley. 1953a. Behaviour of clam larvae in different concentrations of food organisms. Anat. Rec., 117: 586-587.

_____, _____, _____ 1953b. Effect of overcrowding on rate of growth of clam larvae. Anat. Rec., 117: 645-646.

Loven, S. 1848. Utvecklingen af Mollusca Acephala. Ofversigt Stockholm Vetensk. Akad. Förhandl: 233.

Nelson, T.C. 1928. Pelagic dissoconchs of the common mussel, Mytilus edulis, with observations on behaviour of the larvae of allied genera. Biol. Bull., 55: 180-182.

_____ and C.M. Yonge. 1947. On the early development of the oyster and its bearing upon the phylogeny of the ctenidia of Lamellibranchia. Anat. Rec., 99: 607.

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: 156-170.

Owen, G. 1955. Use of Propylene phenoxetol as a relaxing agent. Nature, Lond., 175: 434.

Quayle, D.B. 1952. Structure and biology of the larva and spat of Venerupis pullastra (Montagu). Trans roy. Soc. Edinb., 62: 255-297.

Rees, C.B. 1950. The identification and classification of lamellibranch larvae. Hull Bull. mar. Ecol., 3: 73-104.

_____ 1954. Continuous plankton records: the distribution of lamellibranch larvae in the North Sea, 1950-51. Hull Bull. mar. Ecol., 4: 21-46.

Raven, Chr. P. 1958. Morphogenesis: The Analysis of Molluscan Development. New York: Pergamon Press.

Rice, E.L. 1905. Notes on the development of the gill in Mytilus.
Science, 21: 377-378.

_____ 1908. Gill development in Mytilus.
Biol. Bull., 14: 61-77.

Sigerfoos, C.P. 1896. II. Note on the organization of the larva and the post-larval development of shipworms.
John Hopk. Univ. Circ., 15: 87-89.

Stafford, J. 1913. The Canadian Oyster, its Development, Environment and Culture.
Ottawa: Mortimer.

Steedman, H.F. 1947. Ester Wax: a new embedding medium.
Quart. J. micr. Sci., 88: 123-133.

_____ 1950. Alcian blue 8GS: A new stain for mucin.
Quart. J. micr. Sci., 91: 477-479.

Sullivan, C.M. 1948. Bivalve larvae of Malpeque Bay, P.E.I.
Bull. fish. res. Bd. Can., 77: 1-36.

Walne, P. 1956. Observations on the oyster (Ostrea edulis) breeding experiments at Conway, 1939-1953.
Rapport et Procès-verbaux des Réunions, 140: 10-13.

Wasserloos, E. 1911. Die Entwicklung der Keimen bei Cyclas cornea und andern Acephalen des süssen Wassers.
Zool. Jb., abt. Anat., 31: 171-288.

Winckworth, R. 1932. The British marine Mollusca.
J. Conch., 19: 211-252.

_____ 1951. A list of the marine Mollusca of the British Isles: additions and corrections.
J. Conch., 23: 131-134.

Yonge, C.M. 1946. On the habits and adaptations of Aloidis (Corbula) gibba.
J. mar. biol. Ass. U.K., 26: 358-376.

_____ 1947. The pallial sense organs in the aspidobranch Gastropoda and their evolution throughout the Mollusca.
Phil. Trans. B, 232: 443-518.

_____ 1948. Formation of the siphons in Lamellibranchia.
Nature, 161: 198.

_____ 1949. On the structure and adaptation of the Tellinacea, deposit-feeding Eulamellibranchia.
Phil. Trans. B, 234: 29-76.

_____ 1957. Mantle fusion in the Lamollibranchia.
Pubbl. Staz. Zool. Napoli, 29: 151-171.

Yonge, C.M. 1959. The status of the Protobranchia in the bivalve Mollusca.
Proc. malacol. Soc. Lond.,

_____ 1961. Personal communication.

A COMPARATIVE STUDY OF POST-LARVAL FEEDING MECHANISMS IN THE BIVALVIA

ABSTRACT

Post-larval development in the two sub-classes of the Bivalvia, the Protobranchia and the Lamellibranchia, differs so markedly that it was necessary to deal with each separately. A description is given of post-larvae of three species of Nucula, belonging to the protobranch Family Nuculidae, ranging in length from 160μ, with test newly shed, to 650μ with both ctenidia and palps well developed. This post-larval phase persists at least a year and contrasts with the short larval phase of 60 hours recorded by Drew (1899b and 1901) for Nucula proxima. The post-larval feeding mechanisms are of particular interest since they differ radically from that of the adult.

Feeding activities begin in post-larvae approximately 170μ long and are executed by the foot which, extended beyond the shell, waves to and fro, the cilia encircling its sole wafting particles into the mantle cavity and onto the pedal walls. A curious feature, located on the inner mantle surface, is an arc of cilia whose beat may help to draw in particles and certainly throws them onto the proximal wall of the foot where adoral ciliary tracts carry them to the mouth. In post-larvae exceeding 200μ the activity of the pallial ciliated arc wanes as the ctenidia and palps develop.

With two filaments in each inner demibranch the ciliary feeding mechanism begins to resemble that of lamellibranchs. Particles enter the mantle cavity in the respiratory water current produced by the ctenidia, collect on its surface, and proceed to the filament tips and along the underlying adoral pedal tract. Below this adoral tract the foot develops an antagonistic ciliary tract carrying rejected particles out of the mantle cavity. The palp lamellae of post-larvae 500μ long establish a functional contact with the first filament of the inner demibranch and particles travel directly from one to the other. This type of feeding continues until the post-larva is 650μ long when the palp proboscides probably become functional. The possible phylogenetic significance of the post-larval feeding mechanisms is discussed.

Amongst the Lamellibranchia post-larvae belonging to five families of the Anisomyaria and twelve families of the Eulamellibranchia were examined. In each of the families belonging to the Anisomyaria (Anomiidae, Pectinidae, Limidae, Ostreidae and Mytilidae) the post-larval feeding mechanism is distinctive and in the first four families tends to show a certain complexity. In these four families the monomyarian condition has considerable effect on ctenidial development and hence on the post-larval feeding mechanism. While in the Anomiidae and Pectinidae these effects appear somewhat

disadvantageous, in the Limidae and Ostreidae they are modified by progressive changes in the pattern of ctenidial development. Consideration of the differences in rate and sequence of development reveals a common pattern of development in the four families. One characteristic of this developmental pattern is the disposition and period of activity of certain localized growth zones, the 'embryonic zones', which provide for the elongation and reflection of the filaments.

In the Mytilidae the post-larval feeding mechanism exhibits a simplicity not found in other Anisomyaria. The basic pattern of ctenidial development is also distinctive particularly in regard to the locations and times of activity of the embryonic zones.

In contrast to the Anisomyaria little variety was encountered amongst the twelve eulamellibranch families. The post-larval feeding mechanism closely resembled that of the Mytilidae but the basic pattern of ctenidial development was distinct from that of the latter. Siphon development was examined in the Eulamellibranchia and found to embody two principles: growth from a localized proximal zone and progressive fusion of the mantle folds. The method of siphon extension and withdrawal is described.