A STUDY OF THE LIFE HISTORY

OF

DACTYLOMETRA QUINQUECIRRHA, L. AGASSIZ,

AND

THE TAXONOMIC VALIDITY OF THIS SPECIES

By

Robert A. Littleford

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INTRODUCTION

The sea nettle of the Chesapeake Bay, _Dactylometra quinquecirrha_, L. Agassiz, occurs in tropical and temperate seas throughout the world. It is a coastal form and is found in great abundance in the brackish water of bays and estuaries. In the Chesapeake Bay, as in other brackish water areas, it occurs as two varieties, the red and the white. The red variety possesses sixteen rosin colored pigment areas on the exumbrella surface, and a reddish pigment in the marginal tentacles and oral arms. The white variety differs from the red one in that it is milky white in color and lacks pigment.

The present system of classification of the _Scyphomedusae_ is based in a large part upon the variation in position and number of the marginal tentacles. With the exception of certain groups of the _Semaeostomeae_, notably the families of _Pelagidae_ and _Ulmaridae_, the validity of these variations is unquestioned. In these excepted cases, however, the lack of additional characters and the numerous intergrading developmental stages of the species involved have resulted in a lack of unanimity of opinion with respect to speciation. The genus _Chrysaora_, as defined by Eschscholtz, has twenty-four marginal tentacles and thirty-two marginal lappets, whereas _Dactylometra_ was erected by Agassiz to include those forms

having forty marginal tentacles and forty-eight marginal lappets. The fact that the white medusa may reach sexual maturity in a stage having twenty-four tentacles, a form that may be included in the genus Chrysaora, has led to considerable difference of opinion as to the actual affinities of the two varieties. In spite of this fact, the conditions of development and distribution of this form in the Bay are unknown, and a summary of the reports from other localities presents a very incomplete picture of the whole.

The literature on Dactylometra quinquecirrha is sparse and embodies merely a presentation of generalities substantiated by a few observations. In 1848, Desor (1) reported, in a single sentence, to the Boston Society of Natural History the discovery of a new species of the genus Pelagia, for which he proposed the name quinquecirrha. It is impossible to tell whether or not this observation refers to the species afterwards defined by Louis Agassiz. Dactylometra quinquecirrha was described and named by Louis Agassiz (2) in 1862, and the same description is included in "The North American Acalephae" of Agassiz (3) in 1865 and in the "Systems der Medusen" of Haeckel (4) in 1880. Fewkes (6) adds nothing to our knowledge of this species in his report of 1862, and the faunal survey of Vanhoffen (12), "Nordisches Plankton", merely lists the occurrence of the species.

The occurrence of the genus Chrysaora on the Atlantic

coast was first reported by Bigelow (5) in 1880, when he noted the presence of a white medusa in the Chesapeake Bay. Continuing his investigations, in which he considered tentacle numbers in relation to sexual maturity, he concluded in 1890 (7) that this white medusa was a variety of Chrysaoro mediterranea, Peron and Lesueur. In contrast to this, Agassiz and Mayer (8) in 1895 reported the occurrence of a white medusa in Narragansett Bay which they considered a brackish water variety of D. quinquecirrha. This opinion is upheld by Hargitt (9) in his faunal survey of 1904, and again (10) in his study of tentacle variations in 1905.

Information available concerning the life cycle of Dactylometra quinquecirrha is meagre. Mayer (13) in 1910 reported that reproduction was through a scyphostoma stage having, normally, four tentacles. He also figured the previously unpublished drawings of Brooks on the ephyra. Mayer considered the white medusa of the Chesapeake Bay a "Chrysaora-stage" of D. quinquecirrha. Stiasny (14) in 1919 added further to our knowledge of the scyphostoma in reporting that it developed eight tentacles. In 1921, this same worker (16) reported observations on the ephyra, preserved in the collection at Leiden.

Recent literature has been confined to generalities on distribution and occurrence. Light (15) mentions the occurrence of D. quinquecirrha in the waters of the Philippines. He states that the sting is very severe, at times resulting

in death. In 1930, Menon (17) noted the occurrence of the
"Chrysaora-stage" in the vicinity of Madras and stated that
he believed that the members of the genus Dactylometra be-
come sexually mature in that stage. The yearly fluctuations
occurring in the Chesapeake Bay are reported by Cowles (18)
in 1931. He believed that it was possible that the "form
breeds in the Bay and that Planula, Scyphostomae, and Ephyrae
are present in Summer, Winter, and Spring respectively."

Definite work on Dactylometra quinquecirrha, as it
occurs under conditions of the Bay was begun by Truitt
prior to 1933 and continued by Truitt and Papenfuss in 1933
at the Chesapeake Biological Laboratory. Truitt (19) re-
ported that they had established (1) that fertilization
occurs at night, (2) that metagenesis occurs, and (3) that
the scyphostomae may bud profusely. Papenfuss (20) reported
in 1934 that the embryo was reared from eggs fertilized
under controlled conditions to the scyphostome stage. She
illustrated the four tentacled stage of the polyp. Papen-
fuss believed that the two varieties were the same species
and offered the suggestion that nematocysts might form a
basis for a classification of the Scyphomedusae. In 1936,
Papenfuss (21) reported the results of her investigations
on differences in nematocysts. She classified the white
nettle of the Bay, on that basis, as Dectylometra quinque-
cirrha, var. chesapeakei.

The present investigation, which was started in the

summer of 1935, has concerned itself with a detailed study of the life cycle and medusoid variations of <u>Dactylometra</u> quinquecirrha as it occurs in the Chesapeake Bay.

STATEMENT OF THE PROBLEM

Review of the literature indicates that one of the major problems in the study of the Coëlenterata is that of the common nettle of the Chesapeake Bay. This is true not only of D. quinquecirrha, but also in regard to the order Semaeostomeae, to which it belongs. The classification of the Semaeostomeae is in a chaotic state at present because of the fact that our system of differentiating families and genera is based in a large part upon variable and minor characteristics, a fact recognized by Mayer (13) and others. More recent revisions, based upon the type and the size of the nematocysts, are open to serious objections concerning the validity of the characters used. Since the nettle of the Bay, because of its many variations, fits the description of the two genera, Chrysaora and Dactylometra, it is apparent (1) that our present knowledge concerning the species needs to be supplemented, and (2) that an opportunity is offered to consider the question of basic and valid characters.

The purposes of this investigation have been (1) to determine the stages involved and the length of time required by the organism to complete its metagenic cycle; (2) to determine the manner of cleavage and the method of gastrulation; (3) to extend further our knowledge concerning the development and morphology of the scyphostoma; (4) to consider the variability existing between the red and white medusae; and

(5) to examine the theories of Scyphomedusan relationships
and the validity of certain taxonomic characters.

The problem was outlined to include a study of Dactyl-
ometra quinquecirrha under both natural and controlled
conditions. The study includes (1) the life cycle, (2) the
early embryology, (3) the development and morphology of the
scyphostoma, (4) the ephyra, and (5) adult variations.

PROCEDURE

This investigation has been in progress from the summer of 1935 to December, 1937. The material observed was obtained by rearing the organism, under controlled conditions, from the egg to the medusa. Sexually mature medusae were brought into the laboratory and fertilization was obtained (1) by crowding males and females together in a small container, and (2) by placing segments of ripe gonads in finger bowls, measuring 10 by 4 centimeters, which were partly filled with brackish water obtained from the Chesapeake Bay in front of the Chesapeake Biological Laboratory.

The embryonic material was reared in a basement room of the laboratory where changes in conditions of temperature, humidity, and light were comparatively slight, though not controlled. The temperature of the water in the finger bowls during the summer of 1936 was 24 $\pm$ 2 degrees centigrade and in 1937, 23 $\pm$ 3 degrees centigrade. Light entered the room through a small window just below the ceiling on the eastern wall. The material was placed under the window, thus remaining out of direct sunlight.

The scyphostomae were reared in the laboratory and under natural conditions in the vicinity of Solomons Island. The laboratory material was reared by placing the finger bowl in a battery jar partly filled with bay water. The material placed overboard was protected by a wire cage (Plate I) measuring

24 x 9 x 9 inches. This cage contained five bowls held in
a wooden rack. The protecting wire was of hardware screen
measuring eight strands to the inch. One side of the cage
was closed with screws to facilitate opening, and the cage
was lowered into eight or ten feet of water in a protected
cove near the laboratory.

The water containing the free embryos was changed daily
by pipetting out part of it and refilling with Bay water. The
water on the attached forms was changed weekly, while the
organisms were fed daily on material gathered by means of
plankton tows and on small pieces of oyster.

Studies of the embryonic material were made by use of
hanging drops and depression slides. In this way it was
possible to follow the development of a single egg or group
of eggs from the initiation of development to the planula
stage. Material intended for cytological or histological
examination was fixed in Keiser's, Bouin's, Flemming's,
or Zenker's solution. Chloral-hydrate-menthol was used to
anesthetize the scyphostoma. Staining methods used are as
follows: Iron haematoxylin; Haematoxylin and eosin; Ehrlich's
haematoxylin; Mallory's triple stain; and Lynch-precipitated
borax carmine.

RESULTS

THE LIFE CYCLE

The life cycle, as defined for purposes of this study, includes a consideration of the series of morphologically different stages succeeding one another in the metagenic cycle of development from the egg to the medusa.

The development from the egg to the medusa requires a period of from ten to twelve months, in the vicinity of Solomons Island. Medusae are found abundantly in the Bay from early July until late September. Sexual maturity occurs about the first of August, the developing eggs being set free in the water at that time. Development is rapid and within three to five days the free swimming larvae become attached to some hard objectt.

The attached larvae, the scyphostomae, are colorless. Sixteen or, rarely, twenty tentacles are developed and the polyps undergo no morphological change from late September until the following May. At this time, they become bright pink in color and undergo a process of transverse fission, known as strobilization, a development that results in the liberation of five or six circular discs. These discs are the "ephyral-stage" of the medusae.

Ephyrae reach adult form and size as the result of cell growth toward the periphery of the ephyral arms. This developmental process is rapid and the medusa become sexually

mature in late July or early August. Observations on the
mature medusae over the three years of this study show: (1)
that the number of individuals declines rapidly after mid-
August, at least at the surface of the water; (2) that great
numbers of dead specimens are found in late August; and
(3) that medusae are not present during winter and spring.
It is indicated, then, that the adult medusae do not live
for more than a few months, usually from about July fifteenth
to October first. The exact dates vary from season to season
and in different localities.

The Early Embryology

The male and female of D. quinquecirrha can not be dis-
tinguished from each other, except by means of the microscope,
until they become sexually mature. The gonads of the male
become bright pink at this time, while those of the female
take on a grayish brown or yellowish brown color. The egg is
a colorless, highly vacuolated cell, with a prominent nucleus
and cell wall. As a result of the deposition of yolk material,
the cytoplasm becomes filled, obscuring all structures except
the nucleus. At this time it becomes yellow in color. The
relative state of maturity of the egg can be determined by the
amount and color of the yolk material present in it. The mature
egg (Plate II) varies in diameter from .07 to .19 millimeters

and averages .15 of a millimeter. The sperm cells are developed in sacs (Plate III), which show great variation in size and shape.

Fertilization was obtained in sixty-three tests in each of which a mature female medusa and a mature male medusa were placed together in a small container. Developing embryos were found in the gonads in every case. Similar results were obtained in those tests where segments of the gonads were placed in finger bowls. The eggs released from the tissue were rarely fertilized, whereas over eighty-five per cent of those in the tissue were fertilized. Fifty-one females bearing developing embryos were collected. In all of these, embryos were found in the gonads. Twelve individuals, in addition, had embryos in the gastric cavity, which had reached the morula or early planula stage of development. From these results it may be concluded that fertilization takes place in the gonads.

The relationship existing between the initiation of development and the time of day is shown in the following table involving seven hundred and ten cases:

Table I

Time	Number	Time	Number
3:00 to 6:00 p.m.	0	9:00 to 10:00 p.m.	206
6:00 to 7:00 p.m.	2	10:00 to 11:00 p.m.	24
7:00 to 8:00 p.m.	124	11:00 to 12:00 p.m.	16
8:00 to 9:00 p.m.	329	after 12:00 p.m.	9

These figures show: (1) that fertilization occurs at night; (2) that the greatest sex cell activity takes place between eight and nine o'clock; (3) that the early hours of the evening appear to be less favorable than the later hours of night; and (4) that fertilization does not occur in daylight.

These results are substantiated (1) by the collection of thirty-seven females between eight and nine o'clock in the evening having eggs in the first and second cleavage stages, and (2) by the collection of fourteen females before ten o'clock in the morning having embryos in late morula and early planula stages in the gastric cavity.

The fertilized egg (Plate IV), which is distinguished by the presence of a distinct disc on one end, may divide immediately or it may remain quiescent for six or seven hours after fertilization. The first sign of development is the elongation of one end of the egg (Plate V, Fig. B), producing a prominent knob-like protrusion (Plate V, Fig. C). This knob is resorbed prior to the first cleavage, which occurs a little less than one hour after fertilization. The two celled embryo (Plate V, Fig. D) produced divides almost immediately to form four equal blastomeres (Plate VI, Fig. A; Plate VIII). At the end of three or four hours a third cleavage results in an embryo of eight equal cells (Plate VI, Fig. B).

Succeeding divisions are total and unequal, in that four of the blastomeres divide much more rapidly than the others.

At the end of ten or twelve hours, the embryo has four large cells at one end and an undetermined number of small cells at the other end (Plate VI, Figs. C and D). In sixteen to twenty hours, successive cleavages result in the formation of a bell-shaped aggregate of cells, having those of one end slightly larger than those of the other (Plate VII, Fig. A). Invagination does not occur, and the planula is formed directly from a solid morula (Plate VII, Fig. B).

Certain cells of the external layer of the morula develop cilia and at the end of twenty or twenty-four hours a rotating movement is observed. The free swimming larva or planula at this time has the same general appearance, under low magnification, as the fertilized egg. However, it may be distinguished readily by the use of higher magnification. The planula is now round or oval in shape (Plate IX), but within two or three hours it adopts a pyriform outline (Plate VII, Figs. C and D). It moves through the water by means of a fringe of cilia confined to the cells of the periphery, and from this time on it does not increase in size.

The Scyphostoma

Completing its free swimming stage after a period varying from three to five days, the planula attaches itself by its broad end. The attached larva is known as the scypho-

stoma or hydra-tuba.

Development. The attached larva becomes "ninepin" shaped as a result of the growth of the distal or apical end. This growth, the result of the multiplication of endodermal cells, is known as the oral cone. The mouth is .formed by evagination, and it becomes a gaping opening after one to one and one-half hours following attachment. The sides of the oral cone become secondarily divided to form the four lips common to the cruciform mouth of the older scyphostoma.

The tentacles are produced singly and arise as wart-like evaginations from the region of the body surrounding the mouth. At the end of five days, the scyphostoma has four primary tentacles (Plate X) developed in the perradii of the body. Alternating with these tentacles there arise four taeniolae, or ridges of the endoderm, projecting into the stomach cavity in the interradial axes.

A circular depression (Plate XII, Fig. B) appears on the upper part of the larva on the sixth day. This depression marks off the oral cone (Plate XII, Fig. B) from the bases of the tentacles. Several days later four deep depressions appear in this furrow just above the ˙taeniolae. These de-pressions are the septal funnels. At the end of ten days a scyphostoma with eight tentacles (Plate X) is produced as the result of the formation of four secondary tentacles in the four remaining interradii. This scyphostoma continues to

increase in size and at the end of fiteen days, eight more tentacles have been developed in the adradii of the body of the polyp (Plate XI).

The scyphostoma has reached, in typical specimens, complete development by the middle of August, although longer periods are required for certain individuals. The only observed change occurring from September until the end of the following May is a slight increase in size. The scyphostoma becomes bright pink in color and begins to undergo a process of transverse fission, known as strobilization, during May.

The scyphostoma remaining after strobilization is completed is approximately one millimeter in height. It has a small cruciform oral slit, surrounded by sixteen normal size tentacles produced before the ephyral discs were released. It may be distinguished from those scyphostomae which have not undergone strobilization by (1) the small mouth opening, (2) the short and broad appearance of the body, and (3) the crater-like mouth area in contrast to a normal oral cone. This old scyphostoma regains its normal appearance in from five to seven days. The following spring it again undergoes strobilization, producing the typical number of ephyrae, normal in appearance, structure, and function. Under observation at the time this thesis is being presented, many such scyphostomae are passing through their third winter, apparently normal in all respects.

An associated group of scyphostomae (Plate XII, Fig. A)

consists of seven or eight individuals ranging from one to four millimeters in height. Such colonies are produced (1) by budding of the pedal disc, (2) by means of buds from the stalk of the parent scyphostoma, and (3) by means of stolons. The groups produced as the result of budding from pedal discs may be either linear or irregular in formation, the former resulting from the progressive forward movement of the parent scyphostoma. The colonies formed either by means of buds from the stalk or by means of stolons are irregular in arrangement as a result of the irregular development of buds and stolons.

In December, 1935, it was observed that certain culture dishes in open water no longer contained scyphostomae. Instead, the bottom surface was covered with small, brownish, wart-like cysts. This same condition was observed in November, 1937. In the first case, fifty-one cysts were counted and their positions marked in one of the culture dishes. The following February, twenty-one cysts had disintegrated, while normal scyphostomae had developed in the remaining thirty cases. In November, 1937, several culture dishes containing the cysts were brought into the laboratory. The cysts in these dishes have been under observation since that time. A count of twenty-seven cysts was made in one dish, and two weeks later it was observed that the number was reduced to eighteen. Scyphostomae were produced from these cysts and development took place in a normal manner.

A series of tests was made to determine the food prefer-

ence of the scyphostomae. The results follow:

Table II

Food offered Organism	No. of Polyps	Food Accepted	Food Rejected
Algae	150	0	150
"Worms"	150	90	60
Crab	150	93	57
Shrimp	300	300	0
Copepods	300	300	0
"Coelenterates"	300	237	63
Oyster	300	200	100
Soft Clam	300	140	160

The results show (1) that zooplankton was used as food,
(2) that Copepods and Shrimp were acceptable to all scyphostomae,
and (3) that scyphostomae will accept readily pieces of oyster
and clam, but that in many cases it is not used as food. It
was noted also that the polyps feed readily upon the free
swimming ephyra of their own species.

Morphology. The scyphostoma is a colorless, goblet-
shaped polyp ranging in height from one to five and one-half
millimeters and in diameter from five-tenths to seven-tenths
of a millimeter, the average being three and five-tenths
millimeters in height. The mouth is cruciform and occupies
the entire oral surface of the organism. The body of the
scyphostoma is divided into two distinct regions: (1) the
long, stalk-like, tapering basal region, and (2) the cup-like

body or apical region. The relative size of these two parts is dependent upon the degree of contraction of the polyp.

The solid tentacles, which average six millimeters in length when fully expanded, bear many nematocysts. These nematocysts are regularly arranged, and are developed occasionally to form wart-like thickenings in different areas.

The end of the stalk is fixed to a substrate and is surrounded, at the point of attachment, by a pedal disc (Plate XVI). In older specimens the pedal disc may be one of a group, each of which marks a previous place of attachment.

The body wall (Plates XIV and XV) of the scyphostoma consists of three layers, the ectoderm, the endoderm, and the mesoglea.

The outer layer, or ectoderm, is composed of relatively small cells, which show no variation in size or type except at the base of the stalk. The cells of the basal region vary markedly from the rest of the tissue, being larger and filled with a granular substance. Somewhat regularly arranged throughout the ectoderm are the nematocysts.

The mesoglea is a thin, almost invisible lamella separating the ectoderm and endoderm in the early development

of the scyphostoma. This gelatinous layer increases, after
the eight-tentacled stage, until it becomes a prominent
structure of the mature polyp, when it becomes of consid-
erable importance in the form of the body and in the support
of the more delicate structures. It does not show cellular
structure. The mesoglea forms a supporting shelf for the
endodermal evaginations which form the taeniolae, at which
point it appears slightly granular.

The endoderm is the most prominent of the body layers
and may be divided, loosely, into three areas. The cells of
the stalk (Plate XV, Fig. C) appear highly vacuolated, show
little granulation, and have prominent nuclei near the in-
ternal wall. The central region (Plate XV, Fig. B) is marked
by the infoldings of the taeniolae, which are solely of
endodermal origin. They extend from the mouth to about the
middle of the organism, where they merge with the body wall.
Their free edges are not fused, and hang in the enteric
cavity. The cells of the taeniolae and the region around
them are granular in appearance and bear large nuclei. The
endoderm cells of the mouth and tentacle region (Plate XV,
Fig. A) are palisade-like in appearance, with relatively
thick walls. The cells lining the mouth of the scyphostoma
show clearly their endodermal affinities.

Reproduction. Reproduction in the scyphostoma stage is
of two types: (1) budding, resulting in the production of

scyphostomae, and (2) strobilization, resulting in the pro-
duction of ephyrae. New scyphostomae arise from old ones in
the same manner as in colony formation, that is: budding from
the stalk region, stolons, and pedal discs. The more common
method of increasing the number of scyphostomae among other
species is by somatic breeding. In D. quinquecirrha this
method apparently is rare, being observed only occasionally
in this study. Budding was observed to occur from the base
of the stalk region of the body, with few exceptions. In
budding, the body wall evaginates, forming a new individual,
which develops a mouth and tentacles in the same manner as
does the original scyphostoma. The bud may remain attached
to the parent, or it may attach itself independently to the
substratum.

Reproduction by stolon formation was established, during
the fall of 1937, from material collected in nature. The
stolons are formed from the stalk region of the scyphostoma,
and a new polyp is developed some distance from the parent.
These observations conform with those made by Truitt and
Papenfuss at the Chesapeake Biological Laboratory in the
fall of 1933.*

The most common method of increase is numbers is by means
of the pedal discs (Plate XVI). These discs are formed by
the parent scyphostoma as it moves on the substratum. Move-
ment is accomplished by the extension of the body wall slightly

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*Personal communication from R. V. Truitt.

to one side of the organism's attachment area. After a firm attachment has been obtained in the new area, the body is readjusted to this position, leaving in the original or former place of attachment a circular protoplasmic disc, which is covered by a perisarc-like envelope. New polyps are produced from these discs by the rupture of the covering. They emerge as flask-shaped organisms and develop the mouth and tentacles in the normal manner.

Strobilization occurs in late May or early June. The first sign of the process is the formation of one or more circular furrows (Plate XVII, Fig. A) in the wall of the cup-like body of the scyphostoma. As these furrows become deeper, the oral tentacles of the polyp are resorbed. This process may be completed before further development of the furrows occurs, or the tentacles may remain until after the series of discs has been well defined. The furrows divide the upper part of the body into a series of saucer-like segments which are connected by a central cord of the body wall. Each of these saucers develops eight deep clefts which, in turn, separate the periphery into eight lobes. Each of these lobes again becomes cleft to form a bifurcation. At the apex of each bifurcation a deeply pigmented club, the tentaculocyst, is produced. The scyphostoma in this stage of development is termed a strobila (Plate XVII, Fig. B). The process of strobilization is completed within four or five days and the saucers are then released into the water.

The eight bifurcate lobes become the eight arms of the ephyra, and the eight tentaculocysts are the eight rhophalia of the medusa.

The process of separation of the discs from the base or stalk region of the scyphostoma is completed in from ten to sixteen hours. Shortly before being released, the discs begin to pulsate and continue this activity until release is gained.

The Ephyra

The newly liberated ephyra (Plate XVIII, Fig. A) is about eighty-four one-hundredths of a millimeter in diameter, measured from the distal end of one arm to the distal end of the opposite arm. The most prominent structure of its anatomy is the rhophalia or tentaculocyst, of which there are eight, one in the bifurcation of each of the ephyral arms. Tentacles are lacking. The manubrium measures approximately twenty-three one-hundredths of a millimeter in length and is flared in the radii, forming a cruciform structure. The nematocysts are grouped in capsules of three different sizes and also appear singly covering the exumbrella surface. The ends of the ephyral arms appear knobbed as a result of nematocyst aggregations. The middle of each of the arms is marked by the presence of a pair of large nematocyst capsules, and the region where the arms join the disc is heavily covered with nematocysts.

The ephyra spends the first three or four days of its

existence close to the bottom. During this time the subumbrella surface is outward and the manubrium is carried in an upright position. A single tentacle is developed in each of the deep clefts that separate the ephyral arms (Plate XVIII, Fig. B). These tentacles are the eight primary tentacles of the medusa, and the lobes of the arms are the primary lappets of the bell margin. These tentacles appear four or five days after the ephyra has been separated from the scyphostoma. Following the appearance of the eight primary tentacles, the ephyral disc grows outward, filling the clefts separating the arms until it reaches the radius of the rhophalia. The margin then becomes cleft into a series of lappets, the number of which varies with the age and diameter of the individual.

The manubrium increases in length until it is slightly longer than the bell diameter (four and one-tenth millimeters to three and nine-tenths millimeters, for example). About this time the bell becomes inverted and the manubrium hangs downward from the center of the subumbrella. Inversion of the bell occurs after the formation of the eight tentacles and the increase in length of the manubrium. This occurs between the sixth and eighth days, in typical specimens. The oral lips of the ephyra are simple folds of the body wall, produced from the connecting tube of the scyphostoma. They are heavily covered with nematocysts. As the ephyra develops into the medusa, these arms become folded and develop curtain-like margins on their internal edges.

Four tentacle-like outgrowths appear on the subumbrella surface at the interradii of the manubrium three days after separation. These hollow outgrowths are the first gastric cirra (Plate XIX). They increase rapidly until as many as thirty-five or forty appear in each interradius. An ephyra five millimeters in diameter has eight gastric cirra in each interradius, while the eight millimeter one has ten, and the ephyra of fifteen millimeters has twenty-five. These cirra increase in number as development continues in the medusa.

Development in the ephyra is completed in from six days to two weeks. Upon obtaining the bell shape, it is considered as the early "post-ephyral stage" of the medusa.

VARIATIONS OF THE MEDUSAE

Dactylometra quinquecirrha occurs in the Chesapeake Bay
as two varieties, the red and the white. These two varieties
have been distinguished from one another on the basis of (1)
color, (2) tentacle development, and (3) the growth stage at
which sexual maturity occurs.

Color Differences. Individuals are found showing every
possible step in the intergrading of the two extremes, red
and white. The following tabulation of observations of one
hundred and twenty specimens shows the variation of color.

Table III

Coloration	Male	Female	Number of Tentacles	Total
Bell and tentacles marked	3	2	24 to 32	5
Bell colored	1	11	24	12
Color scattered	8	3	24 to 32	11
Sixteen stripes partially present	15	19	24	34
Central spot on bell	20	27	24	47
Bell spotted	3	10	24 to 32	13
Tentacles and arms colored	7	12	24	19

Color differences of specimens under ten centimeters in
diameter and bearing fewer than twenty-four tentacles also were

investigated, with the following results based upon the
examination of sixty-one specimens:

Table IV

Coloration	Average Diameter	Tentacles	Number
Red variety	6 cm.	8	7
Color on bell	7 cm.	8 to 20	11
Scattered color	4 to 5 cm.	8	25
Striping present	8 to 9 cm.	8 to 20	12
Color on tentacles and oral arms	8 cm.	8 to 20	6

The significance of these results will be considered
subsequently.

Tentacle development. Five hundred and twenty-five
medusae were examined during the summers of 1935, 1936, and
1937 in an effort to determine the relationship between bell
diameter and number of tentacles. The results are presented
in the following table:

Table V

Bell Diameter	Number of Tentacles					Total
	8	16	24	32	36	
1 to 5 cm.	19	8	-	-	-	27
5 to 10 cm.	3	26	49	-	-	78
10 to 15 cm.	-	18	107	43	-	168
15 to 20 cm.	-	-	192	41	5	238
More than 20 cm.	-	-	5	5	4	14

Occurrence of sexual maturity. One hundred and eighty
medusae of the red variety were examined during the last week

of July, 1937, to determine the relationship between sexual
maturity and tentacle development. Seventy-three red individuals
were likewise examined during the same period of 1936. The
combined results are tabulated below:

Table VI

Number of Tentacles	Mature	Immature	Total
36	29	3	32
32	145	15	160
24	56	5	61
Total	230	23	253

A similar investigation was made of two hundred and
twenty white medusae during the last week of July, 1936.
The results were as follows:

Table VII

Number of Tentacles	Mature	Immature	Total
24	131	7	138
32	78	4	82
32 to 36	19	-	19
Total	228	11	239

DISCUSSION

The results of this study are considered under the following divisions: (1) the life cycle, (2) gastrulation, (3) development and morphology of the scyphostoma, and (4) variations of the medusa.

The Life Cycle

The life cycle of D. quinquecirrha is similar in its general outline to that reported for other metagenic species of the Scyphomedusae. In its specific aspects, this life cycle shows closer similarity to that of Chrysaora than to other species for which information is available. Certain points are of considerable interest and justify further treatment here.

In the course of the investigation, the life cycles of both the red and the white forms and the resulting cross have been studied. The life cycles of the two forms are alike in all details, and the individuals produced by a cross between the two forms develops like the varieties in all respects. Noticeable variations in size and rate of development occur within all of the forms mentioned. These variations outweigh any possible differences occurring between the developmental cycles of the red and white medusae. The morphology of the corresponding stages in the life cycles of the three forms is identical. The contention that the red

and white forms of the nettle of the Chesapeake Bay are representative of different species or widely separated varieties of the same species has not received support from this study of the life cycle of the two forms.

Fertilization takes place in the gonads, rather than in the gastric cavity. In this respect, D. quinquecirrha parallels Chrysaora rather than either Aurellia or Cyanea. The place of fertilization apparently depends upon the provision that is made for the retention of the developing embryo. In the case of Aurellia and Cyanea, fertilization occurs in the gastric cavity and the embryos are held either in pockets of the oral arms or in folds of these arms until they reach free swimming development. Dactylometra and Chrysaora, on the other hand, expel the embryos directly into the water and do not retain them in protective pockets or folds of the oral arms.

It has been established that in D. quinquecirrha fertilization takes place at night, the greatest activity taking place between the hours of eight and nine in the evening, as shown by table No. I on page 12. This concurs with the results obtained from closely related forms by previous workers who, as in the present work, have been unable to offer an explanation for this behavior of the germ cell.

Gastrulation

Invagination does not occur in D. quinquecirrha, and the planula is formed from a solid morula. Aurellia and Cyanea

produce the panula as a result of invagination of one end
of the hollow blastula to form a two-layered gastrula. Chry-
saora is similar to Dactylometra in that invagination does not
occur and the planula is produced from a solid morula.

Present day investigators of the Scyphomedusae are agreed
in considering Aurellia and Cyanea as forms showing greater
specialization than Chrysaora and Dactylometra. The former,
however,retain the more primitive method of gastrulation,
whereas the latter have become modified in this regard.
Whether this modification represents specialization or
degeneration is open to question and at present relationships
can not be based upon the method of gastrulation involved.
The fact that gastrulation occurs either by invagination or
by ingression in a single species (Aurellia aurita) lends
support to the contention of Mayer (13) that the method of
gastrulation is of little value in a consideration of
relationships.

Development and Morphology of the Scyphostoma

Closely related to the problem of gastrulation is the
question of the formation of the mouth and taeniolae of the
scyphostoma. Goette (33) in 1891 claimed that the mouth of
Chrysaora hysoscella, Eschscholtz was produced as a result of
ectodermal invagination at the posterior end of the planula.
This claim seemed logical in view of the fact that at the time
it was supposed that the planula was formed by invagination.

The mouth of the scyphostoma was thus considered merely the reopened blastopore of the gastrula. The lining of the oesophagus would accordingly be ectodermal and the stomach pouches partially ectodermal and partially endodermal. In 1894, Hyde (38) reported that ectodermal invagination occurred in Aurellia aurita and later in the same year she reported that invagination produced the mouth of Cyanea capillata var. fulva, L. Agassiz. If this is true, the Scyphomedusae are related to the Actinozoa, where the mouth is ectodermal in origin and the lining of the oesophagus is ectodermal.

The work of Claus (25) in 1877 demonstrated that the mouth of C. hysoscella was formed by endodermal evagination. In 1907, Hadzi (47) showed clearly that the mouth of Chrysaora hysoscella was produced by endodermal evagination, and he suggested that the observations of Goette were erroneous. He denied the possibility of ectodermal invagination in Aurellia aurita. The work of Heric (48) in 1907 corroborates that of Hadzi in C. hysoscella. In 1902, Friedman (42) reported that the mouth of Aurellia aurita was the result of endodermal evagination, the ectoderm being stretched very thin at that point.

The mouth of D. quinquecirrha is formed by endodermal evagination. The cells lining the oesophagus of scyphostomae, having eight or less tentacles, show clearly endodermal characteristics. Certain cells of this lining in the older polyp occasionally show secondary modification to form nematocysts.

The mode of development of the taeniolae of D. quinquecirrha supports the contentions of Hadzi and Heric that the mouth of the scyphomedusan polyp is formed by endodermal evagination. The taeniolae are formed as simple infoldings of the endoderm. The four stomach pouches are merely the passive results of the formation of the taeniolae and are endodermal throughout.

The results of the present investigation indicate that Goette misinterpreted his findings on Chrysaora hysoscella, and furthermore substantiate the work of investigators on Chrysaora and Aurellia, thus establishing the conclusion that the mouth of the scyphomedusan polyp is formed by endodermal vagination. In addition, the Scyphomedusae are established to be more closely related to the Hydromedusae than to the Actinozos. Further support of this contention is to be found in the character of the mesoglea. In the Scyphomedusae, as in the Hydromedusae, the mesoglea is vacuolated and lacks cell structure. The mesoglea of the Actinozos has cellular components, muscle cells, and nerve fibrils.

The adult scyphostoma. General literature repeatedly refers to the scyphostoma as monotonous in structure and sets forth the common conclusion that the polyp form is identical throughout the group. However, sufficient information on the structure and general appearance of the scyphostomae of three genera, Aurellia, Chrysaora, and Dactylometra, is available to make possible the separation of the scyphostomae of these genera.

The scyphostoma of Aurellia normally develops four or eight more tentacles than are developed by the scyphostoma of

either <u>Dectylometra</u> or <u>Chrysaora</u>. Associated with this
development is the formation of four ostia, one in each
taeniola just below the oral cone, resulting in the formation
of the ring-sinus. In the position of the septal funnels four
large invaginations occur. These are the rudiments of the
sub-genital ostia of the medusa. <u>Dactylometra</u> may be dis-
tinguished from <u>Aurellia</u> by the absence of the four large
invaginations and the development of the ring-sinus. The four
septal funnels of <u>Dactylometra</u> are slight depressions rather
than deep ones as in <u>Aurellia</u>. The genus <u>Chrysaora</u> may be
distinguished from both <u>Aurellia</u> and <u>Dactylometra</u> by the pre-
sence of the perisarc. The white medusa of the Chesapeake Bay
is clearly separated from the genus <u>Chrysaora</u> by the absence
of the outer protective perisarc, which characterizes the
latter genus.

<u>Food habits of the scyphostoma</u>. The results of this in-
vestigation show that the scyphostoma of this species feeds
exclusively upon animal plankton, an observation in accord with
the results obtained by Delap on <u>Aurellia</u> (46), <u>Chrysaora</u> (41),
and <u>Cyanea</u> (45). Chuin (50) reports that <u>Chrysaora</u> <u>hysoscella</u>
feeds exclusively upon animal plankton. Miss Delap reports that
Chrysaora feeds particularly on <u>Hydromedusae</u> and <u>Siphonophorae</u>
and other Coelenterate forms. She states that they do not feed
upon Crustacea. <u>Dactylometra</u> <u>quinquecirrha</u>, on the other

hand, feeds principally upon Copepods and Shrimp. The
food is captured and carried to the mouth by the tentacles,
which often force it into the cavity. Examination of the
tentacles after feeding shows that the nematocysts have been
exploded. In most cases, the organisms that escaped from the
scyphostomae dropped to the bottom of the dish as though
benumbed.

The pedal discs. The formation of pedal discs was first
reported by Herouard (49) in 1907, in Aurellia aurita.
He considered this a mere abnormality brought about by
conditions in his aquaria. Whether his work is comparable
to that presented here cannot be told from his report.
Gilchrist (51) believes that Herouard refers to stolon
formation. Herouard's interpretation that the cysts were
the result of abnormal conditions does not stand up in
the light of the present work, since the pedal disc formation
was the common method of reproduction under controlled con-
ditions. The acceptance of this method of asexual reproduction
as normal for the organism is substantiated by the finding
of scyphostomae with pedal discs in nature.

Progressive movement in D. quinquecirrha results in the
formation of a linear series of discs with the scyphostoma
attached to the one formed last. This formation of the
discs is relatively uncommon. This string of discs may
produce a series of scyphostomae extending one behind the other.

The largest scyphostoma is at one end of the series. This individual is the actual "parent" of the polyps in the group. The other polyps differ in size, since they do not develop in the same order as that in which the discs are laid down.

Irregular movement of the scyphostoma results in the formation of a "colony" of discs without orderly arrangement. As in the case of progressive movement, the production of scyphostomae from these discs results in the formation of a colony or associated group of scyphostomae of many different sizes and ages.

Encystment of the scyphostoma. The formation of brown cysts, as previously indicated, was observed twice during the period of this study. Cysts were first observed in December, 1935 in several of the finger bowls which were being held under natural conditions in eight to ten feet of water. Their occurrence under like conditions was again observed during the autumn of 1937, when the dishes showing cysts were held in water that was less than three feet deep at low tide. Scyphostomae were often retained in the laboratory for long periods without food or change of water. During these periods, the polyps resorbed themselves until they had diminished to the size of normal one week old forms. At no time, however, was encystment observed under those conditions. At present, therefore, we can offer no valid explanation for the production of cysts.

The same phenomenon has been observed in _Chrysaora_ by Chuin (51), who has been unable to offer an adequate explanation. In _Chrysaora_ these cysts produce a ciliated larva which swims about and then attaches itself to develop into a polyp. In D. quinquecirrha a larva was not produced, but a large number of these cysts produced new polyps in the same manner as has been reported for pedal discs.

Development after strobilization. Dalyell, the discoverer of the scyphostoma of Aurellia, reported in 1847 (22), that the organism regenerated itself and continued development after strobilization. The present investigation established that the scyphostomae of D. quinquecirrha continue development after strobilization, in that polyps have been reared through two winters, strobilization has been observed to occur two summers in succession in the same individual, and the polyps, in their third year, are normal in appearance.

Variations of the Medusae

The medusae of D. quinquecirrha display great variation in (1) color, (2) tentacle development, and (3) growth stage at which sexual maturity occurs. Several investigators, named in the introduction, have considered the white phase a member of the genus _Chrysaora_. The fact that the scyphostoma of this medusa lacks a perisarc is of sufficient importance to remove it from consideration as a species of _Chrysaora_. Papenfuss (21)

considers it a variety of the red form. Consideration is given here to variation in the three chief characteristics used in the classification of the medusae.

Examination of numbers of medusae shows that color is an intergrading character with considerable variation. In late July an examination was made of one hundred and twenty sexually mature individuals bearing twenty-four to thirty-two tentacles. Five of these specimens had the definite markings of D. quinquecirrha. The others showed variations of the normal color pattern. Those individuals that are partially colored form a series leading to the colorless medusa. A consideration of individuals having fewer than twenty-four tentacles gives similar results. Nettles of the Chesapeake Bay can not fundamentally be divided into two separate color phases. There is no evidence to make it possible to assign partially colored individuals definitely to either of the extremes. It is apparent that the red medusa shows great color variation, and it does not appear logical to use as a specific factor a character showing so much variability of expression, a conclusion reached by Mayer, who worked with the highly variable Chrysaora mediterranea, Peron and Lesueur.

Consideration of the relation of the number of tentacles to the diameter of the bell of D. quinquecirrha show: (1) that the tentacle number increases as the bell diameter increases, (2) that individuals with a bell diameter between ten and twenty centimeters have twenty-four tentacles, with minor exceptions,

and (3) that individuals with a bell diameter greater than twenty centimeters generally have tentacle numbers higher than twenty-four. The rate of tentacle increase tends to diminish when the diameter of the bell exceeds fifteen centimeters. Mayer (13) has suggested that the white medusa of the Chesapeake Bay never attains sufficient diameter to acquire forty tentacles, the number characterizing the genus Dactylometra. Evidence gathered in the present work bears out this suggestion, in that the number of tentacles shows a definite relation to the diameter of the bell.

Closely related to this problem is that of the time of sexual maturity in relation to the growth stage of the organism. A study of two hundred and fifty-three red forms and two hundred and twenty white forms shows: (1) that the red nettle becomes sexually mature at a growth stage of less than forty tentacles, (2) that many of the red form are mature with twenty-four tentacles, and (3) that certain white individuals having more than twenty-four tentacles are still sexually immature.

One fact stands out: that a species can not be erected upon color variations, tentacle numbers, or age at which sexual maturity occurs. The two forms of the Chesapeake Bay show constant intergradation of these characters, so often used in this group as valid systematic characteristics.

The contention of Papenfuss that the white nettle is a distinct variety of the red one has been based on slight

differences in the sizes of two types of nematocysts and a small structural difference of another type. Granting the validity of her data, the question may be raised as to what extent these characters vary over a rather large group of medusae. It appears more logical, in the light of the evidence presented in this study, to consider the white and red varieties as outside limits of variation of a highly variable medusa.

It is concluded that the white and the red forms should be considered as the same species. The following results are presented in support of the conclusion: (1) the red variety matures in the Chesapeake Bay with less than forty tentacles, (2) valid differences can not be established on the basis of color, (3) the increase of tentacle numbers with an increase in bell diameter tends to diminish after a diameter of twenty centimeters is reached, (4) many individuals of the white form do not become sexually mature in the twenty-four tentacle stage, but develop additional tentacles, (5) the two forms interbreed under controlled conditions, and (6) the life cycles of the two varieties and the resulting cross show no developmental or morphological differences. These facts readily make it possible to conclude, in addition, that the genus Chrysaora does not occur on the North American Coast, the white medusa, considered a representative of this genus, being identical with the white medusa shown to be D. quinquecirrha.

SUMMARY AND CONCLUSIONS

This paper presents the results of a study of the varietal differences and morphological and developmental changes occurring in the metagenic cycle of the sea nettle of the Chesapeake Bay, _Dactylometra quinquecirrha_, L. Agassiz. The data reported are based upon field observations and the study of material reared from the egg to the medusa under controlled laboratory conditions.

The metagenic cycle of this species requires from ten to twelve months for completion. Segmentation of the egg is total and unequal. Invagination does not occur, the planula being formed from a solid morula.

The mouth of the scyphostoma is formed as a result of the evagination of the endoderm. The taeniolae are formed by endodermal evaginations which fold into the enteric cavity. The stomach pouches are wholly endodermal, being the passive results of the formation of the taeniolae. These facts support the theory of Claus and Hadzi that the mouth and taeniolae of the scyphomedusan polyp are of endodermal origin. Evidence of ectodermal affinities, as put forth by Goette, was not found in this study.

Reproduction among the scyphostomae occurs more commonly by pedal discs than by somatic budding or stolon formation. The mature scyphostoma differs from that of _Aurellia_ in that it has neither the rudiments of the sub-genital ostia nor the

development of the so-called ring sinus. It may be separated
from Chrysaora by the absence of the perisarc. The number of
ephyrae produced by a single strobila is five or six. The
ephyra grows rapidly, reaching adult size and form in from
one to two months.

The medusa of D. quinquecirrha is highly variable and
occurs in the Chesapeake Bay as two color phases, the red and
the white. A study has been made of the variation existing
in color, tentacle numbers, and stage of development at which
sexual maturity takes place. Results show that the red and
white forms of the Chesapeake Bay are the extremes of a high-
ly variable species and not separate species, as has been
contended by some authors. The white medusa is shown to be
identical with D. quinquecirrha, and not a representative of
the genus Chrysaora. The contention of Papenfuss that the
white nettle is a separate variety of D. quinquecirrha has
been rejected on the basis of results of this study.

The data herein presented on the development and morpho-
logy of the scyphostoma further strengthen the theory that
the Hydromedusae and Scyphomedusae are separate sub-classes
of the Hydrozoa, and refute the theory of Anthozoan affinities
of the Scyphomedusae.

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PLATE I

Photograph of the cage used in rear-
ing the scyphostomae of D.quinquecirrha
overboard. Note the position of the finger
bowls in the rack inside of the cage.
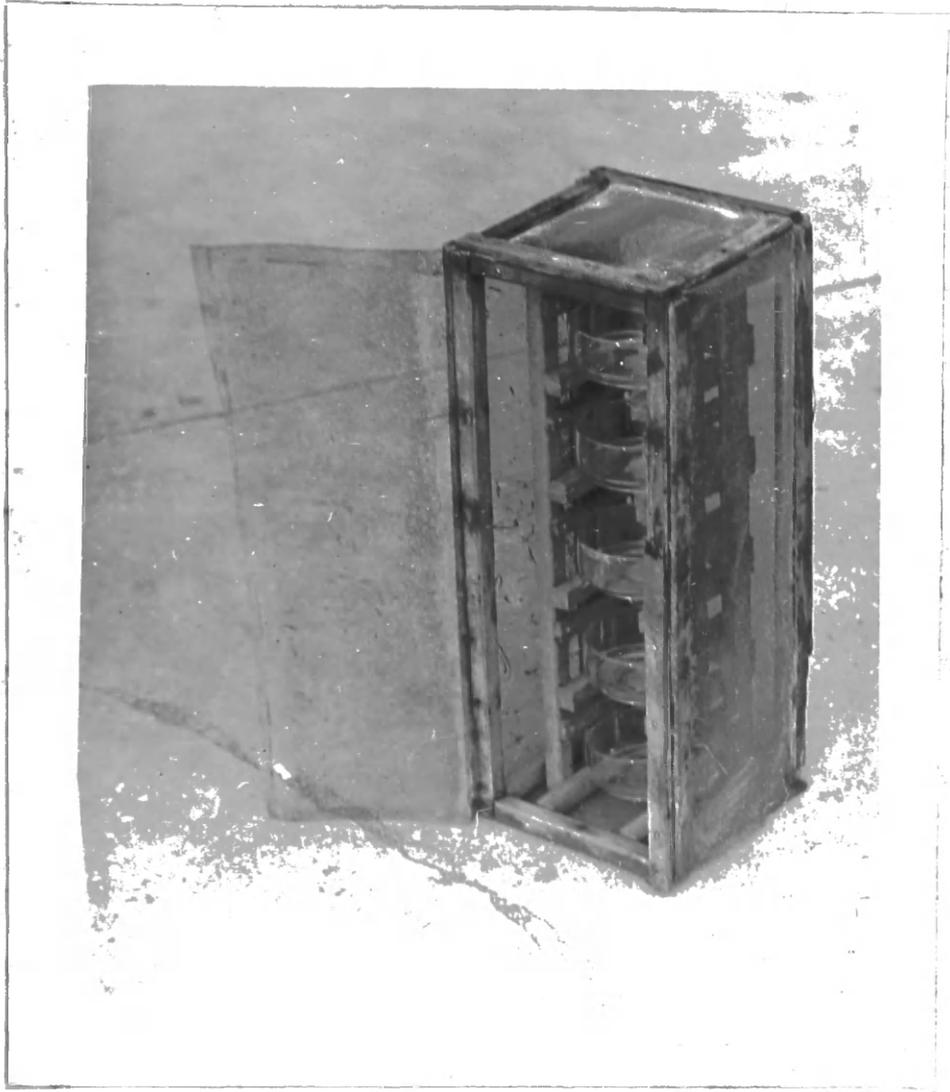
PLATE II

Photograph of a section of the
gonad of a mature female D. quinquecirrha
showing the mature eggs, black, and the
immature eggs, gray.

Magnification - about 300
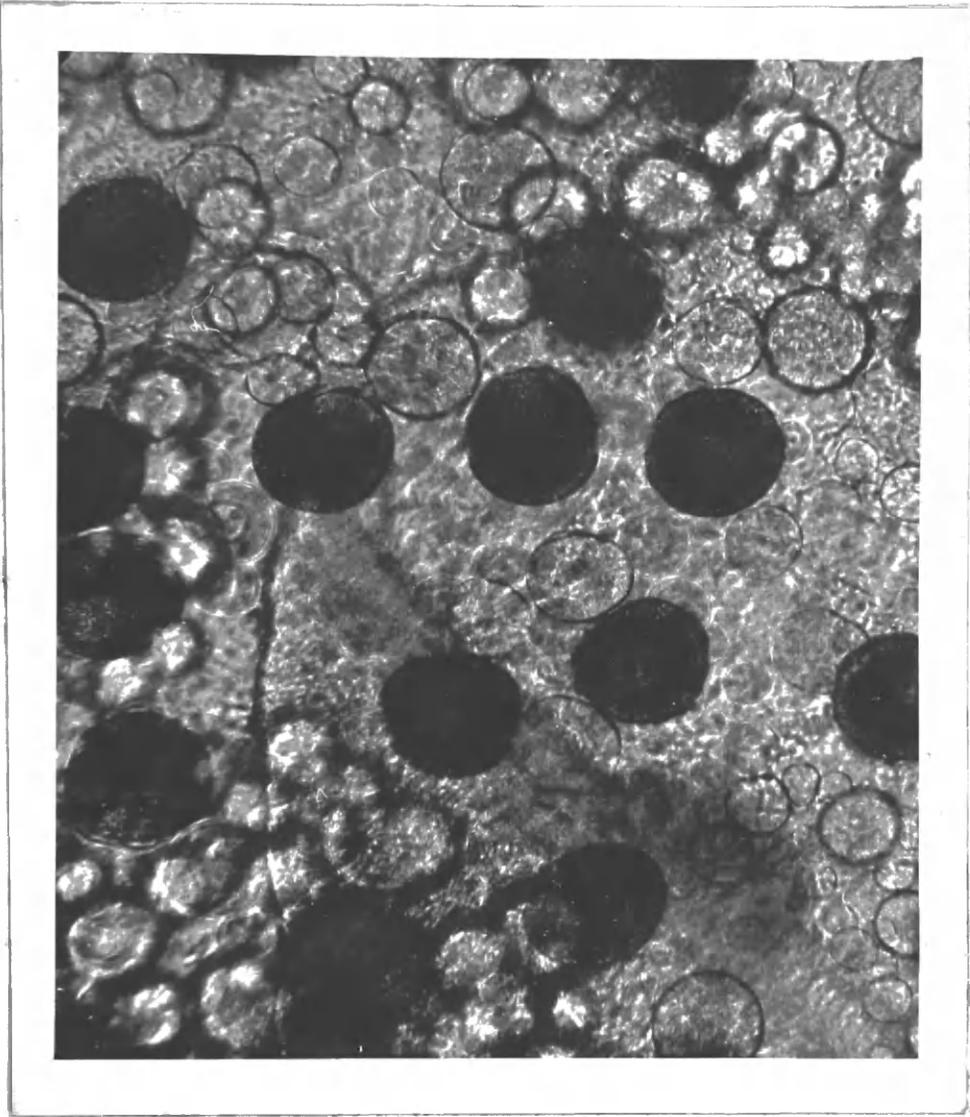
PLATE III

Photograph of a section of the
gonad of the male D. quinquecirrha
showing the sperm sacs.

Magnification - About X300.
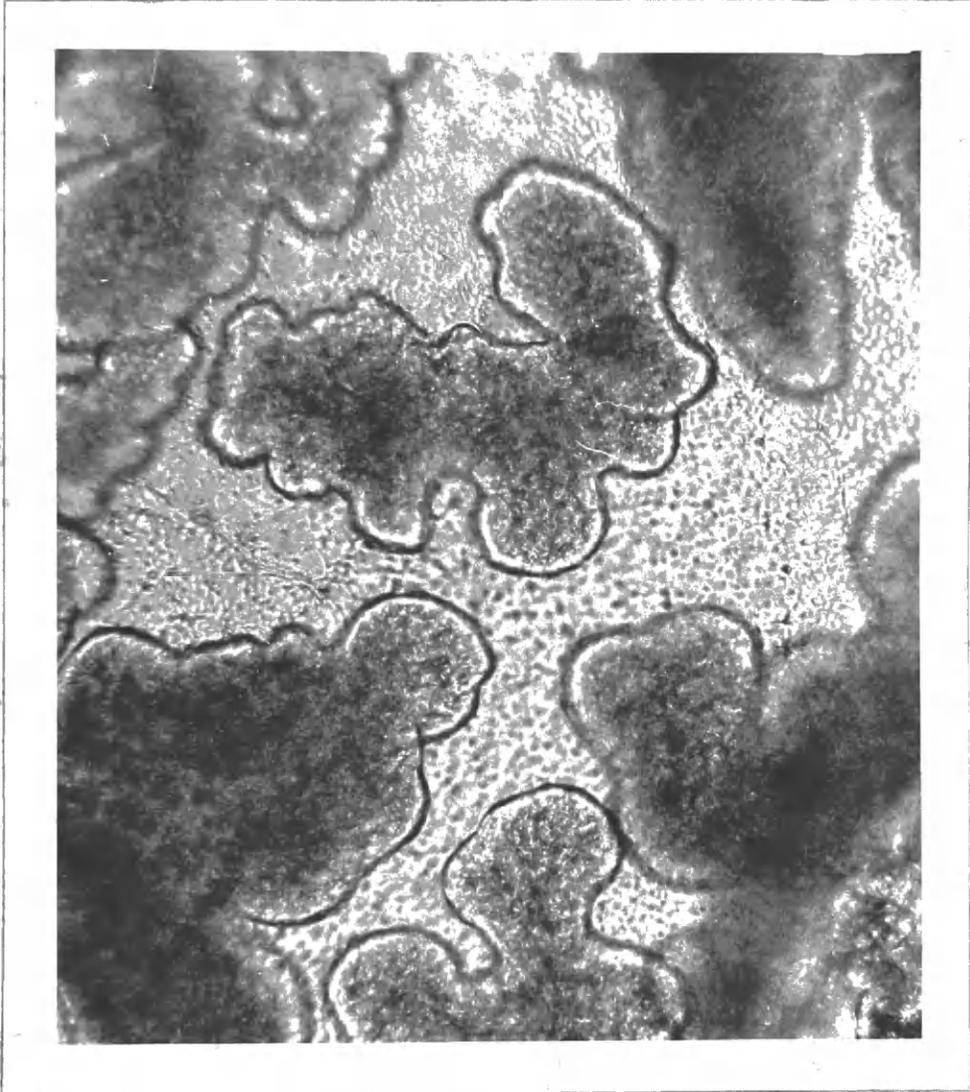
PLATE IV

Section of the gonad of the fertilized'
medusa, <u>D.quinquecirrha</u>, showing: (a) the
fertilized egg bearing a disc on one end,
(b) the mature eggs, and (c) the immature
eggs showing nuclei.

Magnification - About X 300.
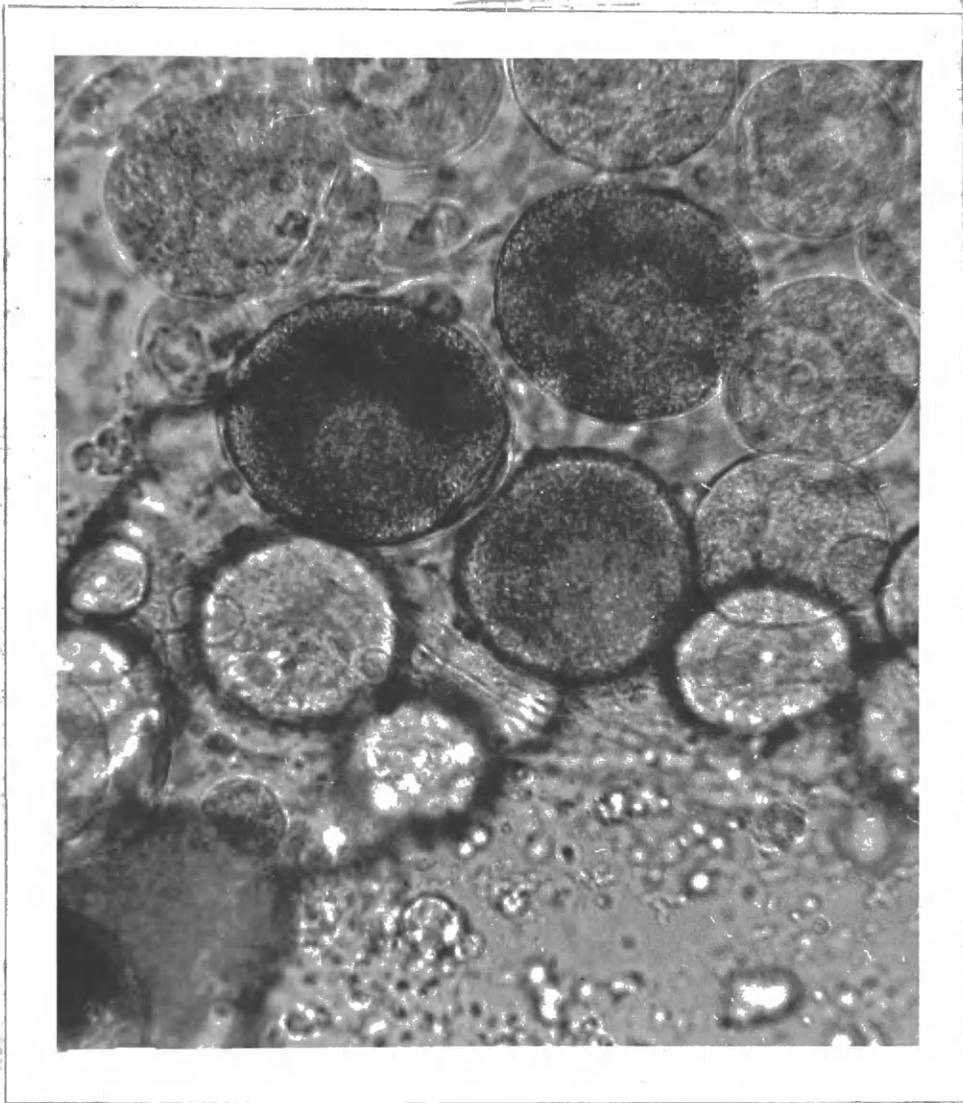
PLATE V

Drawings illustrating stages in
cleavage: (A) the one celled egg, (B)
elongation of the egg, (C) the knob-
like protuberance, and (D) the two
celled embryo.

Camera Lucida drawings from
developing embryos of D.quinquecirrha.

Magnification about X170.
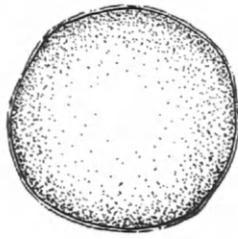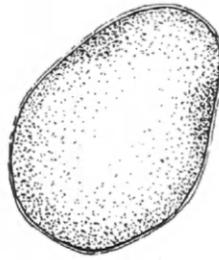
A.   B.
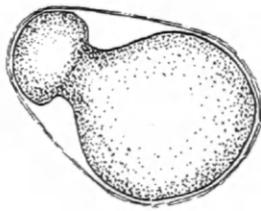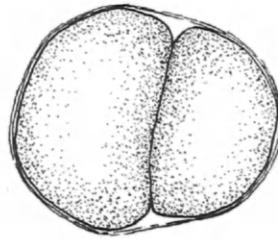
C.   D.

PLATE VI

Drawings illustrating stages in
cleavage: (A) the four celled embryo,
(B) the eight celled embryo, (C) the
early morula stage, end view, and (D)
the same embryo, lateral view.

Camera lucida drawings from
developing embryos of D.quinquecirrha.

Magnification about X 170.
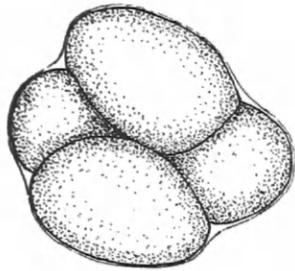
A.
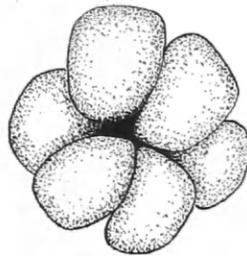
B.
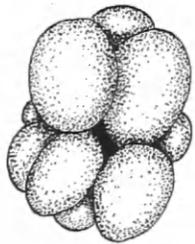
C.
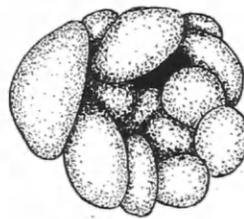
D.

PLATE VII

Drawings illustrating stages in cleavage: (A) late embryo preceeding morula, (B) the morula, (C) an uncommon type of planula, (D) the pyriform planula.

Camera lucida drawings from developing embryos of D. quinquecirrha.

Magnification about X 170.
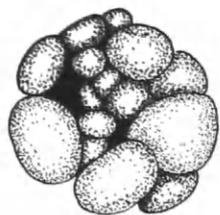
A.
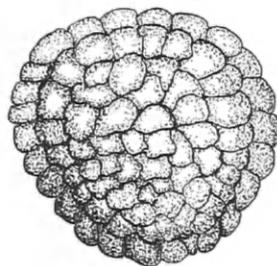
B.
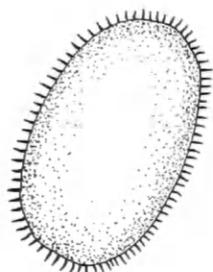
C.
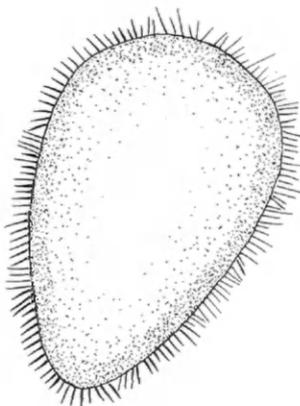
D.

PLATE VIII

Photograph of the four-celled

embryo of <u>D.quinquecirrha,</u> showing the

memorane surrounding the four cells.

Magnification - About X 300.
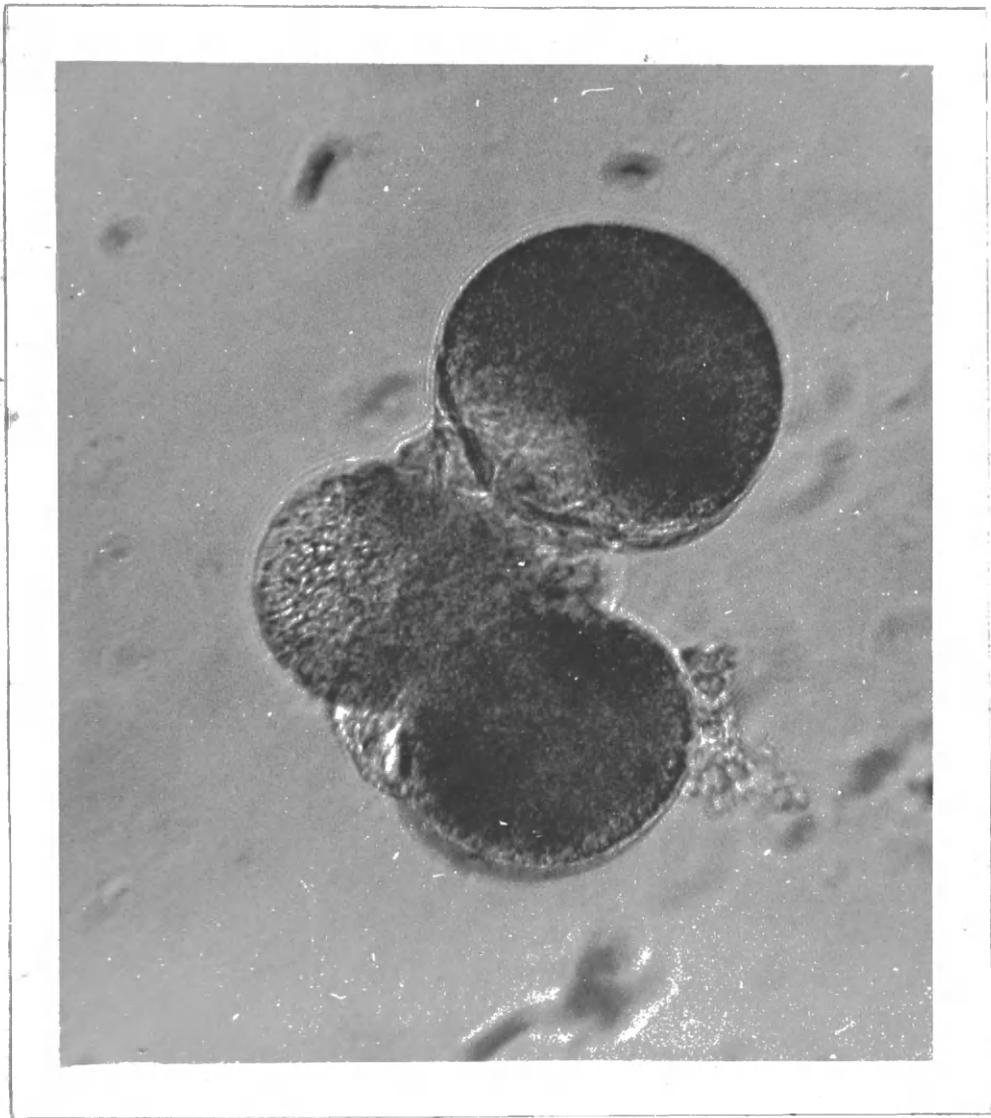
PLATE IX

Photograph of the Planula of
D. quinquecirrha.

Magnification - About X 300.
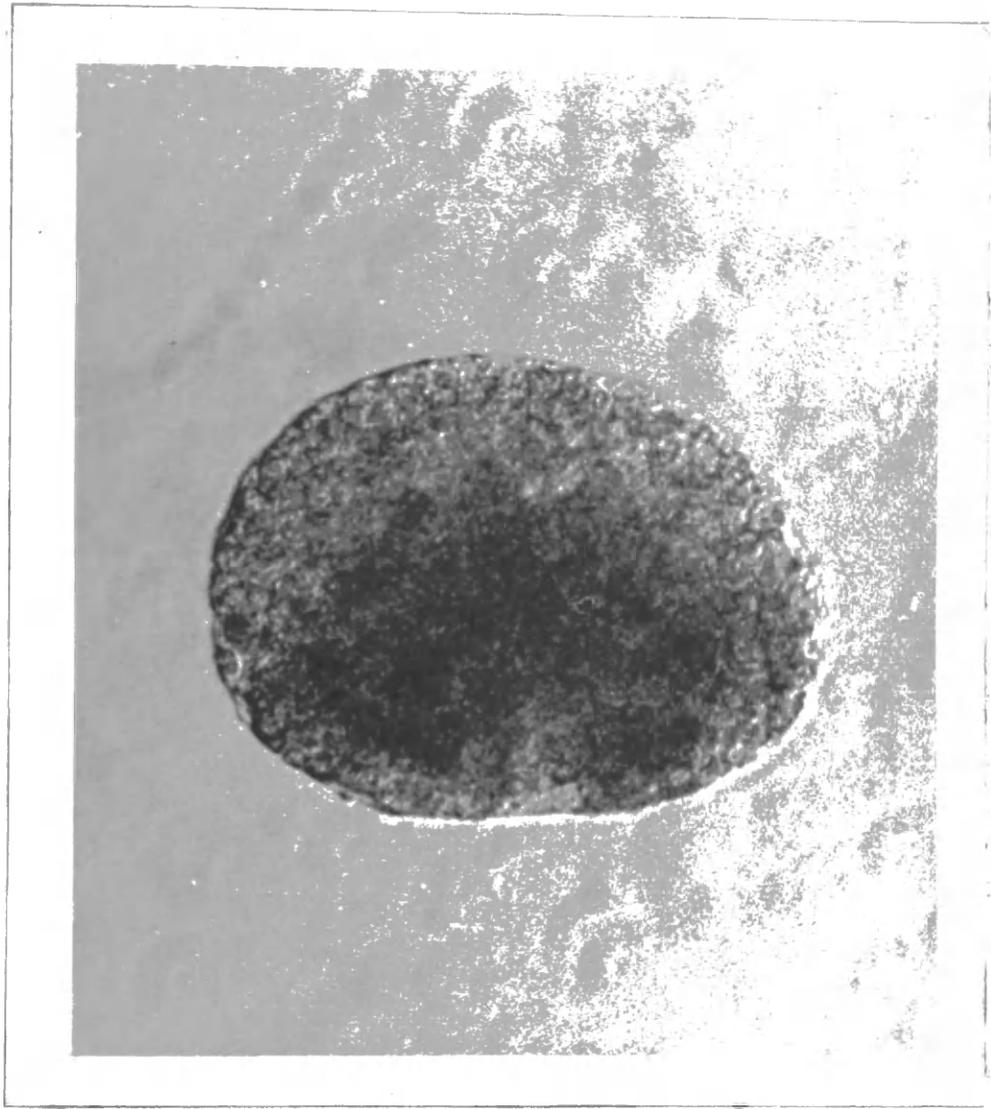
PLATE X

Photograph of several scyphostomae
of D.quinquecirrha six days after attach-
ment. The photograph shows individuals
having three, four, six, and seven ten-
tacles.

Magnification - About X 300.
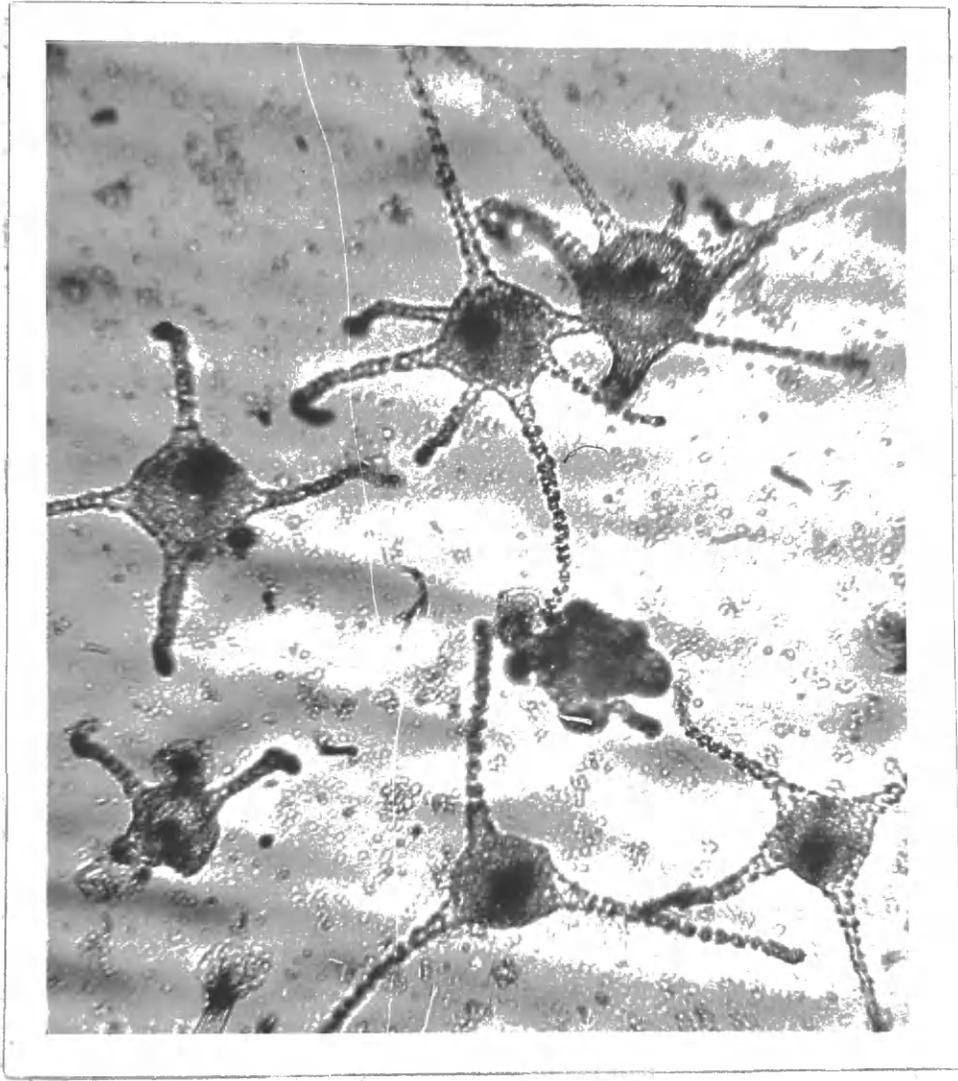
PLATE XI

Photograph of the oral view of the
scyphostoma of D. quinquecirrha showing
the arrangement of the sixteen tentacles.

Magnification - About X 300.
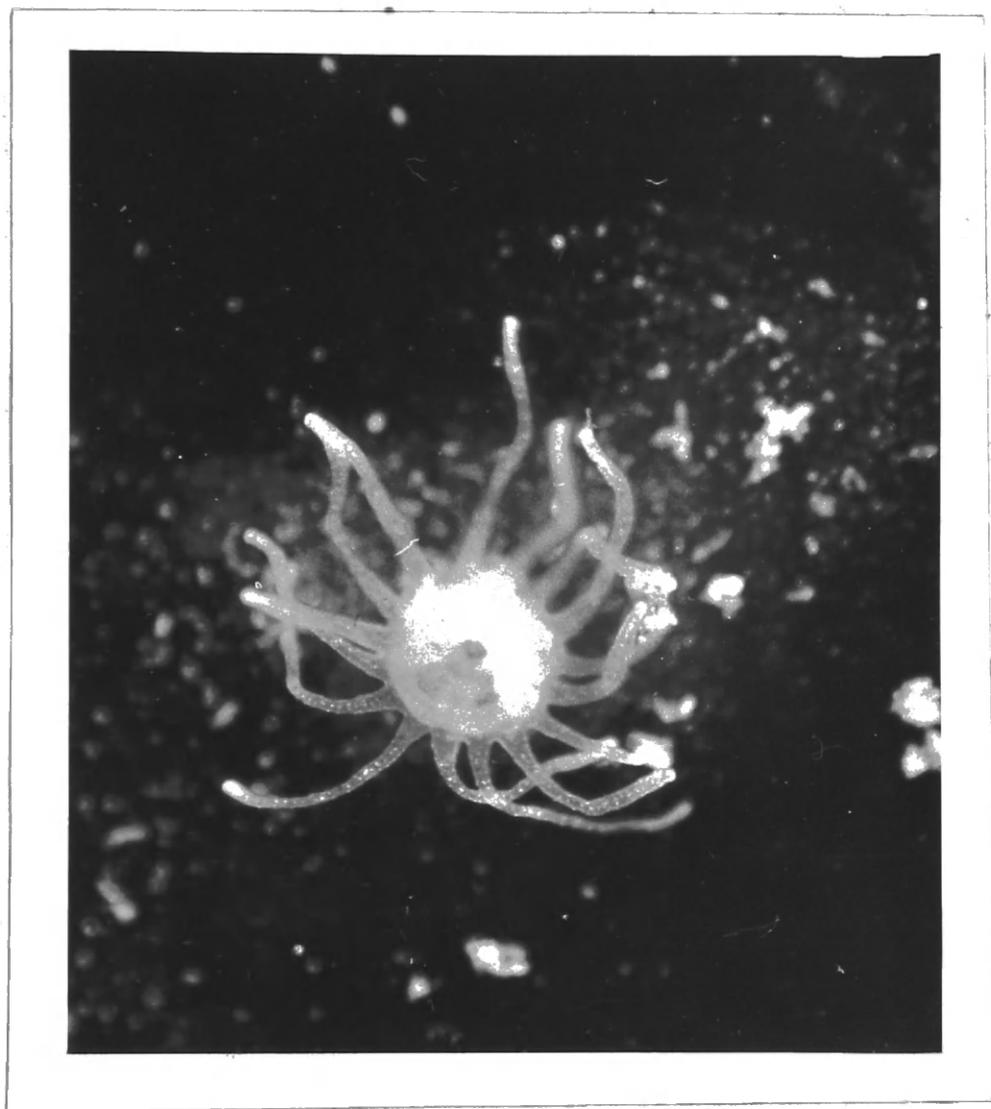
PLATE XII

Fig. A - Photomicrograph of a colony of scyphostomae of D.quinquecirrha. Magnification X 40.

Fig. B - Photomicrograph of a scyphostoma of D.quinquecirrha showing the oral cone and tentacular furrow. Magnification X 50.
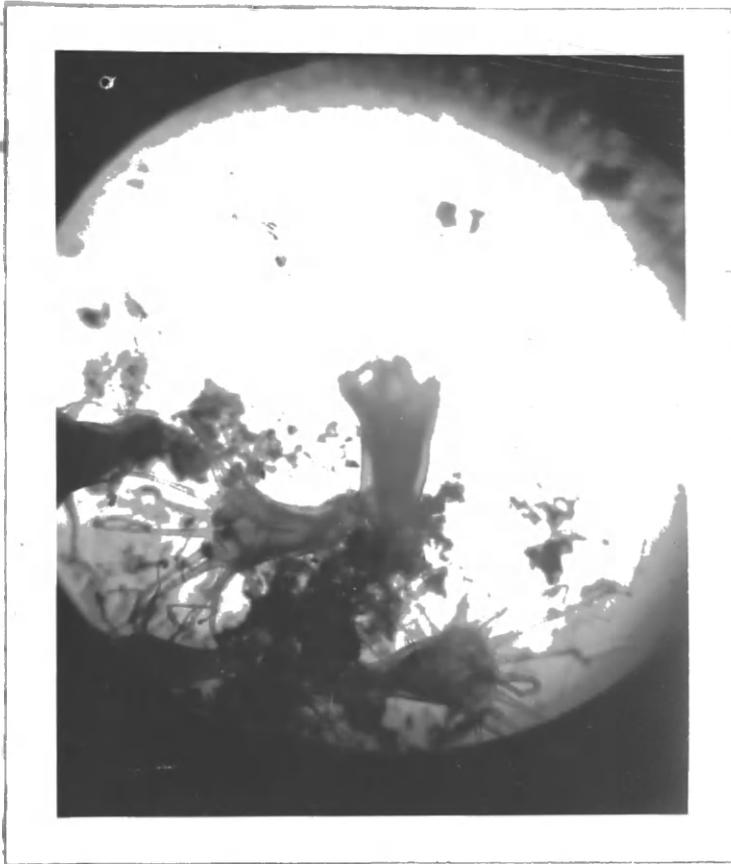
A

B

PLATE XIII

Fig. **A** - Photomicrograph of a
scyphostoma of D.quinquecirrha showing
the arrangement of the nematocysts on
the tentacles. The nematocysts appear
as dark dots on the tentacles.
Magnification X 100.

Fig. B - Photomicrograph of a single
tentacle showing the nematocysts, which
appear as rather large ovoid bodies, and
the nematocyst hairs.
Magnification X 225.
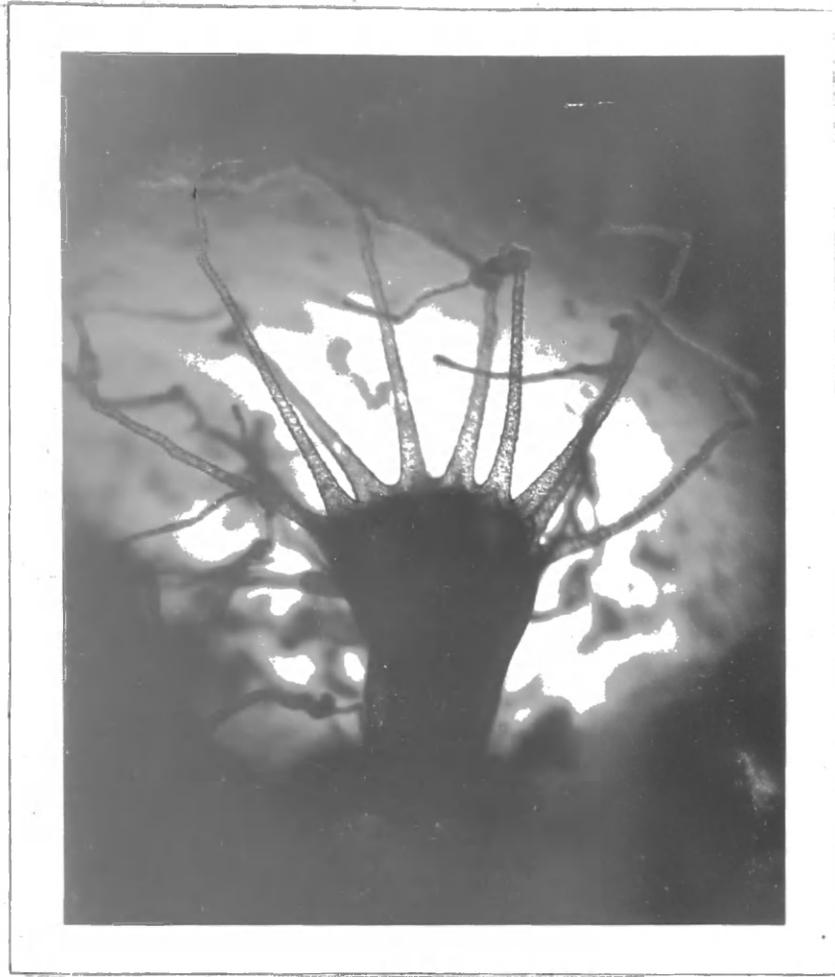
A
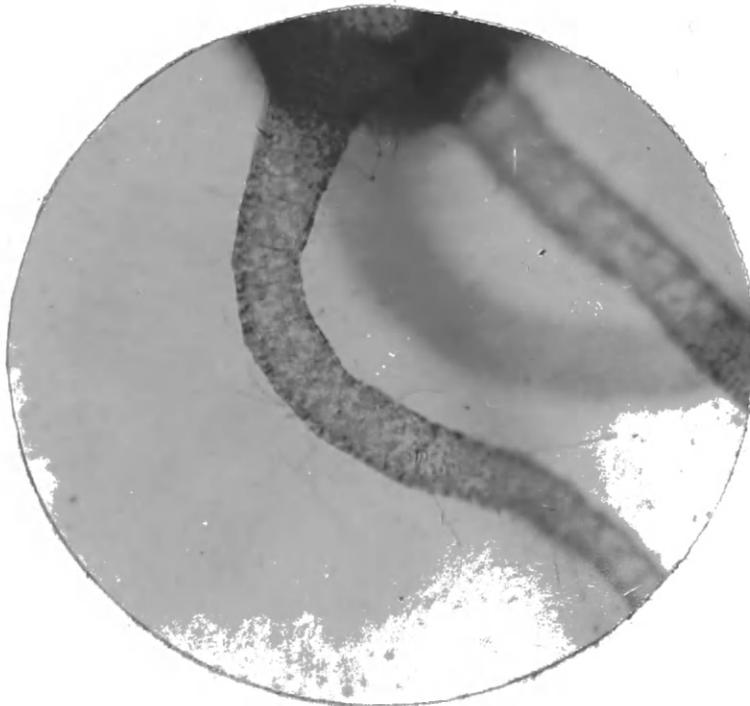
B

PLATE XIV

Fig. A - Photomicrograph of a
cross section of the scyphostoma of
D.quinquecirrha showing the evagin-
ations of the endoderm to form the
taeniolae.
The section is cut on an oblique.
Magnification X 100.

Fig. B - Photomicrograph of a
longitudinal section of a scyphostoma
of D.quinquecirrha showing the form-
ation of the taeniolae.
Magnification X 50.
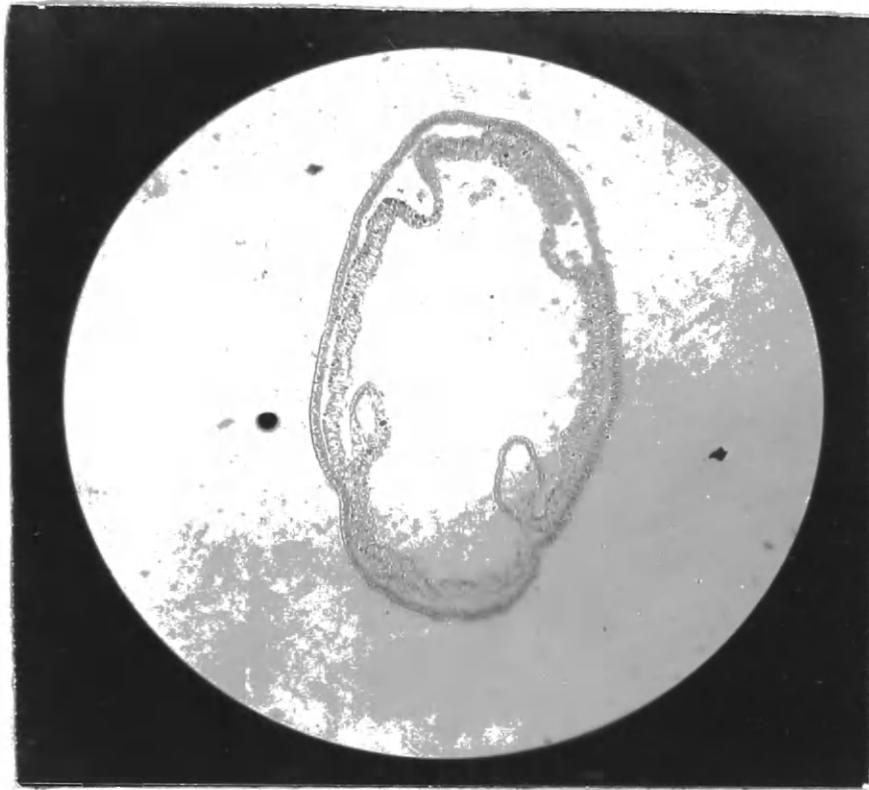
A
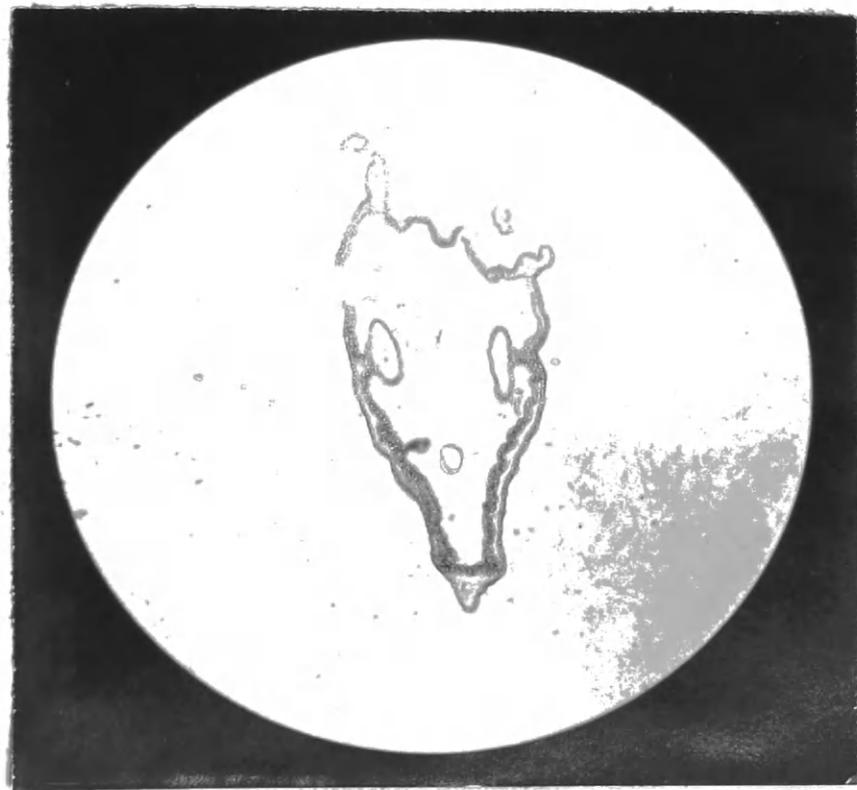
B

PLATE XV

Photomicrograph of a longitudinal
section of the body wall of the scyph-
ostoma of D.quinquecirrha showing the
appearance of the endoderm.

Fig. A - The mouth and tentacle
region.

Fig. B - The region of the taeniolae.

Fig. C - The stalk region.

Magnification X 225.

A.

B.
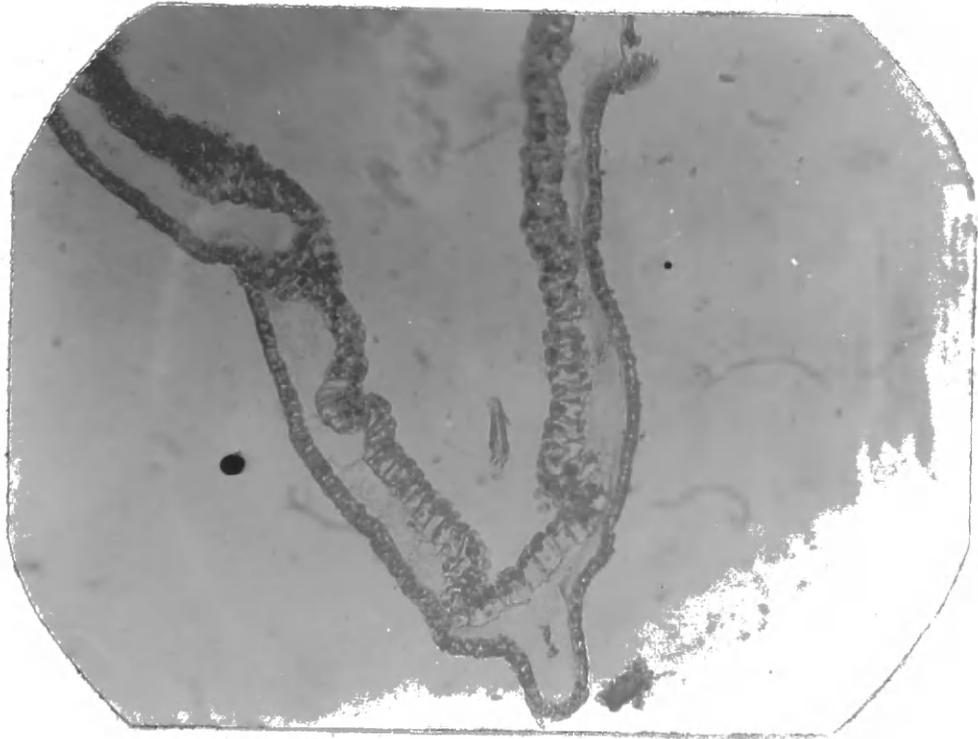
C.

PLATE XVI

Photograph of the scyphostoma
of <u>D.quinquecirrha</u> showing the pedal
discs.

Magnification - About X 300.
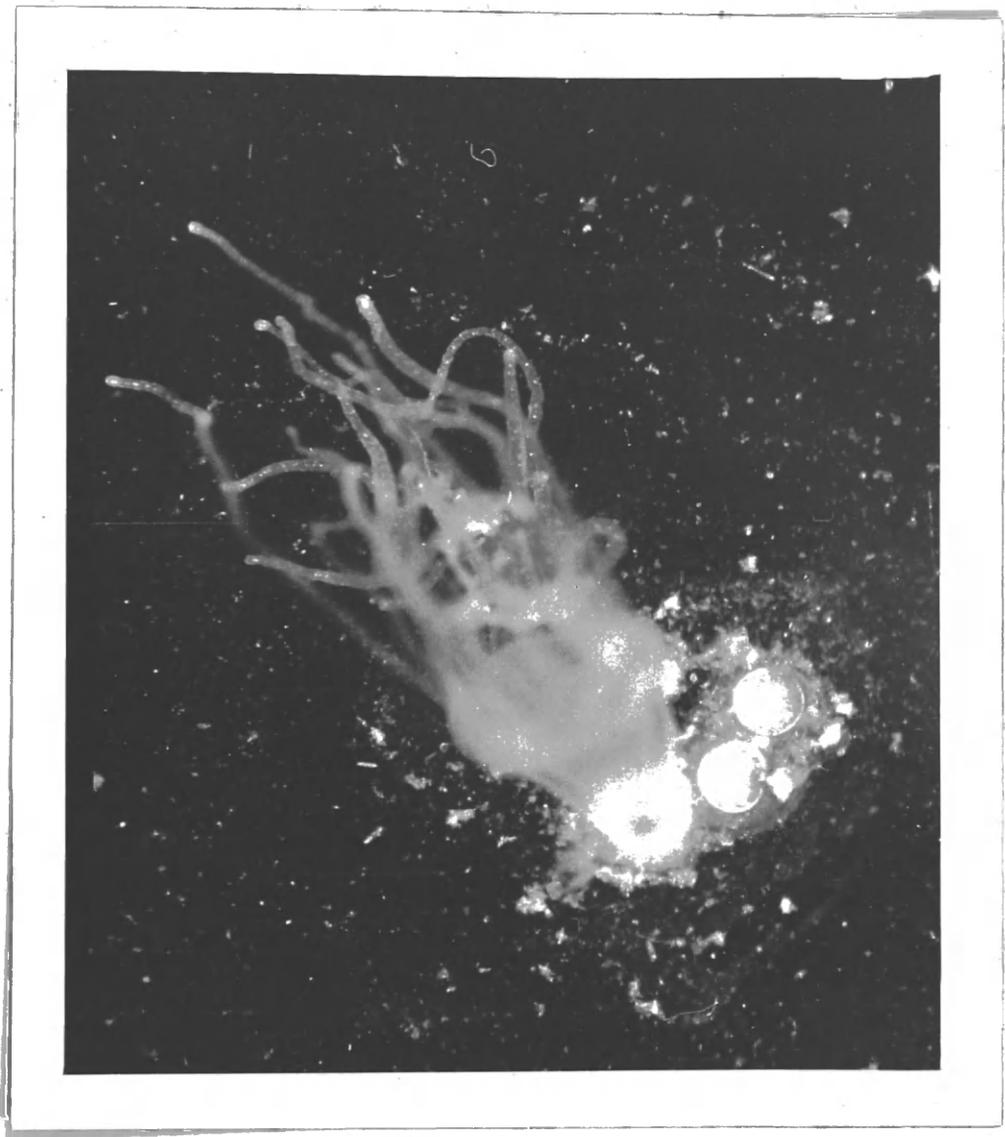
PLATE XVII

Photomicrographs of the scyphostoma
of D. quinquecirrha showing strobilization.

Fig. A - The formation of the circular
furrows.

Fig. B - The strobila.

Magnification X 50.
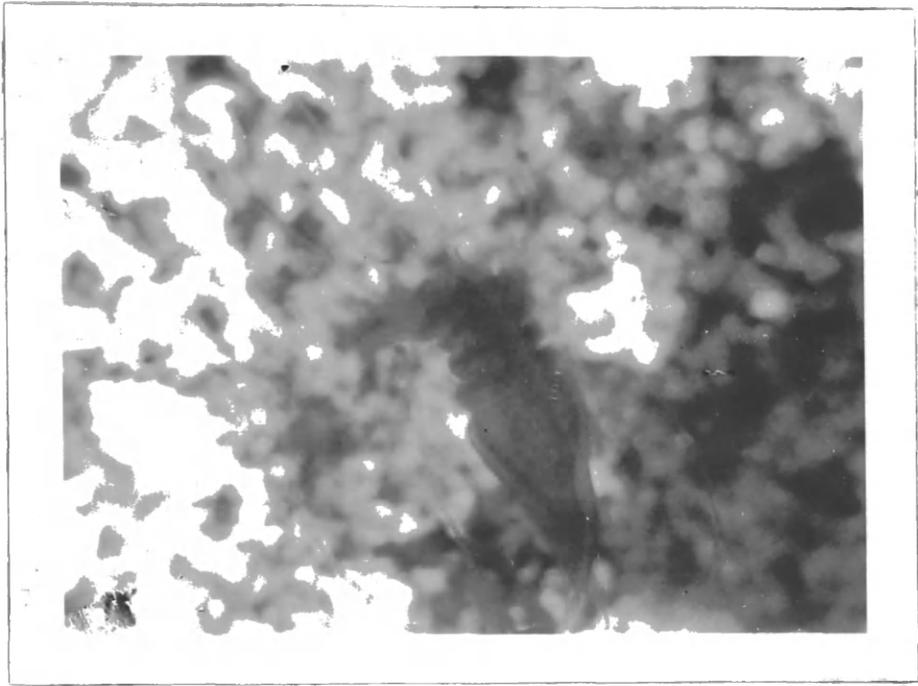
A.
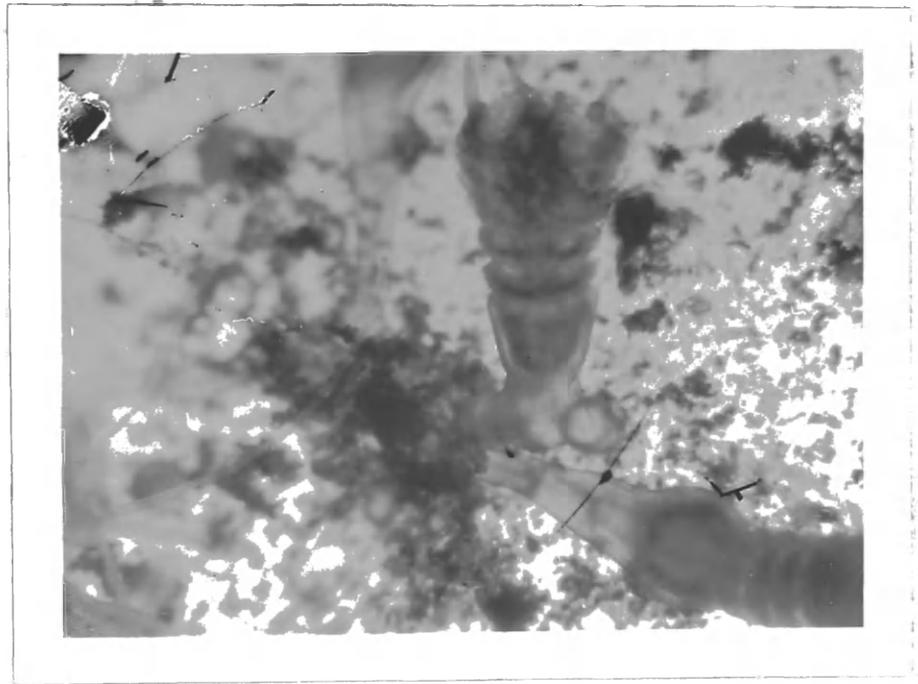
B.

PLATE XVIII

Fig. A - Photomicrograph of the
ephyra of D.quinquecirrha thirty six
hours after liberation. Note the prom-
inence of the tentaculocysts, the cruci-
form mouth, the absence of tentacles,
and the interradial ridges of the future
gastric cirra.

Fig. B - Photomicrograph of the
ephyra of D.quinquecirrha six days
after liberation. Note the eight primary
tentacles, the nematocysts, and the
increased development of the manubrium,
which hides the developing gastric cirra.

Magnification X 100.
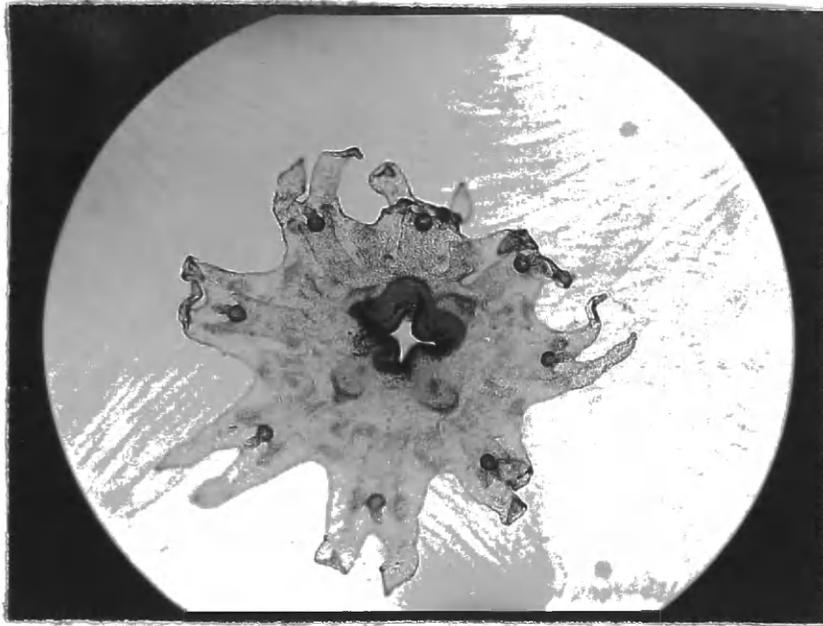
A.
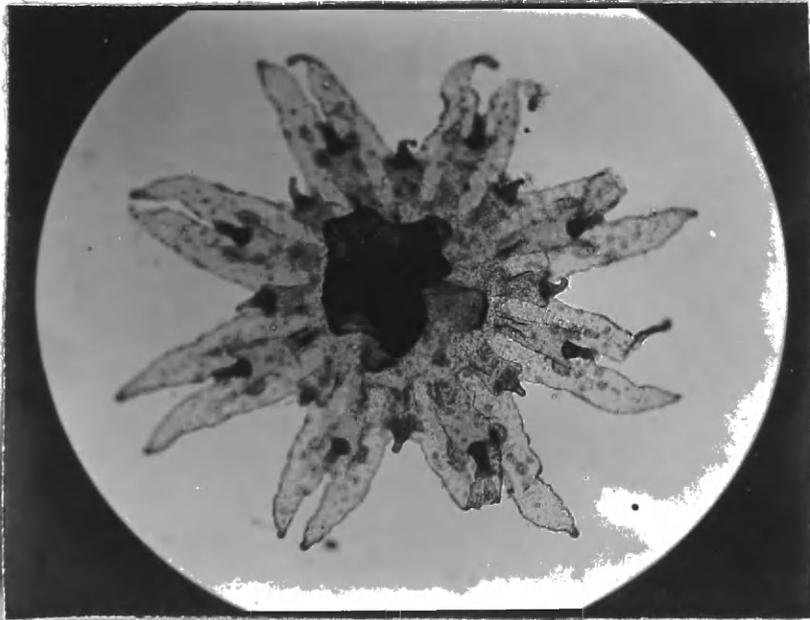
B.

PLATE XIX

Photomicrograph of the ephyra
of D.quinquecirrha eight days after
liberation. Note the four gastric cirra,
the well organized nematocysts, and the
increased development of the manubrium.

Magnification X 100.