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CEPHALODISCUS

By

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By C. C. John, M.A.

(Plates XXXIII-XXXVIII, text-figs. 1-7)

INTRODUCTION

THE genus *Cephalodiscus* was founded on the material dredged by the 'Challenger' in 1876 from the Straits of Magellan. It was first thought to be a compound Ascidian and later referred to the Polyzoa. In 1887 its structure was satisfactorily worked out by M'Intosh and Harmer (1887) who assigned it to the phylum Enteropneusta.

Although *C. dodecalophus* is the first recorded species, Ridewood (1921) has shown that thirteen pieces of *C. densus* were dredged by the 'Challenger' in 1874 at Kerguelen Island. These were at first supposed to be Monaxonid sponges and later regarded as a kind of hydrozoan allied to *Spongicola fistularis*. They were correctly identified only in 1919 and described by Ridewood in 1921. Material of *C. nigrescens* had been obtained as far back as 1841 or 1842 by the 'Erebus' and 'Terror', but remained unidentified until Ridewood described it in 1912.

Under these circumstances *C. dodecalophus* remained the sole representative of the genus until 1903, when Andersson (1907) announced the rediscovery of *Cephalodiscus* by the Swedish South-Polar Expedition. The Siboga report published by Harmer in 1905 added three new species. In the meantime Masterman and Schepotieff devoted several papers to the further description of the Challenger material. The latter also described an interesting new species, *C. indicus*, from Ceylon.

Lankester (1905) described a new species, *C. nigrescens*, from the Discovery material of the 1901-1904 Expedition. In 1906 Ridewood described *C. gilchristi* from South Africa and in 1907 gave an account (1907 *b*) of the two species which had been dredged by the Discovery Expedition of 1901-1904. Among the collections of the "Scottish National Antarctic Expedition" there were some colonies of *C. nigrescens*, *C. hodgsoni*, *C. solidus* and *C. agglutinans* which were described by Harmer and Ridewood (1913).

Finally when Ridewood (1918 *a*) published his reports on *Cephalodiscus* of the Terra Nova Expedition, he gave a complete synopsis of all the species then known. Before that time it was found necessary to break up the genus into three sub-genera. To these I have found it necessary to add one more sub-genus *Acoelothecia* to accommodate one of the new species, *C. kempi*, of the present collection.

Up to now, sixteen species have been described, including those which are regarded as doubtful forms, and the present Expedition adds two more new species to the list.

The material of *Cephalodiscus* collected during the Discovery Investigations occupies twenty-two jars. Although large quantities were collected from some stations, the yield

from others was comparatively poor, consisting of small pieces preserved in tubes. *C. nigrescens* and *C. kempfi* were dredged in large quantities, but *C. fumosus* is represented by one piece and the collection of *C. densus* and *C. hodgsoni* is small. When the zooids had been liberated from the coenocidium and fixed in Bouin's fluid, the results were good. But when entire colonies were fixed and preserved, the zooids are not satisfactory for sectioning, for as the colonies were put into the fixing media, the zooids rushed to the ostia and blocked the passages, thus preventing the entrance of the fixing fluid.

Following the Station List already published, the stations of R.R.S. 'Discovery' are denoted by plain numbers and those of R.S.S. 'William Scoresby' are distinguished by the prefix WS. The symbols used for nets, apparatus, etc., are as follows:

- DLH. Large dredge. Heavy pattern, 4 ft. in length (1.2 m.).
 H. Horizontal.
 N 7-T. Net with mesh of 7 mm. (0.28 in.) attached to back of trawl.
 N 200. 2 m. tow-net. Mouth circular, 2 m. in diameter (6.6 ft.); mesh graded, at cod-end 4 mm. (0.16 in.).
 NRL. Large rectangular net. Frame 8 ft. long and 2¼ ft. wide (2.45 m. × 0.7 m.), with bag of ½ in. mesh (12.5 mm.).
 OTC. Commercial otter trawl. Head rope 80 ft. long (24.5 m.); mesh at cod-end 1½ in. (3.8 cm.).
 OTL. Large otter trawl. Head rope 40 ft. long (12.2 m.); mesh at cod-end 1¼ in. (3.2 cm.).

The following tables give the geographical and bathymetrical distributions:

Geographical distribution

Name of species	Place	Latitude
<i>C. hodgsoni</i>	Off South Georgia Off South Orkneys Palmer Archipelago	54°-64° S
<i>C. nigrescens</i>	Palmer Archipelago	64° S
<i>C. densus</i>	South Atlantic Ocean (station 82) Palmer Archipelago	32°-64° S
<i>C. fumosus</i>	Off Cape Bowles Clarence Island	61° S
<i>C. kempfi</i>	Off South Georgia Between Falkland Islands and South America	49°-53° S

It is interesting to note that all the species of *Cephalodiscus* except *C. indicus*, *C. levinsoni*, *C. gracilis*, *C. sibogae*, *C. evansi* and *C. gilchristi* have been obtained from the Southern Ocean between latitudes 49° and 78° S and of these *C. hodgsoni*, *C. solidus*, *C. densus*, and *C. nigrescens* have been recorded within the Antarctic Circle by previous expeditions. The greater part of the present collection was obtained from the neighbourhood of Palmer Archipelago, Falkland Islands and South Georgia lying between latitudes 49° and 64° S. Only one broken piece of *C. densus* is from station 82 (South Atlantic Ocean, 32° S).

Bathymetrical distribution

Name of species	Depth	Number of specimens	Number of stations
<i>C. hodgsoni</i>	93-130 m.	10	4
	259 m.	1	
<i>C. nigrescens</i>	160-330 m.	1 (fragmentary)	1
	93-130 m.	Numerous	
<i>C. densus</i>	315 m.	1	3
	75 (-0) m.	1	
<i>C. fumosus</i>	140-144 m.	1	1
	93-130 m.	2	
<i>C. kempii</i>	342 m.	2 (including a small fragment)	11
	75-74 m.	2 (Form B)	
	79 m.	1 (Form B)	
	82 m.	4 (Form B)	
	118 m.	1 (Form B)	
	146-145 m.	Numerous (Form B)	
	219-133 m.	7 (Form B)	
	200-236 m.	1 (Form A)	
	245 m.	4 (Form A)	
	401-411 m.	Numerous (Form A)	

I take this opportunity of offering my thanks to Professor E. W. MacBride, F.R.S., for getting the materials on his personal responsibility, and for the facilities he afforded me for carrying on this investigation in the Huxley Laboratory under his guidance and supervision; to Dr Stanley Kemp for having entrusted me with the drawing up of the report on *Cephalodiscus*; to Mr H. R. Hewer for suggesting names for the new species and other technical advice; and to Sir Sidney Harmer, K.B.E., F.R.S., for the trouble he took in revising the original manuscripts and for suggesting corrections and improvements which make this paper acceptable for publication.

SYSTEMATIC ACCOUNT

DIAGNOSIS OF THE SPECIES OF *CEPHALODISCUS*

The most important specific structure is the coenocidium. The classification into sub-genera is based entirely on the nature of colony formation. Harmer (1905, p. 4) considers the length of the body and stalk of the zooids as satisfactory specific characters, but measurement of the zooids of some species does not support this. In *C. hodgsoni* the length of the zooids varies from 2 to 32 mm. and that of the stalk from 4 to 10 mm. In *C. densus*, though normal zooids measure 4 to 7 mm., I have obtained giant zooids 11 to 14 mm. long, with a stalk which varies in length from 25 to 40 mm. The number of arms can be used as a specific character, as this is constant for each species except *C. hodgsoni* in which there may be 10, 11 or 12. The number of buds produced can to a certain extent aid in describing the different species. In some species like *C. fumosus* buds are produced profusely, while in others like *C. hodgsoni* the number of buds is only three to five. I doubt whether the production of buds is confined to a definite

season. Specimens of the same species dredged at different times of the year show uniformity in the number of buds produced and this fact may be sufficient evidence to show that buds are produced all the year round. Living as they do in the cold waters of the Antarctic Seas, where submarine conditions are similar throughout the year, it is not to be expected that the seasons could have much influence on budding. We might expect to find indications of seasonal changes on the forms from shallower waters such as *C. indicus* from the coast of Ceylon, *C. levinseni* from the coast of Japan or *C. gilchristi* from the South African coast, where the changes are very marked; but reports on these do not mention what influence seasons have on budding. The presence or absence of end-bulbs on the arms, and sometimes (e.g. *C. nigrescens* and *C. fumosus*) the presence of dark lines along the axes of the arms are also characters which help identification.

Sub-genus *Demiothecia*

Cephalodiscus hodgsoni, Ridewood. (Pl. XXXIII, figs. 1-5.)

C. hodgsoni, Ridewood, 1907 *b*.

C. inaequatus (Andersson), 1907.

DIAGNOSIS. Irregularly branched colony without cross bars between branches. Width of branch excluding spines usually 4 to 6 mm.; some basal stems 9 mm. Cavity of coenocium continuous, the smooth inner lining sometimes traversed by solid bars. Zooids and buds occupy the cavity in common. Older parts of the coenocium deep amber colour. Ostia numerous, irregularly placed, funnel-shaped and each with two to five simple or forked spines. Zooids: length of a fairly extended zooid from free end of arms to end of body 2 to 3.2 mm. Colour of preserved zooids, reddish or pale brown. Arms, five or six pairs. Axes of each arm have an end-swelling, with refractive beads. Male and female zooids and hermaphrodites occur in the same colony. Buds, two, three or four to each zooid.

MATERIAL. The material of *C. hodgsoni* was obtained from the following stations:

St. 167. 20. ii. 27. Off Signy Island, South Orkneys, 60° 50' 30" S, 46° 15' 00" W. Gear OTL. 244-344 m. One specimen.

St. 187. 18. iii. 27. Neumayr Channel, Palmer Archipelago, 64° 48' 30" S, 63° 31' 30" W. Gear DLH. 259 m. One specimen.

St. 190. 24. iii. 27. Bismarck Strait, Palmer Archipelago, 64° 56' 00" S, 65° 35' 00" W. Gear DLH and NRL. 93-126 m. Twelve specimens.

St. WS 18. 26. xi. 26. 54° 07' 00" S, 36° 23' 00" W. Gear OTL. 160-330 m. Small fragment.

Stations 167 and 187 yielded only two small pieces of dead colonies. Inhabited colonies, dredged from station 190, consisted of twelve fragments, which were labelled in two bottles, owing to differences in the spines. The dimensions of entire colonies given by Ridewood (1907 *b*, p. 50), show that these are only broken bits of large colonies. The basal attachment is found in only one possibly entire colony.

The difference between two distinct types of colonies obtained from station 190 is shown in Pl. XXXIII, figs. 1 and 2. Careful study of their structure shows that the thickness of the coenocium, the number of spines and the short branches on the colony

cause these differences. Between these distinct forms there are colonies which are difficult to assign to either type. The existence of such intermediate forms proves that the external differences are the result of the amount of coenocelial material secreted by the animal. The coenocium and spines are formed by the secretion of the coenocelial substance, laid down in thin lamellae. Increase in size is brought about by the deposition of lamellae over existing layers. Owing to differences in nutrition, and other causes, the amount of coenocelial substance secreted varies and this may account for differences which are observed between colonies dredged from different places.

In the absence of zooids in the colonies obtained from stations 167 and 187, the structure of the coenocium is the only evidence that these colonies are modified forms of *C. hodgsoni*. The colour of the coenocium, the thickness and length of spines and the disposition of short branches are sufficient differences to separate them from Forms A and B (see below).

Owing to subtle variations in the coenocium of *C. hodgsoni* any attempt to give a comprehensive account of the structure may prove to be unsatisfactory. Generalization is rendered difficult by intermediate forms between the extreme types; but since the differences are only due to the amount of coenocelial substance secreted by the colony they do not affect the diagnostic character of the coenocium as a whole.

The colony is formed of a main stem which has many lateral branches. The stem and branches are hollow and the continuous cavity opens externally by numerous ostia. The sides of the lateral

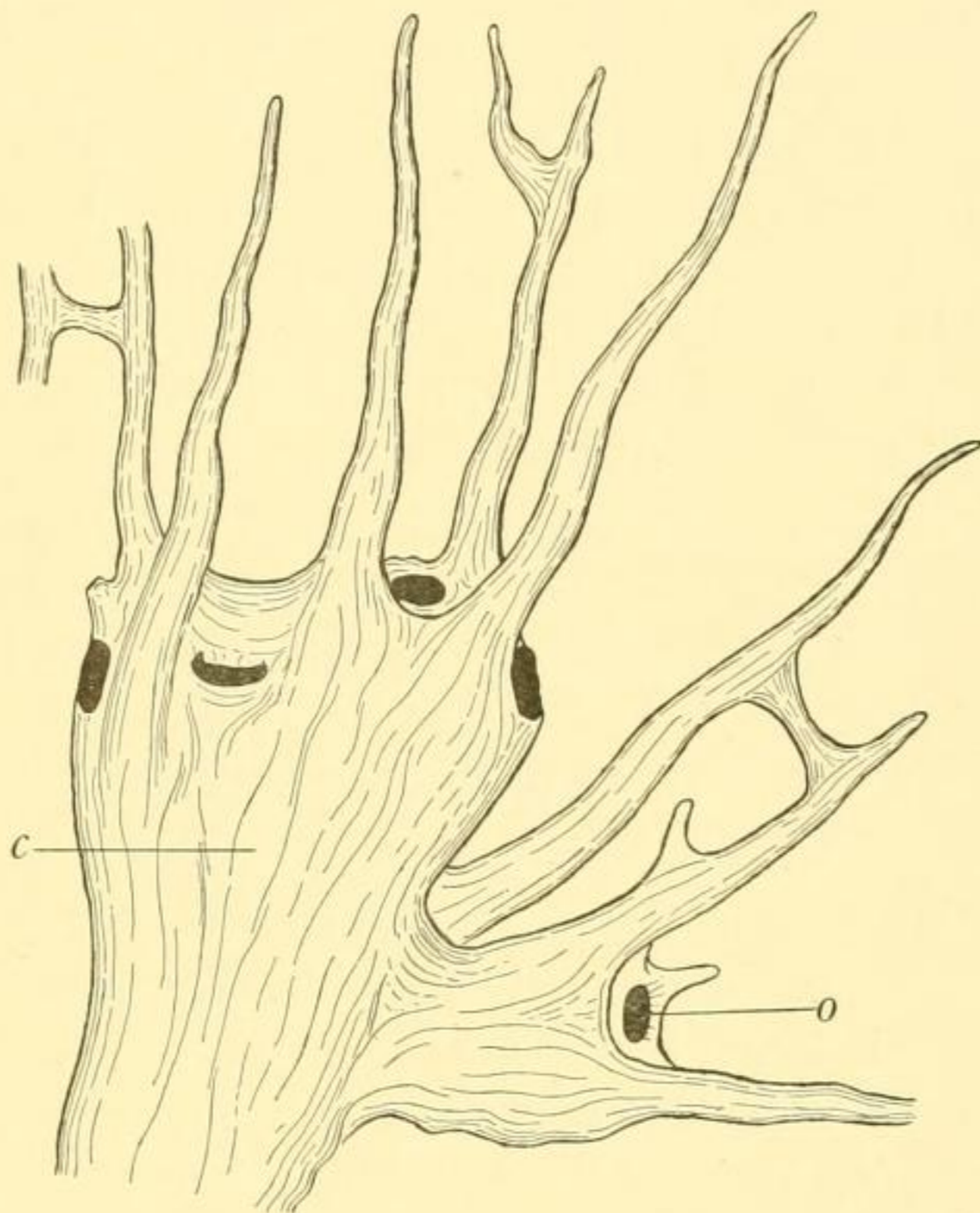


Fig. 1. *C. hodgsoni* showing the disposition in form A of ostia and spines on a short lateral branch. *o*, ostium; *c*, cavity of coenocium.

branches and the edges of the ostia bear varying number of spines. These characters are constant in all the forms, and variations occur only in the disposition of the lateral branches, the spines, the number of ostia and the colour of the colony. Ridewood (1918 *a*, p. 51) defined two forms based on these variations, which he termed Forms A and B respectively. The present account follows the same line with a few new observations.

Form A (Pl. XXXIII, fig. 1). This form is represented only by a few small pieces, mostly of a rich amber colour. The thickness of the coenocium and width of the cavity varies between different parts. At the base, the cavity is small and circular with a diameter of 1.75 mm. and the coenocium is about 1.5 mm. in thickness. Farther up, the cavity gradually widens and the walls become thinner. Towards the tips of the lateral branches

the cavity widens still more and becomes oval in section. The lining of the cavity is smooth, but near the base of the colony there are stout bars extending at intervals across the cavity and fused at both ends with the lining. In one specimen a few pocket-like septa were found on the inner lining, near the base. Pocket-like septa are recorded for the first time, but they are not homologous with the irregular partitions and pockets found in *C. dodecalophus*.

At intervals along the sides of the stem and lateral branches are a number of short branches bearing funnel-shaped ostia. A short branch bears three, four or five spines and one or two ostia. The short branches enlarge by further branching of the spines and the bifurcation of the ostia. In one case as many as seven ostia and fourteen spine-tips have been counted on one small branch. The diameters of the ostia vary from 1.5 to 2.5 mm. and the number of marginal spines ranges from two to five (Fig. 1).

The short branches are not produced at regular intervals. On some branches they are wide apart, and on others closely set. On one branch seventeen short branches were counted in a 5 cm. length; while on another only nine were found in the same length.

The tips of the main branches also bear ostia which are identical with those already described. New ostia are formed by the growth of ridges between the spines. Ridewood (1918 *a*) has given a detailed account of their formation, to which I can add nothing.

The spines are long, tapering and may be simple or forked. The forking first appears as a knob of spine rudiment at some point on the side, very often near the tip of an old spine. It continues to grow in length by the deposition of lamellae. Some of the branches grow upwards, while others, developing horizontally, fuse with adjacent spines or with the spines of adjacent short branches.

Form B (Pl. XXXIII, fig. 2). The short branches are much larger and the spine longer and thicker than those of *Form A*. Broadly speaking it may be said that *Form B* is larger in every way than *Form A*. The two forms are distinguished by the spines and short branches; apart from these there is very little difference in the general structure of colonies. The cavity is crossed by a few horizontal bars in the basal region, but has no side pouches.

The short branches of *Form B* are at least twice as long as those of *Form A*. Each branch has a main central ostium and one or two smaller ostia at the side, a little below the main one (Fig. 2). Typically the main ostium,

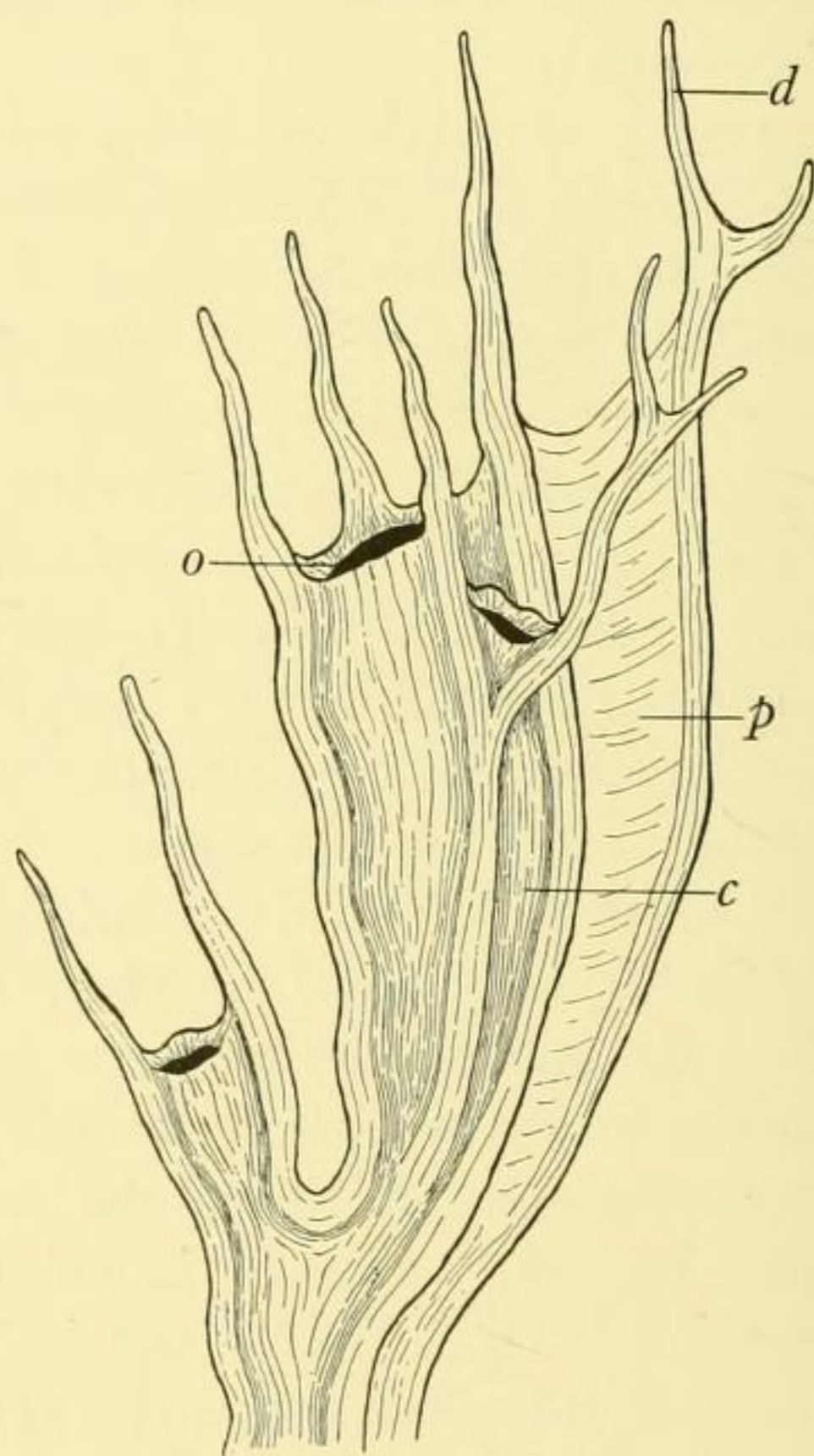


Fig. 2. *C. hodgsoni*. A short branch showing the relation of the spines to the ostium in *Form B*. *o*, ostium; *c*, cavity of coenocium; *p*, plate of coenocium connecting spine *d* with wall of coenocial cavity.

which measures 3 mm. across the longer diameter, is surrounded by four long spines and leads into a funnel-shaped cavity. Two spines project obliquely upwards from the branch and are attached to its sides by a plate of coenocelial substance which spreads as a web between the spines and the side of the branch. Lower there is another small ostium which has two spines, one at each end of its long diameter.

The spines are thick and blunt but are fewer than those of Form A. While fourteen spine-tips were counted in an ordinary short branch of Form A, not more than eight or nine are found in Form B. They are only rarely forked. Many of the spines that are seen projecting freely from the surface of the coenocodium are embedded for a considerable proportion of their total length in the coenocelial wall. These embedded parts were at one time free spines, but were later covered by the growth of the coenocodium, and the support thus given was used as skeletal structure on which the tubes were lengthened. As the growing tubes thus closed round the basal parts of the spines, these continued to elongate by the deposition of coenocelial material at their tips, so that they kept a constant length.

The short branches are fewer than those of Form A. In one specimen, for a distance of 5 cm., there are only six short branches, and in another, for a distance of 6 cm., only eight short branches were counted.

Besides the two distinct types of the species already described two specimens were obtained, one from station 167 and the other from station 187. Since both were dead colonies they cannot be definitely called new forms. Although the coenocodium shows a general structure greatly resembling that of *C. hodgsoni*, I do not venture to base my conclusion entirely on the structure of the coenocodium without examining the zooids. I shall therefore only describe the two pieces, and leave a definite identification to the time when inhabited colonies are obtained in sufficient quantity.

Pl. XXXIII, fig. 4 is a photograph of the specimen obtained from station 167, and Fig. 3 is a short branch of the same. The main stem produces along its sides a number of secondary branches, and one secondary branch is connected with the main stem by a lateral bridge. This bar suggests a resemblance to *C. dodecalophus*, but while the connecting bars of *C. dodecalophus* (M'Intosh, 1887, p. 4) are solid, the one in this form is traversed by the cavity of the secondary branch and main stem.

The main cavity is continuous through the colony and the coenocelial wall is 3 mm.

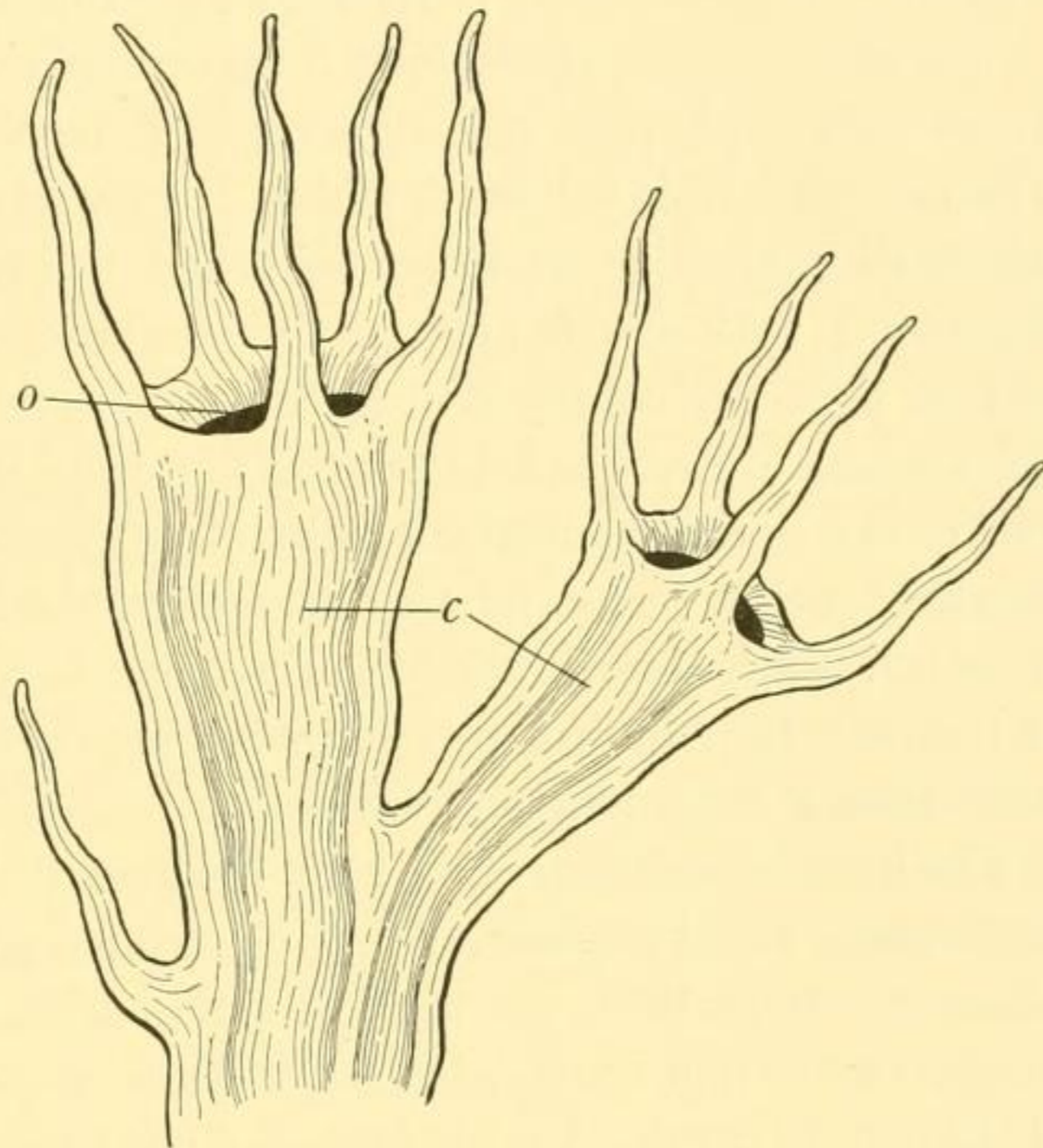


Fig. 3. *C. hodgsoni*. A short branch of the single specimen obtained from St. 167. *o*, ostium; *c*, cavity of coenocodium.

in thickness at the base. It is formed of two distinct layers which can easily be separated one from the other. The inner layer forms the smooth lining of the cavity and is occasionally beset with horizontal bars which run across the cavity. This dark reddish-brown layer is surrounded by a thicker outer layer of a lighter tint.

The main stem and secondary branches bear along their sides a number of short branches each of which carries a single ostium at its tip. The ostia are almost circular and each has four short spines at its edges. These spines, which are pointed, may be forked.

A unique feature of this colony is the dark reddish-brown colour of the coenocium which by itself might serve for regarding this as a new form of *C. hodgsoni*.

The small specimen obtained from station 187 is represented in Pl. XXXIII, fig. 5. From such a fragment it is difficult to draw any conclusions about the entire colony. The coenocium is yellowish white. It may perhaps be thought that the pale colour is due to disintegration after the zooids had died or left the colony; but the experiment of Ridewood (1918 *a*, p. 60) refutes this. In order to test the durability of the coenocium he kept a piece of colony in distilled water partly exposed to air. At the end of two years there was no difference between this piece and the remainder, preserved in alcohol. The pale colour of the coenocium is therefore the natural colour of the entire colony. Short lateral branches with ostia are borne along the sides. The ostia are like those of Forms A and B. Each short branch has three or more ostia which may be divided. The edges of the ostia bear four or more spines which are sometimes forked. The spines are not more than 1.5 cm. long and are blunt.

The internal anatomy of the zooids is treated in a separate section. Points of systematic importance are given here. A fairly extended zooid measures from 2.2 to 3.2 mm., and possesses ten or twelve arms. The stolon arises from the basal region of the body and carries two or four buds. The length of the stolon depends on the amount of contraction at the time of death. A fairly extended one measures up to 6 mm. Very often the zooids are found crowded together into certain parts of the cavity, and the stolons and buds are entangled in such a way that they cannot be easily separated.

The colour of the zooids and the number of arms present an important problem which has not been properly studied until now. Andersson (1907) stated that in *C. inaequatus* the males have twelve arms and females ten. But from the collections of the 'Terra Nova' Expedition Ridewood (1918 *a*, p. 64) showed that there is no great correlation between number of arms and sex. One difficulty of verifying this result is that in most zooids the gonads are immature so that their sex cannot be determined.

In the present collection I was able to distinguish: (*a*) colonies in which all the zooids are crimson-brown and bear six pairs of arms, (*b*) colonies in which all the zooids are pale brown and possess ten or occasionally eleven arms, (*c*) colonies in which both kinds of zooids are present, though the crimson-brown ones predominate. Sections of these two kinds show that the crimson-brown zooids are always females with well-developed paired ovaries, and that the pale brown zooids are males. Therefore some of the colonies are unisexual and others bisexual, although in these female zooids are the more numerous.

In his description of *C. inaequatus*, Andersson (1907) says that female zooids have ten arms and males twelve. This is contrary to my observations and may strengthen the claims of Andersson for regarding *C. inaequatus* as a distinct species. But since the classification of *Cephalodiscus* is based mainly on the structure of the coenoecium, the close resemblance between the coenoecium of *C. inaequatus* to that of *C. hodgsoni* makes the line of demarcation very faint.

Sub-genus *Idiothecia*

Cephalodiscus nigrescens, Lankester.

Lankester, 1905.

Ridewood, 1907 *b*, 1918 *a* and 1918 *b*.

Gravier, 1913.

DIAGNOSIS. Colony massive, branching; maximum width of a single branch 5 to 9 mm., branches roughly cylindrical. Colour greyish, translucent. Ostia placed at the end of peristomial tubes, but in the main stems frequently sessile. Abaxial edge of peristome produced into a blunt lip. No spines. Each ostium leading into a tube which ends blindly in the middle of the branch. The length of the peristomial tube depends on the thickness of the branch. The lower part of the tube is curved downwards slightly and shut off by a septum, so that the zooids inhabit the upper region only. Width of the cavity of the peristomial tube 1.2 to 1.3 mm.; length 14 to 21 mm. Length of the zooid from free end of the body to tip of arms 4 to 6 mm. Preserved zooids blackish, with six or seven pairs of arms. Each arm with two longitudinal black bands running along the whole length of its axis. Arms without end-swellings. Male, female and hermaphrodite zooids occurring in the same colony.

LOCALITY.

St. 190. 24. iii. 27. Bismarck Strait, Palmer Archipelago, 64° 56' 00" S, 65° 35' 00" W. Gear DLH and NRL. 93-126 m. Large quantities. Gear DLH. 315 m. One specimen.

It is interesting that *C. nigrescens* was dredged from the same station which also yielded a good collection of *C. hodgsoni*. Much material was dredged from the depth 93 to 126 m. and only one piece of a branch from a depth of 315 m. No differences in structure or colony formation were observed between specimens from the two depths.

Colonies of *C. nigrescens* are formed of branching cylindrical stems of varying thickness. The test¹ is gelatinous and almost transparent in the growing regions.

The older parts are greyish brown with a maximum transverse measurement of 30 mm. The minimum width of a branch is 5 to 9 mm. The ends of the branches are either blunt or tapering.

¹ The continuous cavity found in *Demiothecia*, occupied in common by the zooids, is replaced by a number of small tubes in *Idiothecia*, each occupied by one zooid and its buds. These are embedded in a common mass of coenoecial substance. Because of this differentiation, Ridewood (1907 *b*, p. 21) introduced the term "Tube" for the individual cavities occupied by the zooids (instead of cavity) and "Test" for the common mass of coenoecial substance (instead of coenoecium).

The tubes in which the zooids live open at regular intervals on the surface of the colony. In the young branches the substance of the test is transparent enough to show the disposition of these tubes. In the older parts they are reddish brown and can easily be distinguished from the surrounding substance of the test. They run from the axial region of the branch obliquely upwards and are not more than 12 mm. long in the young growing points. They project 3 or 4 mm. from the surface, but as growth proceeds, more and more coenoecial substance is laid down in strata, filling the depressions and increasing the thickness of the test so that the ostia come to lie on the surface of the branch. Any further increase in thickness is accompanied by a corresponding increase in the length of the tubes, so that the ostia always open on the surface and the lips alone project.

A longitudinal section passing through the axis of an old stem shows the arrangement of the tubes clearly. Their width is almost constant (1.2 to 1.3 mm.) and they are embedded in the greyish brown mass of the test, forming the bulk of the colony. Near the ostium the cavity of the tube is wider, and the part remote from the ostium is closed. In the oldest regions, the tubes are 20 to 24 mm. long, but the lower part is closed by a septum so that the zooids occupy only the distal half.

The lips are triangular projections of the abaxial margin of the peristomial tube, but on some they are shifted slightly to the sides. They are 2 to 2.5 mm. long, and project at right angles to the surface. On older branches they are shorter and thicker.

Some adjacent branches are attached to each other by the secretion of coenoecial substance. In a few cases the tip of a branch of one colony is attached to the body of a branch of another colony. From this it seems possible to infer that whenever adjacent branches of colonies growing close together touch, they fuse, so that disturbing movements in the water may not injure the zooids.

Each tube is occupied by one zooid and its buds, which in the preserved condition are situated 4 or 5 mm. from the external opening. Owing to their dark colour they are clearly visible through the test. The zooids measure 3.5 to 4.5 mm. from base of body to tip of arms, and are deeply pigmented. The body of a full-grown zooid fits fairly closely in the tube.

The stolon, which is 1 to 1.4 mm. long, projects from the basal part of the body and ends in a knob on which the young buds grow. A fully formed zooid bears two to nine buds. The smallest buds are crowded round the tip and in the preserved condition they are very much contracted, with their stalks twisted about one another owing to the effect of the fixative. The buds at the tip of the stolon are the youngest ones. These have a very short body and proboscis. As the stalks lengthen during growth the buds are removed farther away from the parent stolon. When the mother zooid is freed from the tube, one or two buds are seen pressed to the side of the body, a few entangled among the arms, and rarely one or two projecting beyond the tip of the arms. Such a bud is still connected with the parent stolon by its own stalk, which has grown long enough to carry it to its present position.

The situation of the older buds suggests the possible mode of liberation. The adult

zooid of *C. nigrescens* never completely leaves the tube. It moves forward towards the ostium and may even push its body out, but the stolon always remains fixed to some point on the inside of the tube, so that on the slightest danger the body is withdrawn into the tube (cf. "Observations on living zooids," Andersson, 1907). This habit makes the elongation of the stalk essential for the proper freeing of the buds. The buds when first formed are sessile. They develop slender stalks which rapidly elongate upwards, the buds remaining as thin flat plates. The lengthening of the stalks pushes the buds through the narrow space between the body of the mother and the wall of the tube, and, reaching beyond the arm-tips of the mother, the buds break away as free individuals.

Serial sections were cut of selected zooids from representative pieces of colonies, but no new observation that is worth recording has resulted. The blackish colour of the body is caused by a superficial layer of large brown cells. They occur in great abundance also on the dorsal wall of the proboscis.

The proboscis, which is attached by its dorsal part to the collar region, is oval with indented sides. It measures 1 to 1.2 mm. along the antero-posterior axis, and about 0.8 to 0.9 mm. from side to side. The curved red line runs horizontally between the indentations. The region just above and below the red line is lighter, the pigmentation being deepest on the anterior and posterior edges. The middle part of the ventral face of the proboscis is thick and stains deeper than the rest of the body. In longitudinal sections passing through the middle of the proboscis one or two narrow invaginations are found. These may be tracks through which the coenoecial substance formed by the glandular proboscis flows out.

There are usually seven pairs of arms, but zooids with six pairs are also found. They are devoid of end-swelling with refractive beads and possess two dark longitudinal bands along the axis. Towards the tips the two bands approach one another and fuse into one broad band.

In general, the internal structure of the zooid of *C. nigrescens* agrees with that of all other species. For systematic purposes the only noteworthy difference is the position of the heart and pericardium relative to the notochord. In *C. dodecalophus* the heart and pericardium are placed at the tip of the notochord, but in *C. nigrescens* the pericardial sac is attached to the notochord subterminally.

Sub-genus *Orthoecus*

Cephalodiscus densus, Andersson (Pl. XXXV, fig. 1).

Andersson, 1907.

Ridewood, 1918 *b*.

C. rarus (Andersson), Ridewood, 1918 *a*.

DIAGNOSIS. Colony not branching, a bulky mass or cake, composed of closely set, vertically directed tubes of uniform diameter (1 to 1.2 m.), measuring up to 70 mm. in height. Colourless or pale brown. Longest tubes (which are found towards the centre of the colony) 60 to 70 mm.; those towards the edges, shorter. Ostia transverse and

circular. Tubes ending blindly below, their basal parts held together by common coenoecial substance, which is very soft and spongy and sometimes encrusted with sand grains. Zooids greyish white, orange or brown. Length of a fairly extended zooid from tip of arms to base of body 4 to 7 mm., length from base of arms to end of body 2 to 4 mm. Arms, usually eight pairs, no end-swellings. Male, female and hermaphrodite zooids found in the same colony. Testis elongate and pyriform. Buds, six to twelve on each zooid.

LOCALITY.

St. 82. 20. vi. 26. $32^{\circ} 42' 00''$ S, $2^{\circ} 05' 00''$ W. Gear N200. 75 (-0) m. One specimen.

St. 190. 24. iii. 27. Bismarck Strait, Palmer Archipelago, $64^{\circ} 56' 00''$ S, $65^{\circ} 35' 00''$ W. Gear NRL. 126 m. Two specimens.

St. WS 82. 21. iii. 27. $54^{\circ} 06' 00''$ S, $57^{\circ} 46' 00''$ W. Gear OTC. 140-144 m. One specimen.

The coenoecium of the small piece obtained from station 82 is very much damaged but the zooids are in an excellent state of preservation. The two specimens (broken pieces of colonies) from station 190 are well preserved and the tubes undamaged (Pl. XXXIII, fig. 6). The common coenoecial substance and tubes of one of the specimens contain sand grains, fragments of shells and sponge spicules.

The colonies of *C. densus* are formed by closely set, vertically directed tubes which are held together in the basal region by common coenoecial substance. Since the present collection is formed only of fragmentary pieces, nothing definite can be said about the shape of entire colonies. As the tubes are closely set, and new tubes are formed only at the periphery, the colony increases in bulk laterally. If new tubes are formed uniformly all over, a large colony may have a flat cake-like appearance, but if growth on any one side is obstructed, the colony may have a more or less irregular outline. If this is proved to be the case, the shape of the colony can be regarded only as a secondary factor, depending upon the rapidity with which new tubes are added in any particular region and the presence or absence of obstruction near any part of the colony. On a plane substratum, the colony may extend equally on all sides and assume the perfect shape recorded by Ridewood.

The thickness of the wall of the tube varies. In the specimen obtained from station 82 the external diameter of the tube is 1.3 mm. and the internal diameter 1 mm. But the external diameter in the specimen obtained from station 190 is 1.6 mm., and the internal diameter is only slightly less, the tubular wall being very thin. The tube ends blindly below in the common coenoecial substance and at the upper free extremity opens by a transverse circular ostium devoid of any kind of lip-like outgrowth. They are slightly irregularly curved in the long axis, but there are a few straight tubes in the colony. The smooth inner lining of the tube is formed of thin rings. These are surrounded by an outer layer of irregular thickness. When a tube is dissected out in order to remove the zooids, the outer layer peels off easily, but the thin inner layer adheres closely to the visceral mass of the zooids, so that often it cannot be removed without damaging them.

Andersson (1907, p. 12) separates *C. densus* from *C. rarus* by the nature of the tubes.

He says that in *C. densus* the tubes are straight and that in *C. rarus* they are irregularly curved. While in *C. densus* the tubes are 6 to 7 cm. long and the coenoecial substance at the base free from sand particles, the tubes of *C. rarus* are only 4 to 5 cm. long and are distinguished by the presence of sand grains in the coenoecial substance. But Ridewood (1918 a, p. 40) has shown that these distinctions are the result of variations which do not affect either the structure of the colony or the characters of the zooid. The colony when first formed consists only of a few tubes, which, being unimpeded by anything in the immediate vicinity, are irregular and even straggling. As the zooids multiply, the tubes become more and more closely set and older tubes become longer and straighter, consequently after a study of complete series of gradations between *C. rarus* and *C. densus*, he concluded that *C. rarus* is synonymous with *C. densus*. Even the differences in thickness of the epidermis of the axis of the arms are such as might occur within the same species.

Nothing more need be said to emphasize Ridewood's conclusions. The two specimens obtained from station 190 both possess tubes which are mostly curved. The older tubes are 5 to 6 cm. long and their distal parts straight. In one colony there are a few stray sand grains embedded in the coenoecial substance, but in the other the sand grains and diatoms are numerous.

It may be added that the occurrence of sand grains in the common coenoecial substance is not constant, resulting from selection by the zooids, but depends rather on the immediate surroundings. If the colony grows in unsheltered spots or at the base of submarine rocks the particles which constantly rain from the upper regions of the sea or drop occasionally from the sides of the rocks may fall on the colony and become embedded in the common coenoecial substance. The quantity of sand grains on the colony will depend on the intensity of the rain of particles from above, so that it is possible to find colonies free from sand grains, or with only a few stray particles, growing in the sheltered places. This is supported by the different colonies of the present collection in which the quantity of sand grains, included in the common coenoecial substance, varies markedly.

Each tube is occupied by one zooid and its buds. In the preserved condition the upper tip of the zooid is situated about 7 to 9 mm. below the ostium. The zooids are pale white, but the arms are brownish. The body is straight, longer than that of other species and measures 4 to 10 mm. from base of body to tip of arms. When a zooid is viewed under a lens, two white elliptical patches can be seen slightly bulging out on each side of the pharynx. They arise from the base of the collar region between the opening of the rectum and the pharynx. These are the gonads, which are conspicuous in this species. All the zooids which have been examined in section are hermaphrodite, but both Ridewood and Andersson have observed male and female zooids, with paired testes or ovaries. Ova occupy the upper part of the ovary, the lower part being filled with yolk granules. Sometimes a few eggs are found in the basal part of the tubes. The testis is a thick-walled elliptical tubular organ. The sperm are formed in the thick wall and liberated into the central space from which they pass out through the short vas deferens which opens between the rectum and the pharynx.

Illustrations of sagittal and transverse sections passing through the gill region are given in Plate XXXVI, figs. 3-6. The external gill slit (*eg*) opens into a cavity (*gc*), placed between the body wall and the wall of the pharynx. The wall of this gill cavity is formed of vacuolated tissue, called pleurochord. In other species there is a deep groove running along the entire length of the pleurochords on either side of the pharynx, which starts from the gill slit, and probably the respiratory water traverses these grooves. The gill cavity found in this species may have originated by the enlargement of the groove and the fusion of the lips, resulting in the formation of a tubular space (*gc*) between the pharynx and the body wall, opening on the one side into the external gill slit, and on the other into the pharynx by a narrow slit, which for convenience will be termed the internal gill opening (*ig*). Whereas in other species water passes directly from the pharynx through the gill slit, the intervention of this cavity makes the passage of the respiratory water more complicated. Water flows from the pharynx through the internal gill opening into the gill cavity whence it passes out through the external gill slit.

The proboscis, which is oval with indented sides, is small compared to the zooid. It is 1.1 mm. long and 0.9 mm. broad. The red line runs near the posterior margin.

There are always eight pairs of arms without end swellings. The pinnules on the basal parts are 0.4 to 0.5 mm. long. The dorsal wall of the arm has a thick layer of vacuolated cells each of which encloses a refractive bead similar to those in the end-swellings of *C. dodecalophus* and *C. hodgsoni*. This layer curves over the tip of the arm so that a few refractive beads occur in the tip also. Thus although end-swellings are not found, there are refractive beads in the tips. The arms on the extreme right and left sides are directed downwards on either side of the mouth in the preserved condition. The longest arms measure 1.7 mm., but those towards the sides are shorter.

The stolon varies considerably in length and thickness. In some it is thin and about 25 mm. long, and in others thick and short, with a brownish tint on one side. The difference in length of the stolon is probably due to contraction when the zooids were fixed, but even in the contracted state it is much longer than the stolon of other species¹.

Cephalodiscus fumosus, n.sp. (Pl. XXXIV, fig. 1).

DIAGNOSIS. Colony unbranched, in the form of a brittle arenaceous cake, measuring 90 mm. across and 16 mm. high and consisting of evenly distributed (5 to 7 mm. apart) vertically disposed tubes of uniform diameter. Tubes pale brown, buried in the common mass, which is formed of a dense agglutination of minute sand grains. Each ostium produced on one side into a short thick triangular lip, which can fold over like an operculum. Those in the middle of the colony 14 mm. long, those near the edge shorter. Width of the tube near the ostium 1.4 mm. Length of fairly extended zooid from tip of arms to base of body 3.2 mm., length of arms 1.2 mm., width of body 1 mm. Colour

¹ Sir Sidney Harmer, when reading through this paper, suggested that during life the length of the stolon varies greatly from time to time, but that this point was not sufficiently appreciated by earlier workers who very often cited the length of the stolon of the preserved zooid as a diagnostic character of the species of *Cephalodiscus*.

of preserved zooids—dorsal side of body and stolon light brown, ventral side brownish white. Proboscis with dark brown upper and lower edges. Usually eight pairs of arms, each with two black longitudinal bands running along the entire length as in *C. nigrescens*. No end-swelling with refractive beads. Female and hermaphrodite zooids found in the same colony. Up to ten buds on each zooid. The colony has a smoky grey colour which suggested the specific name.

LOCALITY.

St. 170. 23. ii. 27. Off Cape Bowles, Clarence Island, $61^{\circ} 25' 30''$ S, $53^{\circ} 46' 00''$ W. Gear DLH. 342 m. One entire colony and a broken piece.

The material of this species consists of a single large colony, and another broken piece from which the zooids were removed and separately preserved. Sections were made of the preserved zooids and the large colony was used only for purposes of general description.

The large colony is flat and semicircular in shape, but since the diametrical edge is irregular and broken, it may be assumed that an entire colony is oval or circular with a convex upper surface, thick in the centre and thin towards the edge (Pl. XXXIV, fig. 1).

In most other species of *Cephalodiscus* the colony is formed by the secretion of coenocelial substance, the inclusion of sand grains being only a secondary factor depending on the nature of the surroundings. In *C. solidus* (Ridewood, 1918 *b*, p. 18) large quantities of sand grains, sponge spicules and diatoms are found in the common coenocelial substance of some of the colonies, while others are leathery and non-arenaceous. In *C. agglutinans* foreign particles are included in the soft substance, but some parts of the branches may be devoid of sand grains. In *C. fumosus* the entire mass of the colony is formed of a dense agglutination of sand grains. The particles are very minute and of uniform size and being closely packed together give a homogeneous appearance to the colony. The coenocelial substance is sparsely secreted and is used only for making the thin-walled tubes and binding the sand grains together. Since the bulk of the colony is formed of such a consolidation of sand particles, it is very brittle and easily breaks to pieces when removed from its place of attachment. The basal part has an irregular surface, because the colony grows on a sandy bottom, to which it is fixed by the secretion of a thin layer of coenocelial substance. When the colony is dislodged large particles of the substratum firmly attached to the basal surface come with it. It seems clear from the nature of the particles that they must definitely be selected by the zooids for the construction of the coenocelium, in the same way as certain Foraminifera construct their arenaceous shells. Ridewood (1918 *a*, p. 41) observed that the inclusion of sand grains or foreign particles is not a constant character of any species of *Cephalodiscus*, and that it may be purely local, depending only on the nature of the sea bottom where the zooids first settled down. "It is quite possible that in more rocky parts of the ocean floor the zooids of the species might build up a perfectly clear and transparent coenocelium." Though this is applicable to most species of *Cephalodiscus*, it cannot be said that the arenaceous nature of the colony of *C. fumosus* depends on

chance. If the inclusion of sand grains is regarded as a regular habit of this species, a rocky substratum would be unfavourable for growth and it is possible that the first zooids of the colony always selected a loose sandy bottom. An examination of the coenoecium supports this opinion, but it cannot be definitely established until the habits of the species are known.

The tubes are uniformly distributed 5 to 7 mm. apart. They are thin-walled and vertical. The entire length of the tube lies within the mass of the colony, so that the ostium opens on the surface. On one side the margin of the ostium is prolonged into a vertical triangular lip covered with an outer layer of sand grains. It is capable of folding over the ostium, so that when the lip is closed the ostium cannot be distinguished from the rest of the surface. At the ostium, the tube is 1.4 mm. across, but it becomes slightly narrower at the blind end. The longest tubes in the central region are 14 mm. long. Towards the edge they become shorter and the shortest ones, close to the margin, are inclined outwards.

Each tube is occupied by one zooid and its buds. In the preserved condition the upper tip of the zooid is situated nearly 4 mm. below the ostium. The dorsal part of the body is dark brown, the ventral part and the sides are brownish white. The dark brown colour extends along the entire length of the dorsal part of the stolon as a brown band from the base of the arms to the tip of the stolon.

In the females the ovaries are seen on either side of the pharynx as two conspicuous white masses, which are directed obliquely ventrally. Hermaphrodite zooids could also be distinguished, for the white mass is only on one side; the other side being occupied by the testis, which is not a conspicuous structure. This difference between female zooids and hermaphrodites can be observed only when the gonads are well developed. The ovary is an elliptical organ with seven or eight heavily yolked ova. The short oviduct opens at the base of the collar region between the pharynx and the rectum, just below the lower end of the main nerve mass.

Between the gonads and the rectum there is a small invagination of the ectoderm which dilates into a flask-shaped cavity. This is lined with ectodermal cells and opens through the narrow neck. It is difficult to account for the function of this cavity since it is found to be almost empty. Its position near the ovary and the proximity of its opening to the oviduct suggests that it is a kind of brood-pouch in which the developing ova are received. But since no such structure is found in any other species, this view must be accepted with caution.

The body is slightly curved like that of *C. hodgsoni*. The pharynx runs slantwise, and near the middle of the body opens into the stomach. The ventral wall of the stomach is very much thicker than the dorsal and contains numerous closely set transverse folds. The intestine is a long narrow tract which dilates into a spacious rectum. The epithelial lining of the rectum is also thrown into long narrow folds (Pl. XXXVI, fig. 1).

The stolon originates from the region where the pharynx opens into the stomach. It is directed downwards following the curve of the body. A thin connection keeps the

stolon attached to the body. From the base it continues downwards as the free stolon, which is 4.5 mm. long and ends in a knob.

The proboscis is almost circular. It is of a pale brownish colour, but the edges are dark brown like the dorsal side of the trunk. The ventral glandular wall of the proboscis is not as thick as in *C. hodgsoni* or *C. nigrescens*, and this accords with the habit of secreting a limited quantity of coenoecial substance. In the middle of the ventral wall of the proboscis there is a thin short finger-like protuberance which is directed upwards. Small sand grains might be held between this protuberance and the proboscis and thus carried to the edge of the colony, to be there cemented on to the surface.

There are usually eight pairs of arms which are conspicuous by their dark bands and long pinnules. *C. solidus* also has eight pairs of arms, but they are devoid of the black pigmented bands which are seen only in *C. nigrescens* and this species. The pigmented bands start from the base of the arm and run on each side. Near the tip they converge and fuse into a single broad band. The tip has the appearance of a rounded knob without pinnules. But this knob-like termination cannot be compared with the end-swelling with refractive beads found in *C. hodgsoni* and *C. dodecalophus*. The arms measure 1.2 mm. in length and the pinnules are 0.5 to 0.6 mm. long.

Though the zooids of *C. solidus* and *C. fumosus* are of the same size and possess the same number of arms, the latter can always be distinguished by the presence of the dark bands in the arms. The zooids of *C. solidus* are black in the preserved condition; thus the colour of the preserved zooid of *C. fumosus* will also serve to separate the two species.

Sub-genus *Acoelothecia*, sub-gen. nov.

DIAGNOSIS. Colony small or large, and branching; formed of a meshwork of bars and spines without any definite coenoecial cavities. Spaces between the meshwork irregular and continuous and occupied in common by the zooids and their buds.

Cephalodiscus kemp, n.sp. (Pl. XXXIV, figs. 2-6).

DIAGNOSIS. Colony small and tuft-like or large and branching. The tuft-like colonies are about 3.5 to 4.5 cm. from base to tip of spines. The branching forms sometimes reach a length of 10 cm. and in thickest parts are 3.5 cm. across. The inhabited parts of the colonies are formed of an elaborate meshwork of cross-bars between spines. The coenoecium is devoid of definite tubes such as those found in the other three sub-genera, whence the name *Acoelothecia* for the new sub-genus. Spines with varying length and thickness are found all along the sides of the branches. No definite ostia are present. Spaces between the surface meshwork of bars and spines act as temporary outlets. Colour of the colony from light brown to reddish brown, older parts always of a deeper tint. Length of a fairly extended zooid from base of body to tip of arms 1.8 to 2 mm.; length from base of arms to base of body 1.1 mm.; width of body 0.9 to 1 mm. Colour of preserved zooids amber. Arms usually five pairs, with end-swelling and refractive beads. Male, female and hermaphrodite zooids found in the same colony.

LOCALITY.

- St. 152. 17. i. 27. $53^{\circ} 51' 30''$ S, $36^{\circ} 18' 30''$ W. Gear DLH. 245 m. Two specimens.
 St. 156. 20. i. 27. $53^{\circ} 51' 00''$ S, $36^{\circ} 21' 30''$ W. Gear DLH. 200 to 236 m. One specimen.
 St. 158. 21. i. 27. $53^{\circ} 48' 30''$ S, $35^{\circ} 57' 00''$ W. Gear DLH. 401 to 411 m. Large collection.
 St. WS 71. 23. ii. 27. 6 miles N 60° E of Cape Pembroke Light, East Falkland Islands. $51^{\circ} 38' 00''$ S, $57^{\circ} 32' 30''$ W. Gear OTC. 82-80 m. Three specimens.
 St. WS 72. 5. iii. 27. $51^{\circ} 07' 00''$ S, $57^{\circ} 34' 00''$ W. Gear OTC. 95 m. One specimen.
 St. WS 84. 24. iii. 27. $7\frac{1}{2}$ miles S 9° W of Sea Lion Island, East Falkland Islands. From $52^{\circ} 33' 00''$ S, $59^{\circ} 08' 00''$ W to $52^{\circ} 34' 30''$ S, $59^{\circ} 11' 00''$ W. Gear OTC. 75-74 m. Two specimens.
 St. WS 85. 25. iii. 27. 8 miles S 66° E of Lively Island, East Falkland Islands. From $52^{\circ} 09' 00''$ S, $58^{\circ} 14' 00''$ W to $52^{\circ} 08' 00''$ S, $58^{\circ} 09' 00''$ W. Gear OTC. 79 m. Small fragments.
 St. WS 97. 18. iv. 27. $49^{\circ} 00' 30''$ S, $61^{\circ} 58' 00''$ W. Gear OTC. 146-145 m. Large collection.
 St. WS 211. 29. v. 28. $50^{\circ} 17' 00''$ S, $60^{\circ} 06' 00''$ W. Gear OTC. 161-174 m. Four specimens.
 St. WS 216. 1. vi. 28. $47^{\circ} 37' 00''$ S, $60^{\circ} 50' 00''$ W. Gear N7-T. 219-133 m. Seven specimens.

From stations 158, WS 97, and WS 211 a considerable quantity of material was obtained. The material from station 158 consisted of small tuft-like colonies with radiating spines. The yield from stations 152 and 156, WS 71, WS 84, WS 97, WS 211, WS 216 consisted of long cylindrical branching colonies.

For the sake of convenience the short tuft-like colonies obtained from station 158 will be called Form A and the branching cylindrical form Form B. Although the habit of growth of the two forms is quite distinct the structure of the coenocium and zooids is the same in both forms.

Form A. Most of the material was collected at station 158, from a depth 401 to 411 m. Small pieces were obtained from stations 152 and 156 at depths of 245 m. and 200 to 236 m. respectively. Since variation in size and structure is not met with, this form can be regarded as a distinct type of the species. The coenocium in the preserved condition is light brown. The colony consists of a basal region of thick bars and spines forming a meshwork from which spines radiate on all sides except basally. The spines are thick, straight and tapering and measure 12 to 17 mm. They may be forked or branched. The origin and growth of spines are the same as in *C. hodgsoni*, that is, by deposition of coenocial substance locally in the form of lamellae. A section of the spine shows two distinct regions. A transparent core of thin consistency surrounded by a firm, reddish brown, outer layer formed by a number of close lamellae.

A few colonies are slightly larger than the rest and have longer spines with pointed tips, though generally the spines measure 1.2 to 2.3 cm. and possess blunt or pointed tips. They are straight except for slight occasional curvature of the distal part of the spine by preservation.

When lamellae are deposited on the spine they may enclose any particles which are adhering to the surface of the older layer. Masses of sand grains, enclosed between layers of lamellae, appear like nodules on the side. In one instance a slender branch of a polyzoan colony was attached to the tip of the spine and had been almost enclosed by coenocium.

The structure of the coenocium of this species is such that it cannot be included in

any of the three sub-genera previously recognized. The absence of a definite cavity forming tubular spaces individually or occupied in common by the zooids is unique. The spaces between the bars and spines on the surface of the meshwork are the openings through which the zooids come out and are not homologous with the ostia of other species, being only temporary outlets, which become part of the internal meshwork when new bars are formed above the existing ones.

Most of the colonies are attached to calcareous tubes of Polyzoa¹. Some colonies are attached to the tips of these tubes, while in others they are horizontally embedded in the basal region, surrounded by a thin layer of coenoecial substance.

The sexual development of *Cephalodiscus* has not been thoroughly worked out. Harmer (1905, p. 102) described the embryonic stages of *C. gracilis* and *C. levinseni*, and Gilchrist (1917) gave an account of the larvae of *C. gilchristi*, but nothing definite is known about the metamorphosis and habits of the later stages of the larvae, as they were not studied in the living condition. In spite of this ignorance, we may assume that at the end of the free-swimming stage the larvae of *C. kempfi* settle down on some suitably firm support, such as the calcareous tubes of Polyzoa, and secrete a thin layer of coenoecial substance which envelops part or whole of the supporting object.

Rudiments of spines are laid down on the surface of this envelope which project at various angles. As the spines increase in length, lateral bars are formed, which grow at right angles to the axis and fuse with adjacent spines. A complicated meshwork is thus produced by the formation of four or five cross-bars between each adjacent pair. By the additional deposition of coenoecial substance the lateral bars and spines increase in thickness, the angles become smooth and curved so that the original rectangular spaces become circular or ovoid. As the zooids increase in number and more space is required, new lateral bars are formed above, but the colonies do not grow beyond the tuft-like form.

Two growing colonies have been found attached to flat surfaces (one to the mantle of an Ascidian, and the other to a broken piece of Lamellibranch shell). In both of these, a flat, plate-like secretion was first formed. Colonies were also attached to fragments of sponges. Whatever the object to which the colony is attached, a layer of coenoecium is spread on the surface of the object, which as growth proceeds becomes partly or wholly enclosed.

Form B. This form is represented by material obtained from stations WS 71, WS 75, WS 84, WS 88, WS 97, WS 211 and WS 216. Stations WS 97 and WS 211 gave most of the collection, while from each of the other stations only one or two pieces were obtained.

Colonies are formed of massive cylindrical branching stems with a close array of spines along the sides. The length, thickness and nature of the spines depend on their

¹ "The Polyzoon which is associated with *C. kempfi* is *Ogivalia elegans*, the *Vincularia elegans* of D'Orbigny, a species which is abundant in the 'Discovery' collections. This is a branching form with brittle branches. It seems not unlikely that the *Cephalodiscus* was growing on it and that the dredge merely broke off the tips of the branches." *Letter from Sir Sidney Harmer.*

position. In the basal regions the spines are long, stiff, thick and tapering, while towards the tips they are slender, shorter and very pliable.

The main stems are 3.7 cm. across in the thickest parts, but the width of the apical regions is not more than 1 to 1.8 cm. The older parts of the coenoecium are dark reddish brown and very opaque, so that the zooids inside cannot be seen, even by strong transmitted light. Nearer the tip, the dark mass of zooids can be seen distinctly through the light brown semi-transparent coenoecium. Usually the main stem grows vertically, producing secondary branches from its sides. A single stem 8 cm. long may bear as many as four to six branches. Branches are produced on all sides of the stem, but if the main stem is horizontal they are found only on the upper side. Entangled among the branches arenaceous tubes of Polychaetes, calcareous branches of Polyzoa, Ostracods and small Ophiurids are often found. Big sand particles and masses of mud are also deposited locally.

The colonies are a meshwork of bars and spines constructed as in Form A, but more elaborately, due to the greater length and thickness of the colonies. The spines of the tip of the branch are directed upwards so that the growth of the spines, accompanied by the formation of lateral bars between them, increases the length of the branch, while the production of lateral bars between the obliquely directed spines on the sides increases its thickness.

Although the meshwork is very distinct in the apical regions, the bars and spines lose their identity below by the addition of coenoecial substance around them. As in Form A, spaces in the surface meshwork form the openings for the zooids.

A hand-cut longitudinal section, from the interspaces of which the zooids are carefully washed out, shows the structure of the coenoecium given in Fig. 4. Spines *A* and *B* grow in opposite directions from the axial part of the branch. A lateral bar between them at the base results in the formation of a closed mesh which is at first rectangular. Since these two spines diverge, if a second bar is formed between them above the first one, the space enclosed would be much larger than the first one, so in the middle of the first bar the rudiment of a new spine is laid down, which grows up as spine *C*. Between *A* and *C* and *C* and *B* two bars are formed simultaneously, thus enclosing two spaces which are of almost the same size as the one below. As the spine *C* continues to increase in length one or two more bars may be formed between *A* and *C* and *C* and *B*, without appreciably increasing the size of the spaces enclosed. Now the spines *D* and *E* are produced. These may be formed in the same way as spine *C* or may arise as branches from the side of *A* or *B*; but whatever the origin they serve the same purpose as spine *C*.

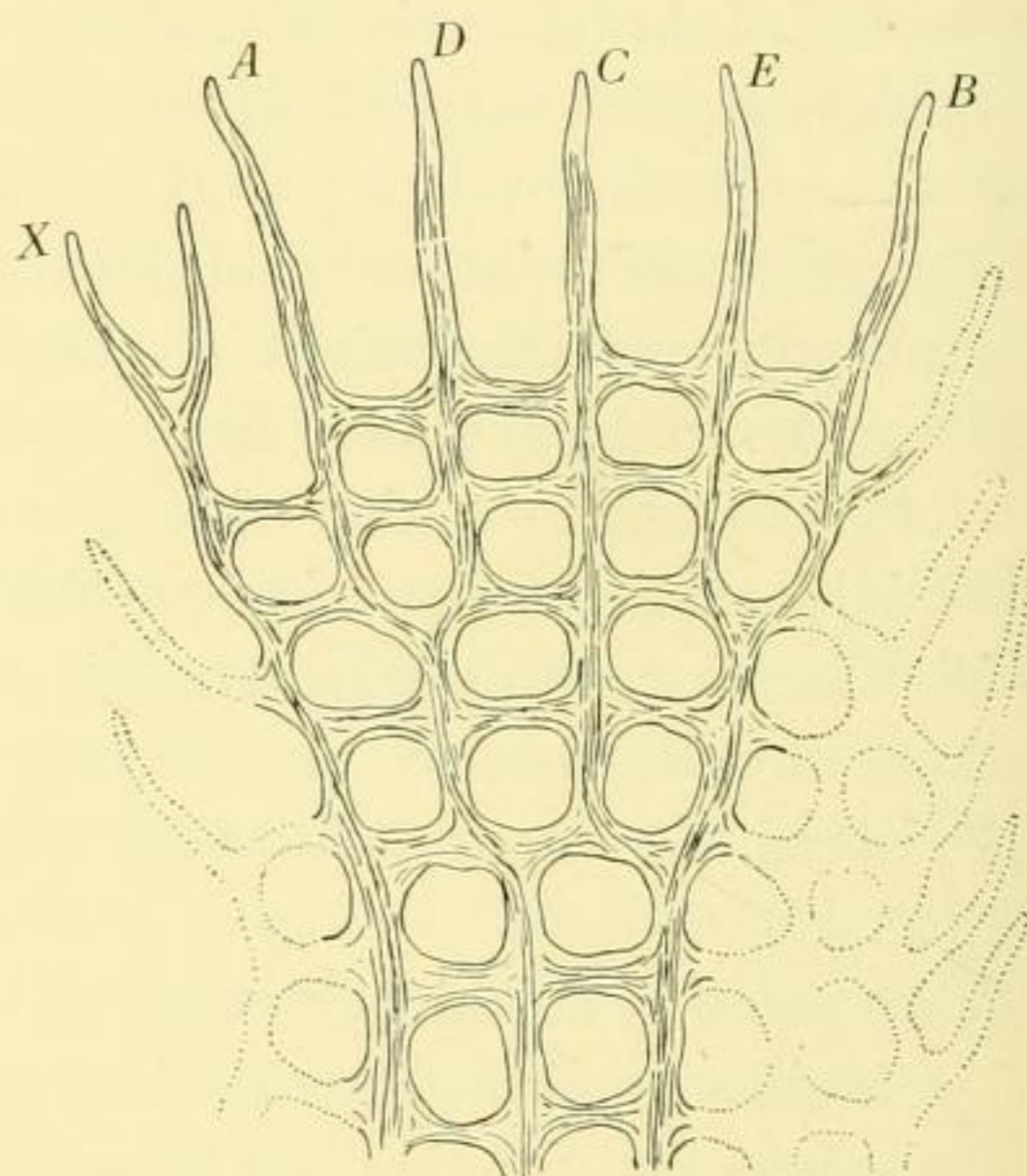


Fig. 4. *C. kempi*. Structure of the meshwork.

When these spines elongate, bars are formed between *A* and *D*, *D* and *C*, *C* and *E*, *E* and *B*. These intermediate spines limit the spaces in the meshwork and also increase the number of these spaces in almost geometrical ratio. Between diverging pairs of spines lateral bars are formed on this system, but when two spines run parallel to one another, as *A* and *X* do, a number of bars may be formed between them without intermediate spines. This meshwork is the inhabited part of the colony, beyond which the spines project.

The spaces between the bars on the surface form the openings for the zooids, but as the spines increase in length and new bars are developed above the older ones, the former openings become part of the internal meshwork.

In some branches the upper half is slender and pliable; this represents the growing part of the colony. When first formed the coenoecium is almost transparent and the spines are short and slender, but later by the successive deposition of coenoecial substance, the internal meshwork becomes thicker, and the spines stiff and straight. Between the fully developed colonies and the newly formed semi-transparent pliable pieces, branches representing different stages of growth are found. The differences between them consist mainly in the thickness of the branch, the length and thickness of the spines, and the colour of the coenoecium.

The zooids are small and measure 1.8 to 2 mm. from tip of arms to base of body. There are always five pairs of arms which are 0.9 to 1 mm. long and possess end-swellings with refractive beads. The stolon which is 1.3 to 1.7 mm. long originates from the base of the trunk and carries two to five buds. The rest of the anatomy agrees with that of *C. dodecalophus*.

INTERNAL ANATOMY

ORIENTATION

Two opinions are held about the orientation of the zooid. Ridewood considers the long axis of the body as longitudinal, while Harmer (1905, p. 23) regards this as transverse. The reason advanced for this view is that a section of the adult zooid passing through the collar region and proboscis at right angles to the long axis of the body shows all the five coelomic cavities like a frontal longitudinal section of *Balanoglossus*. Considering the U-shaped alimentary canal, the positions of the proboscis and the anal opening, this seems very acceptable. But with the lack of adequate knowledge of the development this opinion has at least one difficulty; during the development of the bud, before the arms are formed, the coelomic cavities are arranged in the long axis, so that a section passing medianly through the long axis shows the same arrangement of the coelomic cavities (Fig. 6) as a longitudinal section of *Balanoglossus*. At a later stage, when the arms are developed, the proboscis shifts forward and the coelomic cavities take up the new positions seen in the adult. Although the condition in the young bud is not regarded as the basis for correct orientation, it has been found convenient to

adopt Ridewood's orientation, so that in the following account the long axis of the body is regarded as longitudinal (Fig. 5).

The internal anatomy of *Cephalodiscus* has been worked out very thoroughly by Harmer (1905) and Andersson (1907). From sections of the zooids of different species

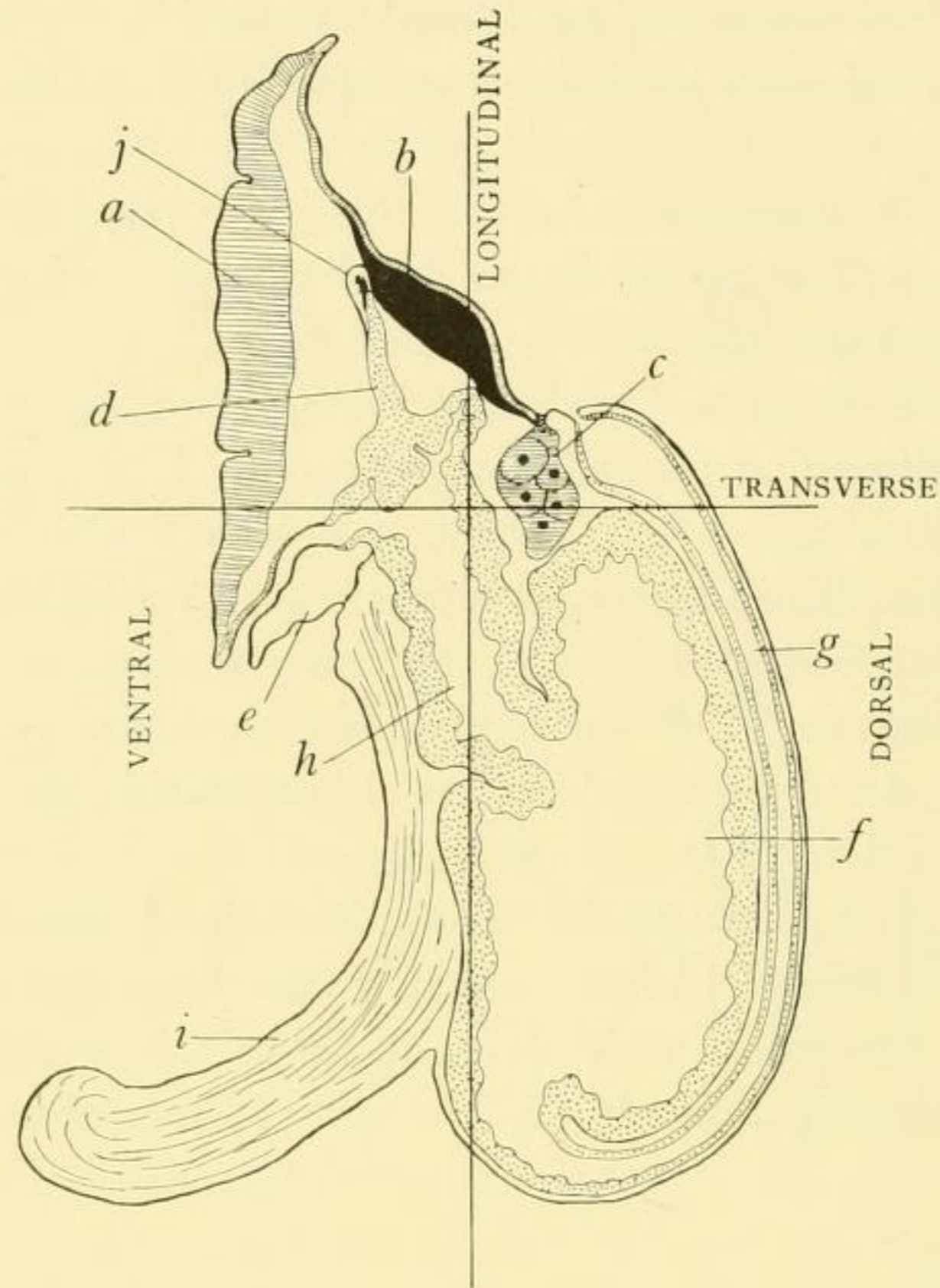


Fig. 5. Orientation of the zooid. *a*, proboscis; *b*, central nervous system; *c*, gonad; *d*, notochord; *e*, post-oral lamella; *f*, stomach; *g*, intestine; *h*, pharynx; *i*, stolon; *j*, heart and pericardium.

of the present collection it has been possible to verify these results. The following account does not attempt to give a complete description of all parts, but only deals with those organs and systems about which new observations have been made.

PROBOSCIS

The proboscis of *Cephalodiscus* varies in size and shape, as will have been seen in the systematic accounts. The discoidal part of the proboscis is attached to the body by a very short neck, which is always capable of a little extension. That this gives the disc great mobility is clear from the diverse positions of the proboscis in the preserved individuals. Observations made on the living zooids show that they come out of the coenocidium and creep on the surface of the colony, with the disc acting as a sucker. This was first recorded by Andersson (1907, p. 59) and confirmed by the observations of Dr Stanley Kemp during the present expedition. The disc is flattened dorso-ventrally.

The ventral wall is formed of elongated gland cells, and in the thickest part, at the base of the gland cells, there is a thin transparent layer, which looks like nerve tissue. The ventral wall of the anterior lobe of the proboscis is composed of a thin layer of epidermal cells, basement membrane, and coelomic epithelium, but in *C. densus* this region is comparatively thick and the epidermal cells have vacuoles like the refringent vesicles in the end-bulbs of *C. dodecalophus* (Pl. XXXVI, fig. 2). Behind the attachment of the proboscis to the collar, the dorsal and ventral walls approach each other, diminishing the proboscis cavity. Ultimately by the apposition of the two walls a thin lobe is formed, the posterior lobe of the proboscis, which functions as the roof of the passage into the mouth. The point where the two walls touch is the posterior boundary of the glandular part of the ventral wall, which is invariably marked by a line of red pigment, extending transversely from edge to edge.

It is difficult to explain the functional significance of this red line. It is surrounded by a group of minute nuclei and lightly stained large protoplasmic cells which can be distinguished easily from the glandular cells of the ventral wall. A similar patch of pigment occurs in the oviduct and M'Intosh (1887) suggested that the pigmented oviduct was a phosphorescent organ. Harmer (1905, p. 27) assigns to it a sensory function, though according to him the nerve supply to these regions seemed inadequate for this purpose. In the account of the nervous system it will be seen that there is a distinct nerve originating from the back of the main ganglion which runs to the oviduct, and that the nerve plexus at the base of the glandular region of the ventral wall of the proboscis does not extend beyond the red line. Although no distinct nerve connection with the red line is visible, the nerve plexus may end in the pigmented line by breaking up into very minute branches. The distinct nerve tract in the oviduct suggests that a similar connection exists in the pigmented line of the proboscis, and this definite relation to the nervous system confirms the suggestion of Harmer that the red pigment has a sensory function. This is emphasized by the occurrence of the red line in all known species, where it is prominent from very early stages in the development of the bud.

The proboscis cavity is traversed by thin strands of protoplasmic fibres and opens externally by two pores, the proboscis pores, which are on either side of the pericardium above the end of the anterior horns of the collar cavities.

COLLAR CAVITIES

The two collar cavities together form a ring encircling the pharynx. Dorsally the cavities are large and are separated into the right and left collar cavities by the dorsal coelomic mesentery. They descend downwards and extend into the post-oral lamella, where the two cavities are continuous; there is no ventral coelomic mesentery. The collar cavities open by the right and left collar pores, on either side of the pharynx, at the base of the post-oral lamella, just above the gills. The collar pores are thick-walled ciliated openings which lead by short canals into their respective collar cavities and control the water currents to maintain the turgidity of the collar and arms.

The arms are situated on the dorsal side of the collar. Each arm is a hollow tubular axis which may have an end-swelling (e.g. *C. hodgsoni* and *C. kempi*). The ectodermal cells of the end-swelling are vacuolated and contain refractive beads. In *C. nigrescens* and *C. fumosus* end-swellings are absent, but in *C. densus* and *C. sibogae*, although there are no end-swellings of the type described by Cole (1900, p. 256), refractive beads are found the whole length of the dorsal side of the arms. Sections of *C. densus* stained in Mallory show the vesicles and refractive beads very clearly (Pl. XXXVI, fig. 2). Some of the beads are stained blue and others red. They are ovoid or elliptical homogeneous bodies and normally are in the middle of the vacuolated spaces of the ectodermal cells. Some of these beads are sometimes found partly protruding from the surface of the cells.

M'Intosh (1887, p. 11), who first observed the refractive beads in the end-swellings of *C. dodecalophus*, described them as glandular. Masterman (1898 *b*, p. 344) suggested that they were crystalline refractive lenses, and drew the inference that these organs are rudimentary monostichous compound eyes similar in structure to the branchial organs found in sedentary Annelids. Later he discarded this view, and Cole (1900, p. 356) thought them rhabdite-producing organs. The greatest distribution of these refractive beads occurs in *C. densus* and *C. sibogae*; in others they are restricted either to the swollen tips of the arms or completely absent. The refractive beads therefore cannot have any general function, but serve more or less a specific purpose which at present is not understood.

The arms grow from the dorsal wall of the collar on either side of the central nervous system, and the collar coelom continues to the tip of each arm and into the pinnules on each side; the whole system thus recalls the water-vascular system and tube feet of Echinoderms. On the ventral side of the arm there is a longitudinal groove, termed the food groove. The movements of the pinnules convey food particles into the groove along which the particles move to the base of the arms. The food grooves of each side of the body open into a space between the posterior lobe of the proboscis and the ridge on the anterior margin of the collar. These together form an efficient tract for food particles to the mouth.

ORGANS OF THE TRUNK

The greater part of the trunk is occupied by the alimentary canal. The pharynx is a thick-walled chamber which in nearly all species extends half-way down the body and opens by an obliquely directed narrow oesophagus into the large stomach; this, on its postero-ventral side, in turn leads into the intestine. The intestine is a narrow tube which forms a loop and running upwards between the stomach and dorsal body wall opens into a large rectum. The anus is on the dorsal side just below the collar, at the base of the central nervous system. The gill slit on each side opens into the pharynx laterally at the base of the post-oral lamella, below the collar pores. The wall of the gill slits is formed of vacuolated cells. Transverse sections of the gill region show that the vacuolated cells in the roof of the gill slit do not extend to the extreme front end of the pharynx as described by Masterman (1898 *b*, p. 353), but that the floor of the gill slit continues backwards on

each side of the pharynx as a band of vacuolated cells with a deep internal groove communicating with the cavity of the pharynx. The insertion of these lateral bands, the pleurochords, divides the wall of the pharynx more or less completely into four distinct regions, two lateral, a mid-dorsal and a mid-ventral. The two lateral regions are formed of the bands of vacuolated cells, and the mid-dorsal and mid-ventral walls of ordinary cells of the pharynx. The groove on the inner side of the pleurochords is deep and conspicuous in *C. hodgsoni*, and, as already mentioned, in *C. densus* a tubular space completely lined with vacuolated cells lies between the external gill opening and a cavity of the pharynx. This has been termed the gill cavity, and its opening into the pharynx the internal gill slit. The respiratory water passes through the gill cavity before it finds outlet through the external gill slit. This gill cavity could have been formed only by the fusion of the lips of the groove in the pleurochords. In other species where the lips of the groove stand apart, the respiratory water probably traverses the groove before passing through the gill slit. Assuming this to be so, it is clear that the pleurochords and the grooves play a definite part in respiration. Further, the pharyngeal blood vessels lead to the vacuolated region of the roof of the gill slit, but the mode of exchange of gases still remains a problem.

A rod-shaped structure with a narrow lumen projects upwards from the dorsal wall of the anterior diverticulum of the pharynx. This organ has been variously termed by different writers. Harmer (1887, p. 40) compared it with the notochord of *Balanoglossus*. Later, Willey (1902) described it as the stomatochord, and Masterman (1898 *b*, p. 351) regarded it as the subneural gland; but the view most generally accepted was that this organ corresponds to the vermiform process of certain Enteropneusta. In this paper it is called the notochord in accordance with the view of Harmer. The lumen of the notochord opens into the dorsal diverticulum of the pharynx.

Masterman thought this the enlarged base of the duct, but the evidence is not strong enough to support the glandular nature of the notochord: I did not find a trace of mucus inside the lumen.

Since the development of *Cephalodiscus* has not been worked out thoroughly it is difficult to say anything definite about the origin of the notochord, but it may be worth mentioning that during the development of the bud it is very conspicuous. In Fig. 6, A and B, drawings are given of sagittal sections of the young bud. The proboscis is very large and the collar cavities have just appeared as a ring. Within the trunk-cavity is the rod-shaped primitive gut, which has not as yet mouth-opening or intestinal loop. Later,

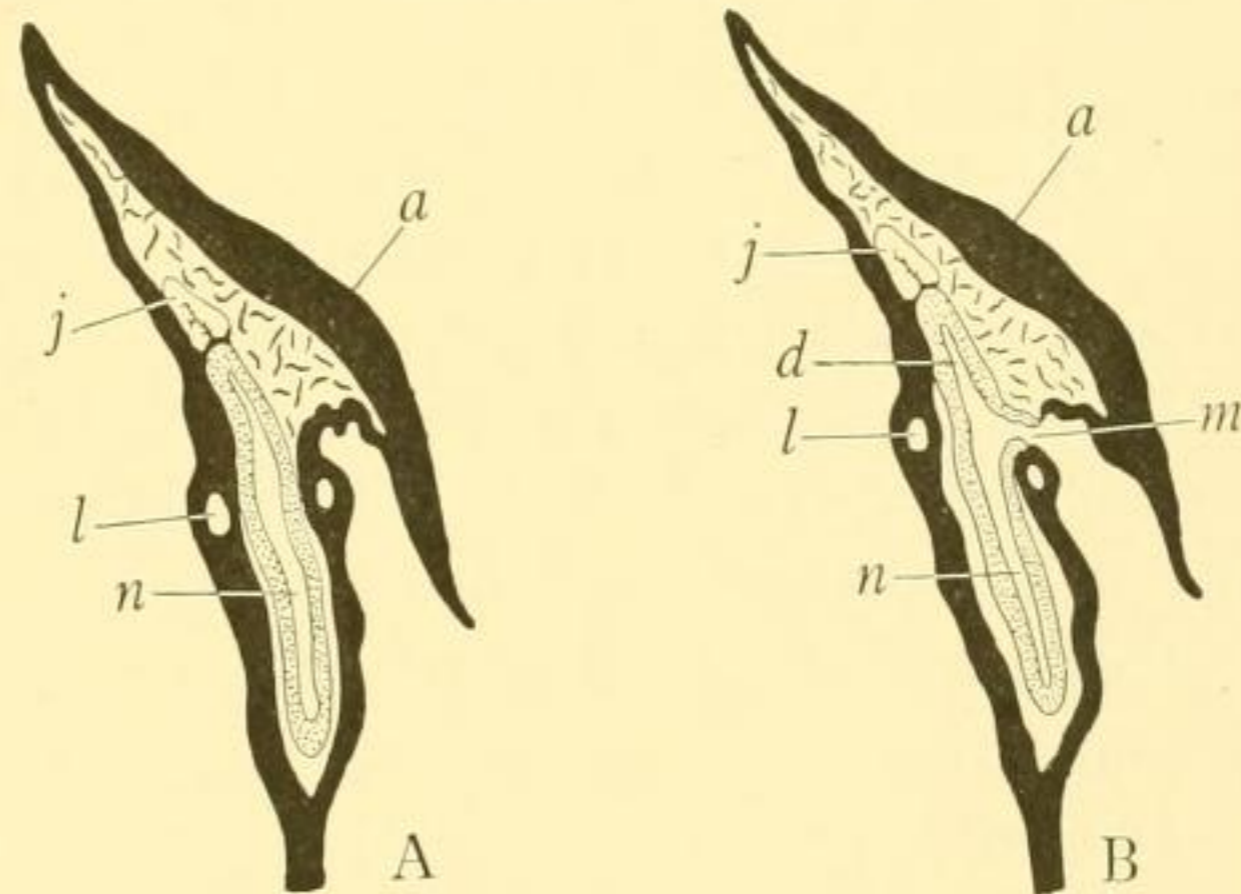


Fig. 6. Young bud of *C. nigrescens* (sagittal sections). A, early stage; B, later stage. *a*, proboscis; *d*, notochord; *j*, heart and pericardium; *l*, collar cavity; *m*, mouth; *n*, primitive gut.

the mouth is formed at about one-third the distance from the anterior end of the primitive gut. This stage has been figured by Harmer (1905, Pl. XIII, fig. 173). Later still, the pre-oral region of the primitive gut develops the characteristic appearance of the notochord. From the earliest stage its homology is revealed by the position of the heart and pericardium.

To draw any general conclusion from the development of the bud may not be justifiable, but it is recorded here since it shows a distinct stage in the formation of the notochord, which may serve for comparison when the embryonic development is worked out.

MUSCULAR SYSTEM

The muscular system of *Cephalodiscus* is well developed, and the zooids are capable of vigorous contraction. The chief muscles can be grouped as follows: (*a*) the muscles of the stalk, which are continuous with (*b*) the postero-ventral longitudinal muscles of the trunk, (*c*) longitudinal muscles of the collar, (*d*) longitudinal muscle of the arms, (*e*) transverse muscles of the proboscis and (*f*) "problematic" tissue situated on the roof of the collar pores.

Longitudinal muscles of the stolon are reflected on the ventral wall of the trunk. At the junction of the stolon and the body these muscles form three distinct tracts, which, diverging and broadening out slightly, run along the ventral body wall towards the bases of the right and left collar pores. On their course forwards some of the fibres terminate in the ventral body wall, so that the two bands become weaker as they approach the collar pores and are finally inserted into the septum between the trunk and collar cavities.

Two strong muscles are given off from the region of the collar canals; these traverse the collar cavities on each side of the mouth and end in the septum between the proboscis and collar cavities. From their relation to the mouth they are called the oral muscles. In the arms there are four bundles of longitudinal muscles, two strong bundles ventrally, one on each side of the food groove, and two weaker bundles in the dorsal wall.

The transverse muscles in the proboscis are grouped into bundles, which radiate from the septum between the proboscis and collar cavities. These muscles are attached to the ventral wall of the proboscis and their contraction enables the disc of the proboscis to be used as a sucker for the creeping movement of the zooids when they come out of the ostia.

Besides these definite muscle fibres there is a very prominent bundle of "problematic" tissue situated on the roof of each of the collar canals. These were regarded as lateral skeletal masses forming a fulcrum for the pre-oral muscles (Masterman, 1898 *b*, p. 348), but Harmer (1905, p. 46) observed that they constitute a series of oval lamellae which stain like muscle fibres, each connected along half its circumference with the roof of the collar canal and with the external body wall, the other half being freely exposed in the collar cavity. The oval lamellae appear in all details to be muscle fibres. They originate from the roof of the collar pore and radiate towards the dorsal and ventral walls of the collar. Most of these fibres are inserted into the collar septa, only those towards the middle remaining free in the collar cavity. In *C. densus* the distal ends of these fibres

appear to be torn away from their attachments in the dorsal wall of the collar (Pl. XXXVII, fig. 1, *pt*). It is therefore probable that these are dilator muscle fibres which widen the lumen of the collar pores when water is drawn in, the connection of some of the fibres having been torn away by vigorous contraction when the zooids died.

VASCULAR SYSTEM

The vascular system of *Cephalodiscus* was described first by Masterman (1898 *b*, p. 350). He observed that it is composed of a pericardium situated on the tip of the notochord, a dorsal vessel running downwards in the mesentery of the collar, a system of sinuses round the stomach, vessels to the ovaries, a ventral vessel which divides into two at the base of the notochord and passes round the mouth to the anterior side of the body and stolon, vessels on the dorsal side of the body cavity of the arms and dorsal and ventral vessels in the stolon. He stated that the vascular system of *Cephalodiscus* is identical with that of *Balanoglossus*. The dorsal vessel communicates with the heart, and glomeruli occur in the ventral wall of the pericardium and in the ventral blood sinus. He also described a blood sinus running in the dorsal wall of the proboscis which was connected with the anterior glomerulus. Harmer (1905, p. 75) denied the existence of certain of the vessels described by Masterman. It was difficult to demonstrate that the dorsal and ventral vessels of the stolon were connected with similar vessels in the trunk; so he distinguished the spaces in the body as (*a*) vessels, the vascular nature of which was very clear, and (*b*) doubtful spaces. He recognized (1) the existence of the dorsal vessel which starts from the anterior caecal projection of the stomach and runs upwards parallel to the pharynx. This vessel, he believed, functioned as a reservoir of blood. He recognized also (2) vessels in the lateral mesentery passing ventral to the oviduct into the ovary and supplying it with nutriment, (3) two vessels in the stolon, the anterior vessel passing into the anterior part of the ventral mesentery and the posterior vessel passing into the ventral mesentery as far as the alimentary canal. To this detailed account there are only a few additions to make, and they are based only on the sections of *C. densus*. The space inside the heart as well as all the discernible vascular spaces are deeply stained and so it is easy to distinguish them from non-vascular spaces in the body.

In *C. densus* the heart is not situated on the tip of the notochord as in *C. dodecalophus* but on its ventral surface, so that the pericardium extends backwards almost parallel to the notochord. The heart is thick-walled and formed by the invagination of the posterior wall of the pericardium. The space inside the heart is dilated and deeply stained (Pl. XXXVII, figs. 1-4). This communicates directly with two blood vessels. A blood vessel originating from the dorsal side of the heart passes round the tip of the notochord, gives off a branch which runs forwards to the dorsal wall of the proboscis and proceeds backwards between the collar cavities close to the dorsal side of the notochord. Glomeruli occur on its walls in the hinder part, where it is very thick. On reaching the roof of the dorsal diverticulum of the pharynx it divides into two. These branches which I propose to call the pharyngeal blood vessels (Pl. XXXVII, fig. 2, *pv*₁ and *pv*₂) pass backwards close

to the right and left sides of the pharynx to the base of the collar pores. The roof of the gill opening occurs immediately behind the collar pores and the right and left pharyngeal blood vessels on reaching the gill region come to an end abruptly. Though it could not be demonstrated in my material, it seems probable that the pharyngeal blood vessels break up into smaller branches which pass into the vacuolated cells of the gill region where the blood is oxygenated.

From the ventral posterior side of the heart is given off the ventral blood vessel, which at the base of the notochord divides into two lateral branches which pass along the dorsal wall of the collar cavities into the arms. In the arms these vessels are seen as deeply stained wavy lines running between the basement membrane and the coelomic epithelium. On the ventral side of the arms similar vessels occur which are directly connected with the median dorsal vessel. Pl. XXXVII, figs. 3 and 4 are transverse sections of the heart showing the cavity of the pericardium and heart. The pericardial cavity is not stained at all, whereas the space inside the heart is deeply stained. The wall of the heart is very thick and glomeruli occur on it. The section passes through the lower region of the heart and so the heart and pericardium appear only on the ventral side of the notochord. Dorsal to the notochord in the median septum between the right and left collar cavities runs the dorsal vessel already described. On the ventral posterior side of the heart there opens into it a very large vessel, the ventral blood vessel, which runs on the ventral side of the notochord. This dilates into a large space before it opens into the heart (Pl. XXXVII, fig. 1, *vv*). The dilated part has thick walls with glomeruli occurring on them. It is not certain whether the walls of the vessel are muscular. It follows the curve of the notochord and ends abruptly on the roof of the pharynx. The vessel which occurs in the median septum between the pharynx and the rectum is very probably a continuation of this vessel.

It has not been possible to work out the complete course of the circulation since the vessels are indistinct in parts of the body. But from the evidence it seems possible that the dorsal vessel conveys blood from the heart to the gills, arms and proboscis and that the ventral vessel collects blood and returns it to the heart.

In the stolon there are two vessels, the dorsal and ventral, but I have not been able to discover the connections of these vessels with the vessels of the body. Considering the specific differences in the relation of the stolon to the trunk, the connection of these blood vessels may not be the same in all species. In *C. hodgsoni* the stolon originates from the mid-ventral side of the body, in *C. densus* from the posterior extremity, and in *C. fumosus* near the mouth in the pharyngeal region (Pl. XXXVI, fig. 1). How far the position of the stolon would affect the connection of the stalk vessels with the vessels of the body is difficult to estimate.

NERVOUS SYSTEM

Detailed accounts of the nervous system of *Cephalodiscus* were given by Masterman and later by Harmer. Masterman (1898 *b*, p. 342) recognizes (1) the main ganglion on the dorsal wall of the proboscis and collar; (2) an anterior pre-oral nerve over the tip

of the proboscis and spreading out as a thin plexus under the glandular part of the ventral wall; (3) nerves to the arms; (4) a pair of lateral nerves; (5) a post-oral ring from the posterior edge of the collar and (6) nerves into the stolon. I was not able to find all the nerves which Masterman described and the main course of the nerve tracts which I have determined seems to be somewhat different.

Fig. 7 is a drawing of the nervous system. From the anterior end of the main ganglion arises a thin plexus of nerves which spreads out laterally between the basement membrane and coelomic epithelium of the dorsal wall of the proboscis, the separate nerves become fused, round the lateral edges, with a thin plate of nerve plexus found under the

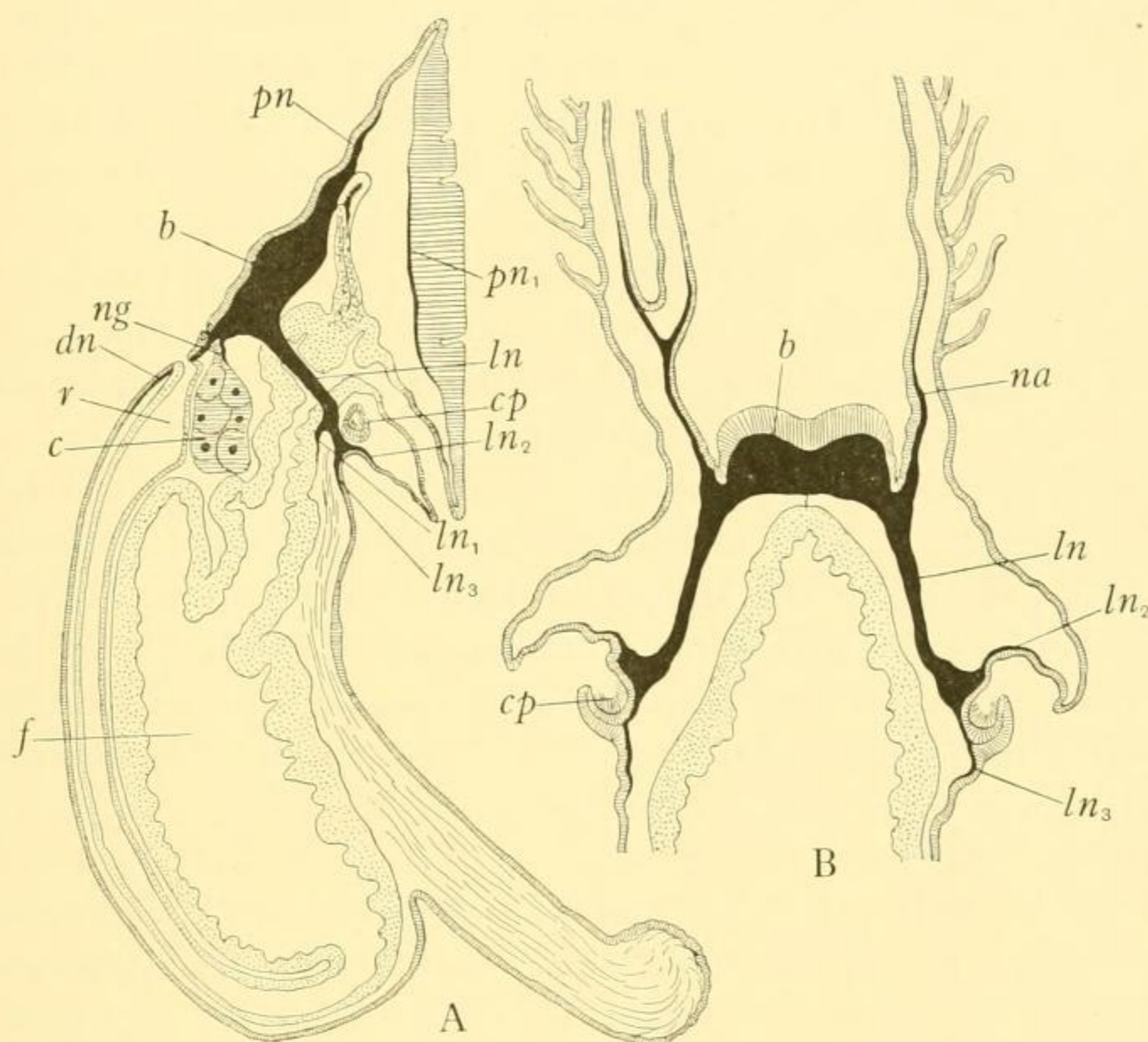


Fig. 7. *C. densus*. Nervous system. A, sagittal section; B, frontal section. *b*, ganglion; *c*, gonad; *cp*, collar pore; *f*, stomach; *pn*, pre-oral nerve plexus; *pn₁*, nerve plexus in ventral wall of proboscis; *ln*, post-oral nerve; *ln₁*, nerve to pharynx; *ln₂*, nerve to post-oral lamella; *ln₃*, nerve to ventral body wall; *ng*, nerve to gonad; *dn*, nerve to dorsal body wall; *na*, nerve to arms; *r*, rectum.

glandular region of the ventral wall. This pre-oral nerve plexus does not extend to the anterior tip of the proboscis, so that Masterman's description of its course is incorrect. From the dorsal side of the ganglion arise the nerves to the arms; from the posterior end, a pair of post-oral nerves and a median nerve which runs in the dorsal wall of the trunk. This median nerve gives off a pair of small branches which enter the ducts of the gonads. The post-oral nerves, homologous with the "post-oral ring" of Masterman, proceed backwards on either side, and at the base of the collar pores each divides into three branches which enter the pharynx, post-oral lamella and body wall respectively.

Pl. XXXVIII, figs. 1 to 8 are transverse sections which show the course of the main nerve

tracts. Fig. 1 passes through the anterior region of the proboscis in front of the ganglion. Apart from the three layers of the body wall no trace of nerve plexus is seen in this region, and this supports my opinion that the pre-oral nerve plexus does not pass round the anterior tip of the proboscis. Harmer (1905, p. 72) also doubted the existence of such a nerve, though he believed the nerve plexus at the base of the glandular region of the ventral wall to be connected with the ganglion by a nerve which passed through the tip. Fig. 2 shows the region of the proboscis in front of the notochord. The proboscis cavity is very wide and contains inside it the proboscis canals and the heart and pericardium. Dorsal to the heart is the thick pre-oral nerve plexus which spreads out laterally on each side and becomes continuous with the nerve plexus of the ventral wall. Fig. 3 shows the ganglion, and, ventral to this, the heart and pericardium, the two proboscis pores and the anterior horns of the right and left collar cavities. The lateral plexus is more prominent and is seen extending to the sides. Fig. 4 shows the continuation of the ganglion in the dorsal wall of the collar from which nerves are given off to the arms. These nerves pass along the dorsal wall of the axis of the arms, and at the base of each arm spread out laterally forming a complete ring of nerve plexus. Fig. 5 shows the tip of the dorsal diverticulum of the pharynx and the origin of the main lateral post-oral nerves. These nerves proceed downwards along the right and left sides of the pharynx and in fig. 6 they are seen at the base of the post-oral lamella below the right and left collar pores. They give off three branches on each side, the first (ln_1) proceeds to the wall of the pharynx, the second (ln_2) passes along the posterior wall of the post-oral lamella, and the third (ln_3) goes to the ventro-lateral body wall. By the time fig. 8 is reached the lateral nerves become so small that they cannot be easily distinguished from the surrounding tissue. Beyond the region of the gill opening no distinct nerve tract is visible, and I was not able to discover the nerves in the stolon nor any sign of the lateral nerves extending into it.

In conclusion it may be pointed out that the pre-oral and lateral plexus together form a continuous plate of nerve plexus which spreads out from the anterior and lateral sides of the main ganglion in the dorsal wall of the proboscis. In the present account this is called the pre-oral nerve plexus. The paired lateral nerves and the "median pre-oral" nerve of Masterman are not distinct branches, but are only parts of this continuous plate of nerve plexus which in individual longitudinal and transverse sections appear like branches. The paired post-oral nerves do not form a complete ring but break up into branches at the base of the right and left collar pores.

CLASSIFICATION OF THE SPECIES OF *CEPHALODISCUS* WITH A LIST OF KNOWN FORMS

Ridewood (1918 *a*) gave a synopsis of the species of *Cephalodiscus* and a list of all recorded specimens in his contribution to the 'Terra Nova' reports. The present expedition has brought to light two new species. I therefore feel justified in revising the classification especially in view of the fact that a new sub-genus *Acoelothecia* had to be

made for the new species *C. kempfi*. With the incomplete knowledge of the limited number of species, it would be futile to search for a primitive type among them. The zooids of all recorded species, except for differences in the number of arms, size of body and position of stolon, are uniform in structure except *C. densus*, in which the structure of the gill region marks a distinct advance on the general type. The coenoecium of *Cephalodiscus* is marked by great diversity of form and structure upon which the classification into sub-genera is based.

In *Orthoecus* the colonies are in the form of cake-like masses, each zooid occupying a tube of its own. The different tubes are not continuous but are held together by the secretion of coenoecial substance between them. In one species—*C. fumosus*—the individual tubes are arranged vertically inside a common mass which is formed by the agglutination of minute particles of sand. This species and the diminutive disc-like colonies of *C. indicus* can be regarded as the bases upon which a hypothetical primitive type can be founded. Such a form will be a solitary individual which constructs a tube of its own, buried in the sand or mud of the sea-bottom, with habits like those of the allied group Enteropneusta.

The sub-genus *Orthoecus* is an intermediate stage between the primitive solitary hypothetical type and the typical colonial forms included in *Demiothecia* and *Acoelothecia*. In fact *Orthoecus* is only a gregarious group of organisms, each individual having an independent existence of its own. The tendency towards complete colonial life is more definite in *Idiothecia* where the colonies grow vertically. Though in *C. nigrescens* each individual has a tube of its own, the elaborate branching of the colonies and other habits are the evidence of a more communal life. This is accentuated in *C. agglutinans*, in which the different tubes are connected with each other resulting in a tubular labyrinth in the middle of the branch and this may be regarded as the bridge between *Idiothecia* and *Demiothecia*. Complete colonial life is met with in *Demiothecia* and *Acoelothecia*. The spaces inside the colony are continuous and the zooids occupy them in common, but of these two, *Acoelothecia* is more advanced, since the central tubular cavities are replaced by the elaborate meshwork which in Form B of *C. kempfi* reaches great size and thickness.

In the following classification the diagnoses of the species not recorded in this report are adopted from Ridewood.

CEPHALODISCIDA

Genus *Cephalodiscus*, M'Intosh

Sub-genus *Orthoecus*, Andersson

Colonies in the form of a cake or cone or mass of irregular shape. Zooids occupying individual tubes, each with an ostium of its own, embedded in a common coenoecial substance or mass formed by the agglutination of minute particles. The tubes either closely set and parallel or irregularly bent and straggling.

C. indicus, Schepotieff. Colony diminutive, in the form of a small round plate; diameter 7 to 10 mm., height 3 to 4 mm. Ostia without any definite peristomial lip. Length of zooid 2.2 mm., arms three pairs, no end-swelling with refractive beads. South coast of Ceylon and Mahé (Malabar coast of India).

C. fumosus, n.sp. Colony in the form of a flat cake-like mass formed by agglutination of minute sand particles. Tubes vertical and parallel, with triangular peristomial lips. Length of zooids 3.2 mm.; dorsal side of body light brown. Arms eight pairs, with two black bands in the axis. No end-swelling with refractive beads. Buds on each zooid up to ten. Off Cape Bowles, Clarence Island.

C. solidus, Andersson. Colony not branching, in the form of a bulky mass or cake, measuring up to 300 mm. across, and 100 mm. high; the mass consisting of closely set vertically disposed tubes each with an ostium and peristomial tube at the upper end. The common coenoecial substance with or without sand grains. Length of zooid 4 to 5 mm. Colour of preserved zooid blackish. Arms eight pairs; no end-swelling with refractive beads. North of Joinville Island and off Mertz Glacier, Adélie Land.

C. densus, Andersson. Colony in the form of a bulky mass or cake, measuring up to 70 mm. high, consisting of closely set vertically disposed tubes of uniform diameter, each with transverse ostium at upper end. Common coenoecial substance soft and spongy, with or without sand grains. Length of zooids 4 to 11 mm. Colour of preserved zooids greyish or brownish white. Arms usually eight pairs. Buds on each zooid up to fourteen. Graham Land region, south-east of Seymour Island; Palmer Archipelago; off Queen Mary Land; McMurdo Sound, Ross Sea.

C. rarus, Andersson. Probably a synonym of *C. densus*.

C. anderssoni, Gravier. Colony a ragged bulky mass, measuring up to 105 mm. across; consisting of radially disposed tubes of uniform diameter, each with a transverse ostium devoid of peristomial lip. Basal parts of tubes cemented by common coenoecial substance into groups of four or five; partly incrustated with sand grains. Length of zooid 4 to 4.5 mm. Arms in buds six pairs, number in adult doubtful. South of Jenny Island, near Adelaide Island.

Sub-genus *Idiothecia*, Ridewood

Colony branching, each ostium leading into a tube occupied by one zooid and its buds. Tubes embedded in common coenoecial substance, and disposed at a more or less constant angle to the surface, either blind at their inner ends, or connected up in the middle of the branch.

C. nigrescens, Lankester. Colony branching, branches roughly cylindrical, colour greyish translucent; ostia at the end of short tubular peristomes, abaxial edge of peristome produced into a blunt lip. No spines. Each ostium leading into a tube which ends blindly in the middle part of the branch. Length of zooid 4 to 6 mm. Arms usually seven pairs, sometimes six or eight pairs, axis of arms with two black bands; no end-swelling with refractive beads. North-east of Coulman Island, Victoria Land; south

of Jenny Island, near Adelaide Island; Palmer Archipelago; off Queen Mary Land; McMurdo Sound, Ross Sea.

C. levinseni, Harmer. Colony reddish orange, slightly branched. Width of branch not including peristomial tubes 3 to 5 mm. Ostia numerous, each leading into a tube that ends blindly in the middle part of the branch. Peristomial tubes projecting beyond the general surface about 4 mm. Length of zooids 2.5 mm. Colour of preserved zooids whitish. Arms six pairs; no end-swellings with refractive beads. Off west coast of Japan, at the south end of Corea Strait.

C. evansi, Ridewood. Colony massive, branching, coenocidium friable, cream coloured, speckled, containing large quantities of shells of Foraminifera, and fragments of shells of Molluscs and Echinoids. Ostia at the end of tubular peristomes that project 2.5 to 4.5 mm. from the surface of the branch. Length of the zooids 3.5 mm. Colour of preserved zooids, pale green or white. Arms usually eight pairs, no end-bulbs with refractive beads. Buds up to nine. New Zealand, Three Kings Islands.

C. gilchristi, Ridewood. Colony of long branches, some of the branches connected across by solid bars. Width of terminal branches 5 to 8 mm., colour brown or pale brown. Ostia numerous, except on main stem. Spine-like processes on the coenocidium numerous, slender, simple or forked. Zooids 1.6 to 1.8 mm. Colour of preserved zooids brown. Arms usually six pairs; no end-swellings with refractive beads. Off Cape St Blaize, Knysna Heads; Cape St Francis; East London; other localities on the south coast of Cape Colony, South Africa.

C. agglutinans, Harmer and Ridewood. Colony massive, branching. Coenocidium friable, cream coloured, speckled, opaque, containing large quantities of shells of Foraminifera, fragments of shells of Mollusca and spines of Echinoids and rounded particles of slate. No peristomial tubes. Each ostium with a thick lip or spine that projects about 3 mm. beyond the general surface. Each ostium leading into a tube that communicates at its inner end with a tubular labyrinth in the middle part of the branch. Length of the zooid 4.5 mm. Colour of preserved zooid blackish, arms eight or nine pairs, no end-swellings with refractive beads. Burdwood Bank, south of Falkland Islands.

Sub-genus *Demiothecia*, Ridewood

Colony branching. Each ostium leading into a cavity which is continuous through the colony, and is occupied in common by the zooids and their buds. The walls of the coenocial cavity usually of irregular thickness and sometimes with inwardly projecting bars and ridges.

C. dodecalophus, M'Intosh. Colony irregularly branched and straggling; some of the branches fusing to form a network, the cross-bars being usually solid. Coenocidium pale orange-brown or colourless; width of branch excluding spines, 3.5 to 6 mm.; cavity of coenocidium continuous, but partially divided up by bars and incomplete

partitions; occupied in common by zooids and their buds. Ostia numerous, irregularly placed, oval and without peristomial tubes. Spines obviously not related to ostia, simple, forked or branched. Length of zooids, 2 mm. Colour of preserved zooids, whitish or cream-coloured. Arms usually six pairs, sometimes five pairs, with end-swelling with refractive beads. Buds two or three. Straits of Magellan; east of southern end of Tierra del Fuego, Beagle Channel; between Falkland Islands and Burdwood Bank.

C. hodgsoni, Ridewood. Colony irregularly branched, cavity of coenoecium irregular, continuous and occupied in common by the zooids and their buds, inner surface smooth and sometimes traversed by solid bars. Ostia numerous, irregularly placed, lateral or terminal, each ostium with two to five more or less radiating spines, forked or branched. Length of zooids 2 to 3.2 mm. Zooids dimorphic; red zooids with six pairs of arms, females; brown zooids with ten or eleven arms, males. Arms with end-swelling with refractive beads. Buds two, sometimes three or four to each zooid. Ross Sea, east end of Barrier; in McMurdo Sound, south of Ross Island; Commonwealth Bay, Adélie Land; off Shackleton Glacier, Queen Mary Land; Graham Land Region, south-east of Seymour Island.

C. inaequatus (Andersson). Regarded as synonymous with *C. hodgsoni* by Ridewood.

C. aequatus, Andersson. Nearly related to *C. hodgsoni* and *C. dodecalophus*. Colony irregularly branched and straggling; coenoecium containing diatoms in great numbers. Length of zooids 2 mm. Colour of preserved zooids crimson-brown, fading to pale brown. Arms, six pairs in both sexes, with end-swelling with refractive beads. Buds two to four on each zooid. Graham Land Region, north of Joinville Island.

C. gracilis, Harmer. Colony very small and delicate, irregularly branched, creeping on a species of Polyzoa. Coenoecium almost colourless, the orange-coloured zooids within imparting a yellow tint to the colony. Cavity of coenoecium continuous, occupied by zooids and their buds in common. Ostia at the ends of branches, funnel-shaped; margin produced into three, four or five spines. Length of zooids 1.3 mm. Stolon with black pigment in the median line of the ventral surface. Arms five pairs; end-swelling with refractive beads found on the first pair of arms of the bud, occasionally on the second and third pairs also, sometimes persisting in the adult. East coast of Borneo.

C. sibogae, Harmer. Colony very small and delicate, irregularly branched, orange-coloured with dense basal encrusting part of coenoecium attached to stones; cavity of coenoecium continuous, occupied in common by the zooids and their buds. Ostia at the end of very short side branches, more or less alternate on opposite sides of the branch, funnel-shaped, with margin produced into two or three spines. Ordinary zooids, sterile, with large operculum and four pairs of arms. Male zooids with a single pair of arms without any trace of pinnules; the dorsal wall of the arms constituted by large number of refringent vesicles; the alimentary canal vestigial and the operculum absent. Colour blackish. Zooids, which otherwise resemble neuters, sometimes with functional testes. Northern entrance of Buton Strait, south-east of Celebes.

Sub-genus *Acoelothecia*, sub-gen. nov.

Colony small or large and branching, formed of a meshwork of bars and spines without any definite coenoecial cavities. Spaces between the meshwork irregular and continuous and occupied in common by the zooids and their buds.

C. kempfi, n.sp. Colony small and tuft-like or large and branching. Inhabited part of coenoecium formed of an elaborate meshwork of bars and spines. Spines found all along the sides of branches; not related to ostia. Colour of coenoecium light brown to reddish brown. Length of zooid 1.8 to 2 mm. Arms five pairs, with end-swellings with refractive beads. Off Falkland Islands; off South Georgia.

NEW DATA SUMMARIZED

1. Two kinds of zooids are found in *C. hodgsoni*. Red zooids with twelve arms (female) and brown zooids with ten or eleven arms (males). Dimorphism being thus established, it is possible that *C. inaequatus* of Andersson is synonymous with *C. hodgsoni*, as suggested by Ridewood.

2. In *C. densus* a gill sac lies between the external gill opening and the pharynx.

3. *C. fumosus* is a new species, the zooids of which resemble those of *C. nigrescens*, but the coenoecium is formed by the agglutination of minute sand particles.

4. *C. kempfi* is a new species which constructs a coenoecium formed of a meshwork of bars and spines. Because of this unique structure and the absence of distinct tubes for the zooids it is found necessary to create a new sub-genus *Acoelothecia*.

5. The red line on the proboscis and the pigmentation in the oviduct are believed to be sensory in function.

6. It has been shown that the dorsal vessel gives off two branches—the pharyngeal vessels—which enter the gills.

7. The main ganglion gives off the pre-oral plexus; and the paired post-oral nerves divide into three branches.

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PLATE XXXIII

- Fig. 1. *C. hodgsoni*. Form A, St. 190.
Fig. 2. *C. hodgsoni*. Form B, St. 190.
Fig. 3. *C. hodgsoni*. Form B, St. 190.
Fig. 4. *C. hodgsoni*. The single specimen obtained from St. 167.
Fig. 5. *C. hodgsoni*. The single specimen obtained from St. 187.
Fig. 6. *C. densus*. From St. 82.



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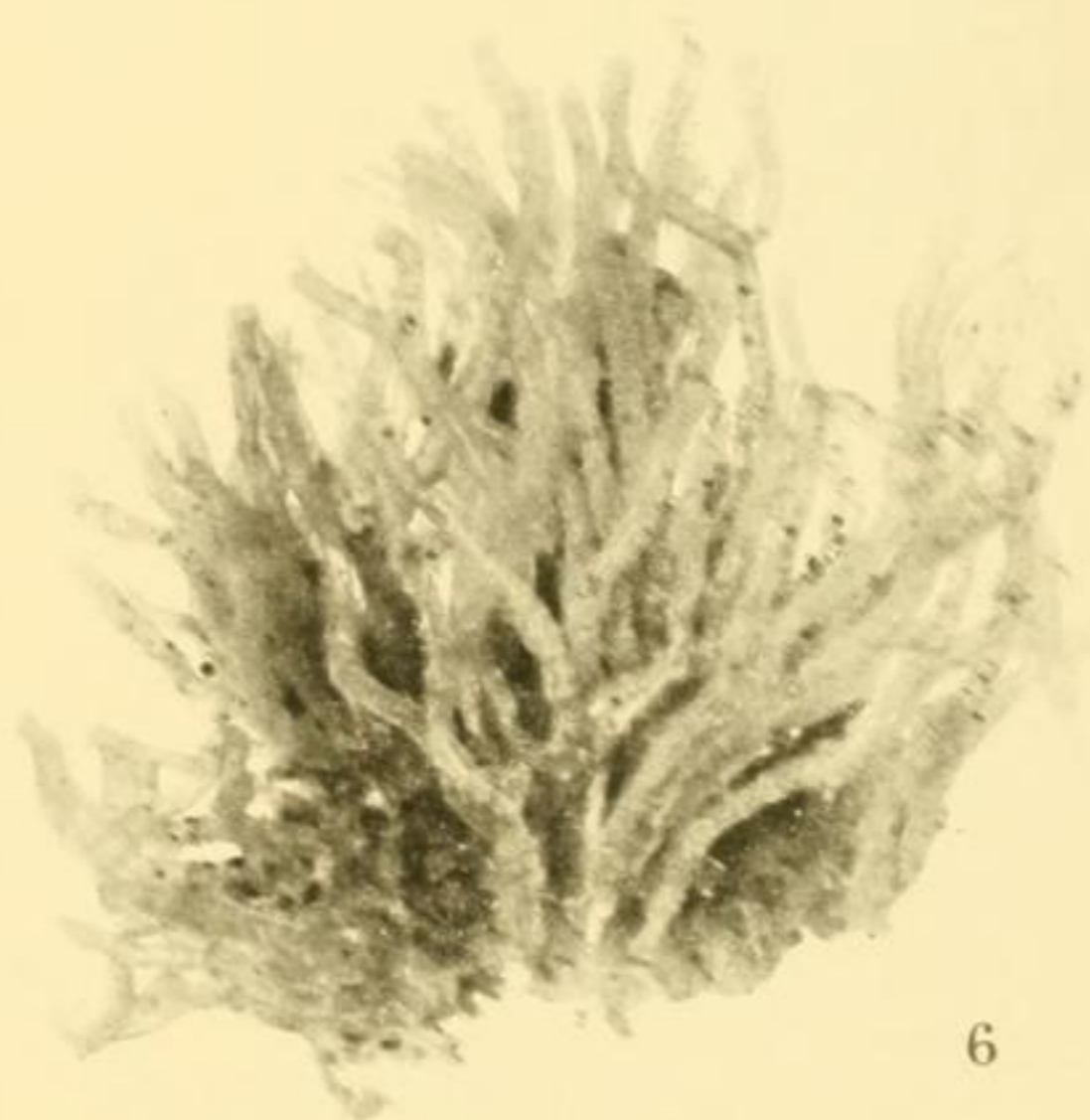
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CEPHALODISCUS



PLATE XXXIV

Fig. 1. *C. fumosus*. St. 170.

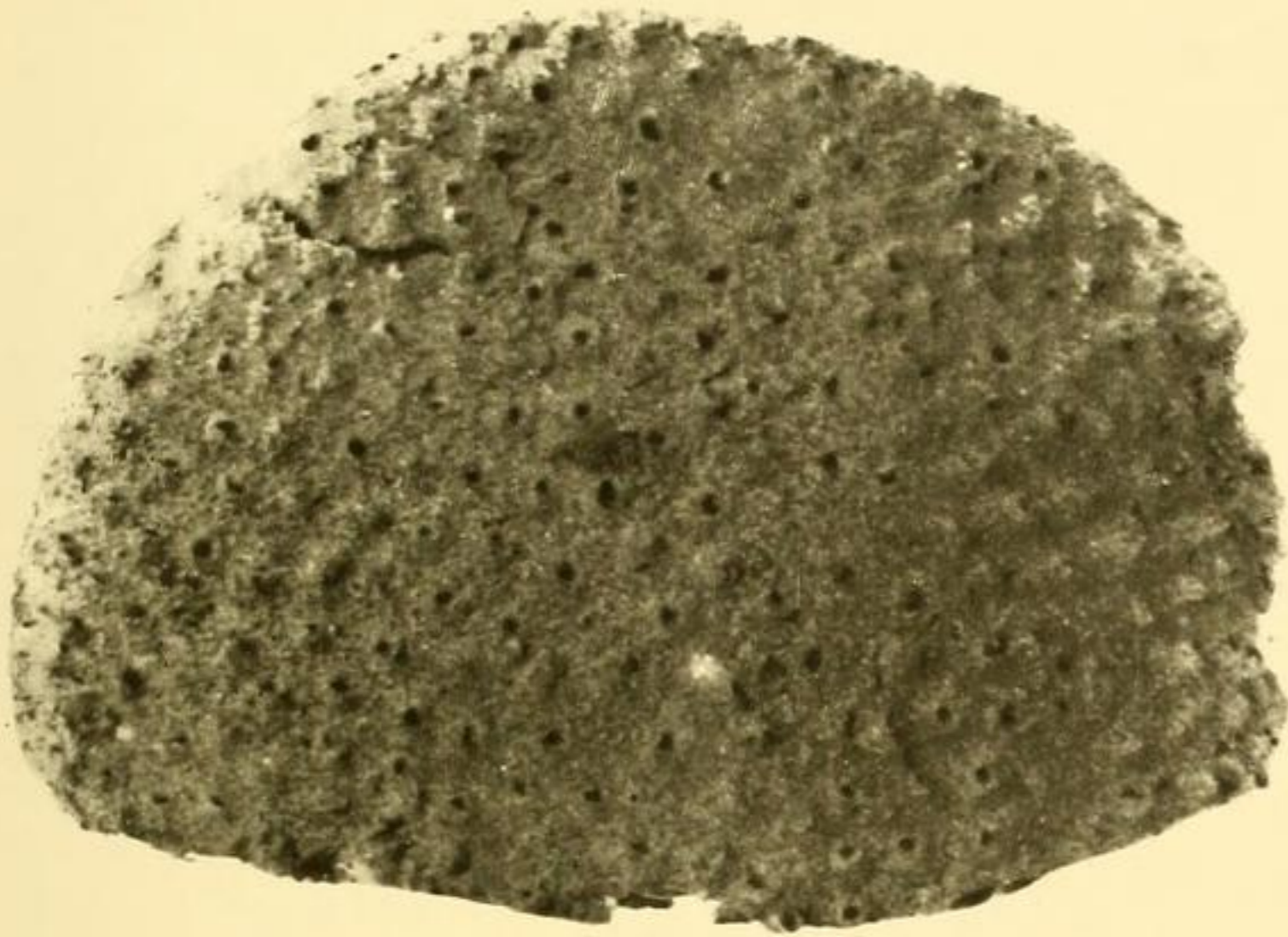
Fig. 2. *C. kempfi*. Form B, from St. WS 97, basal part of a large colony.

Fig. 3. *C. kempfi*. Form B, from St. WS 97, distal end of a branch showing the transparent growing region.

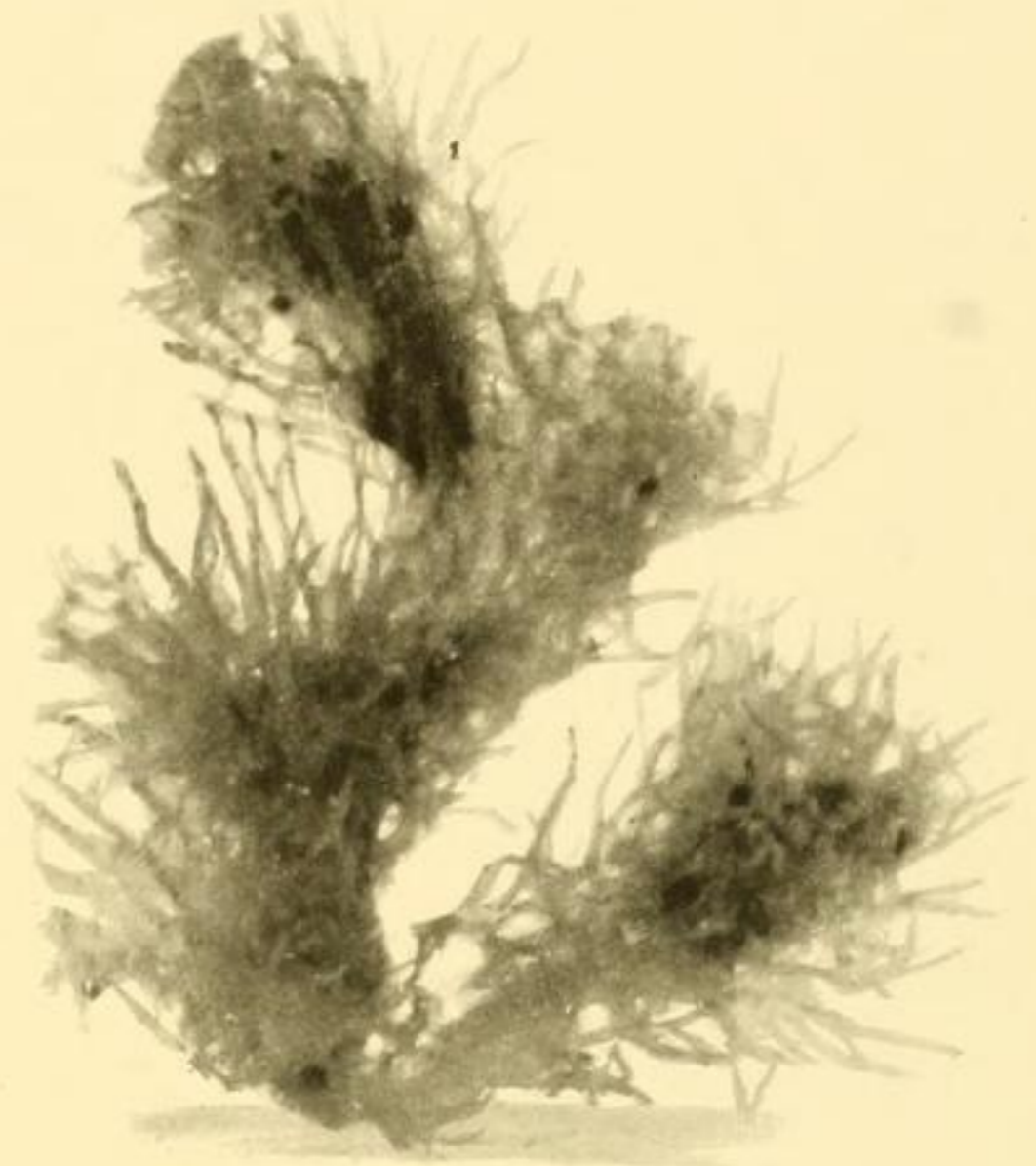
Fig. 4. *C. kempfi*. Form A, from St. 158.

Fig. 5. *C. kempfi*. Form B, from St. WS 97, the basal part of a thick branch photographed by transmitted light, showing the meshwork of the coenoecium.

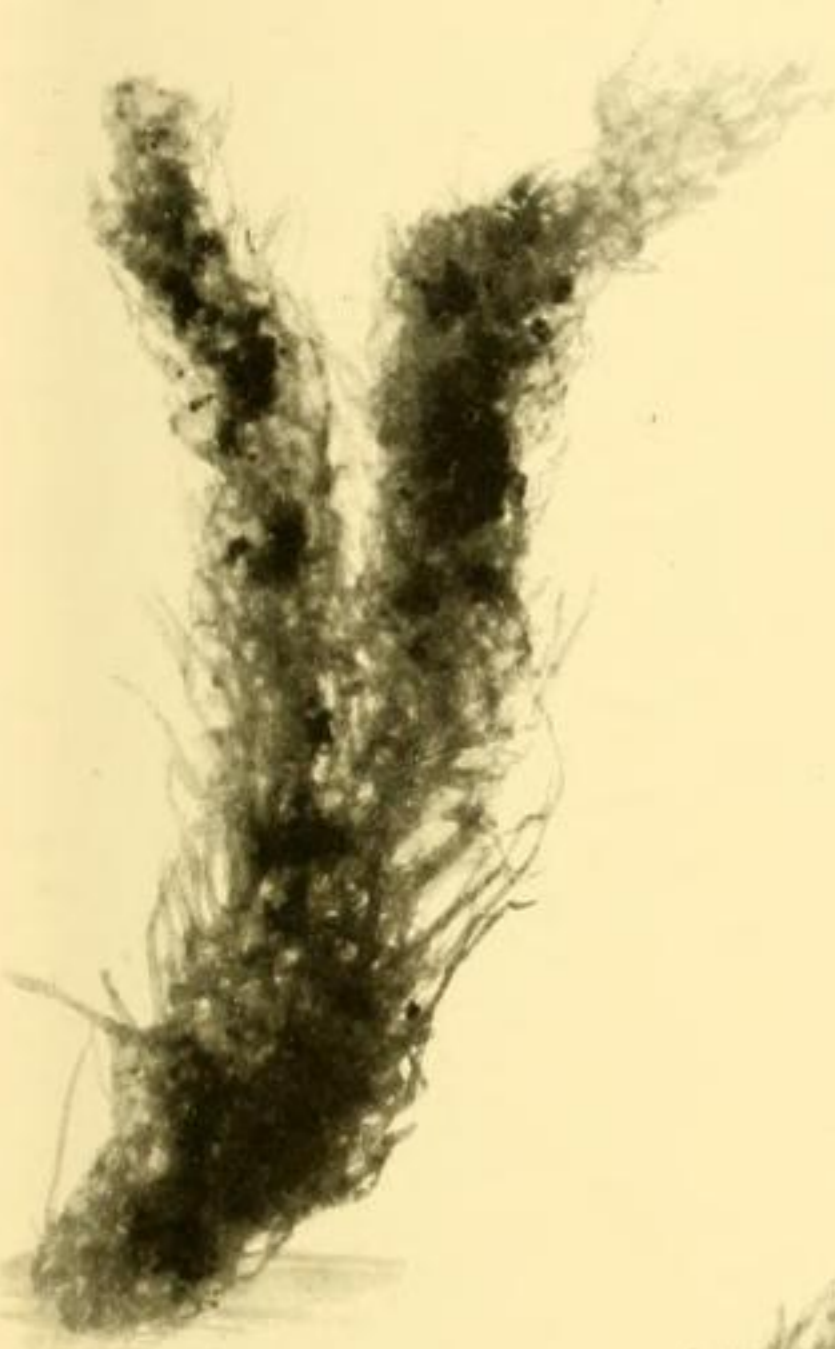
Fig. 6. *C. kempfi*. Form B, from St. WS 97, distal end of a branch photographed by transmitted light, showing the meshwork of the coenoecium and the mass of zooids.



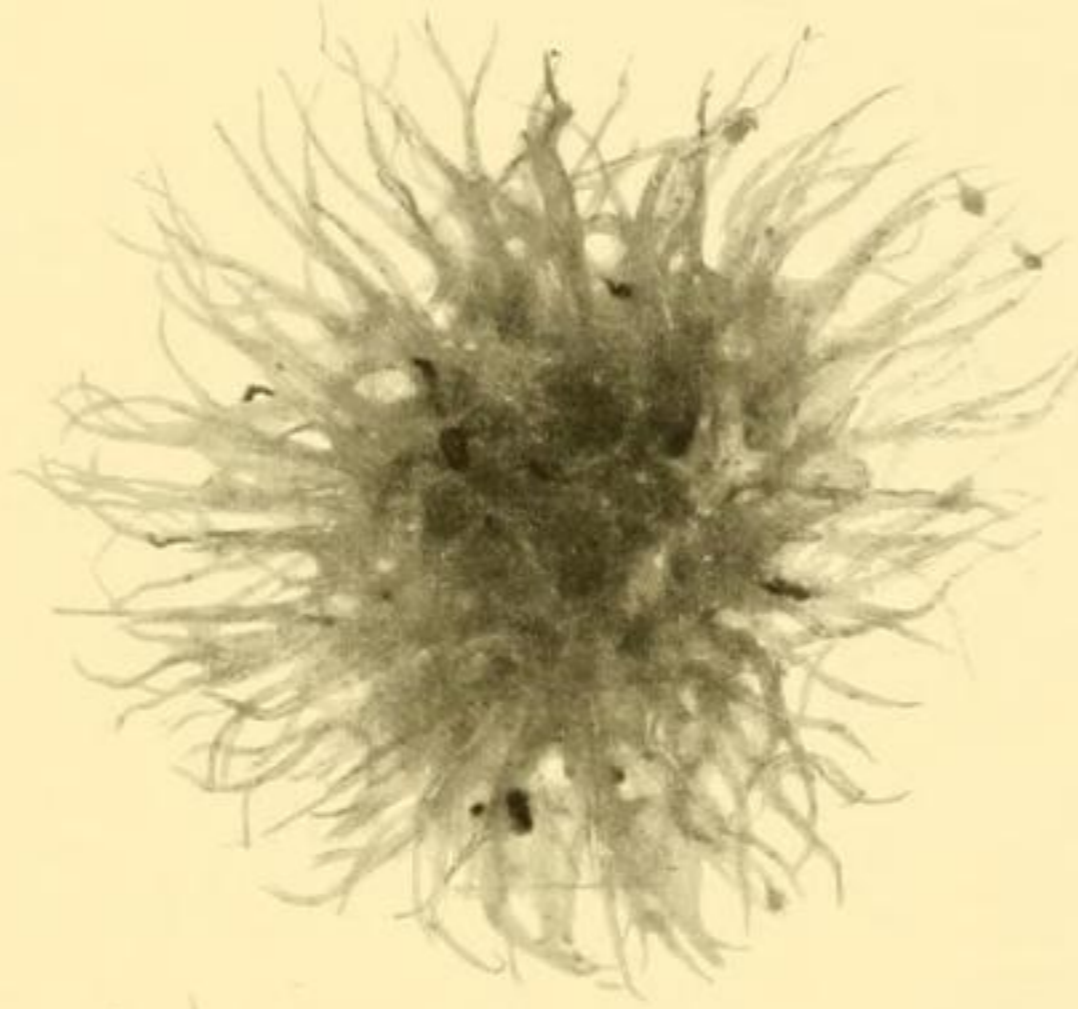
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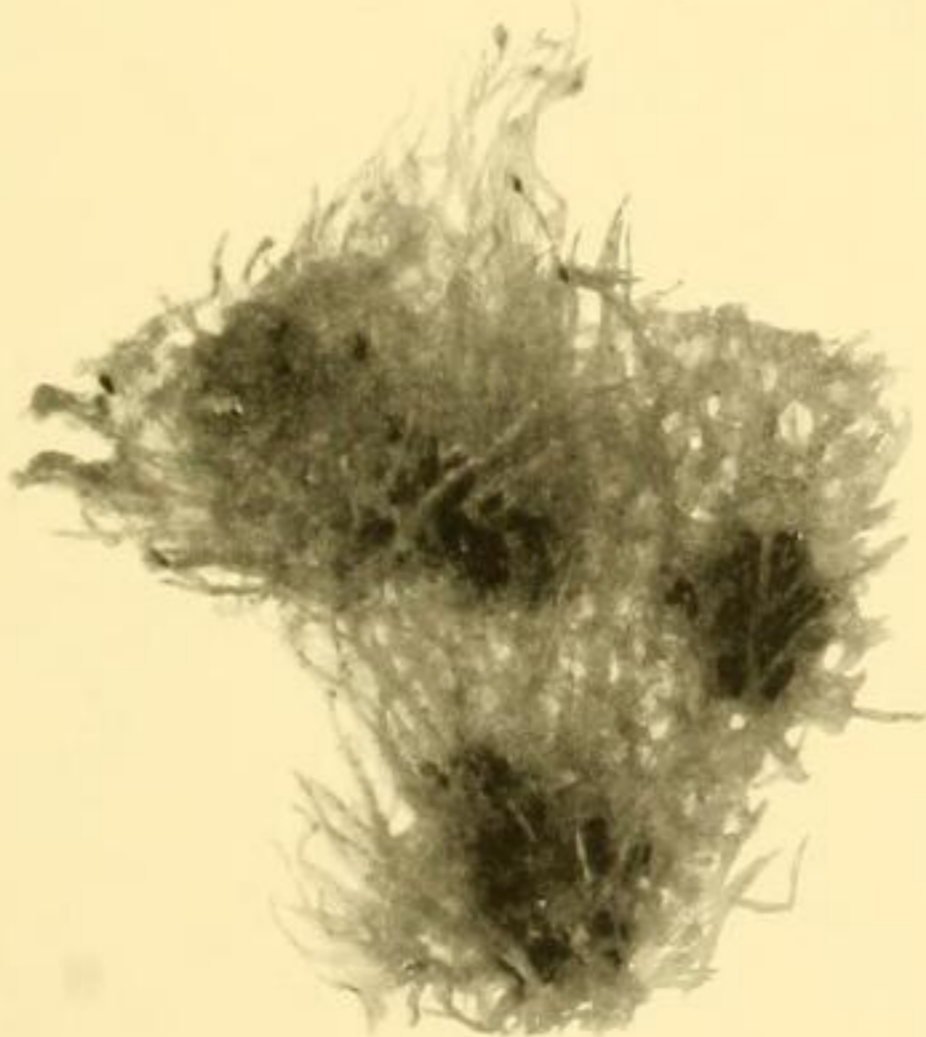
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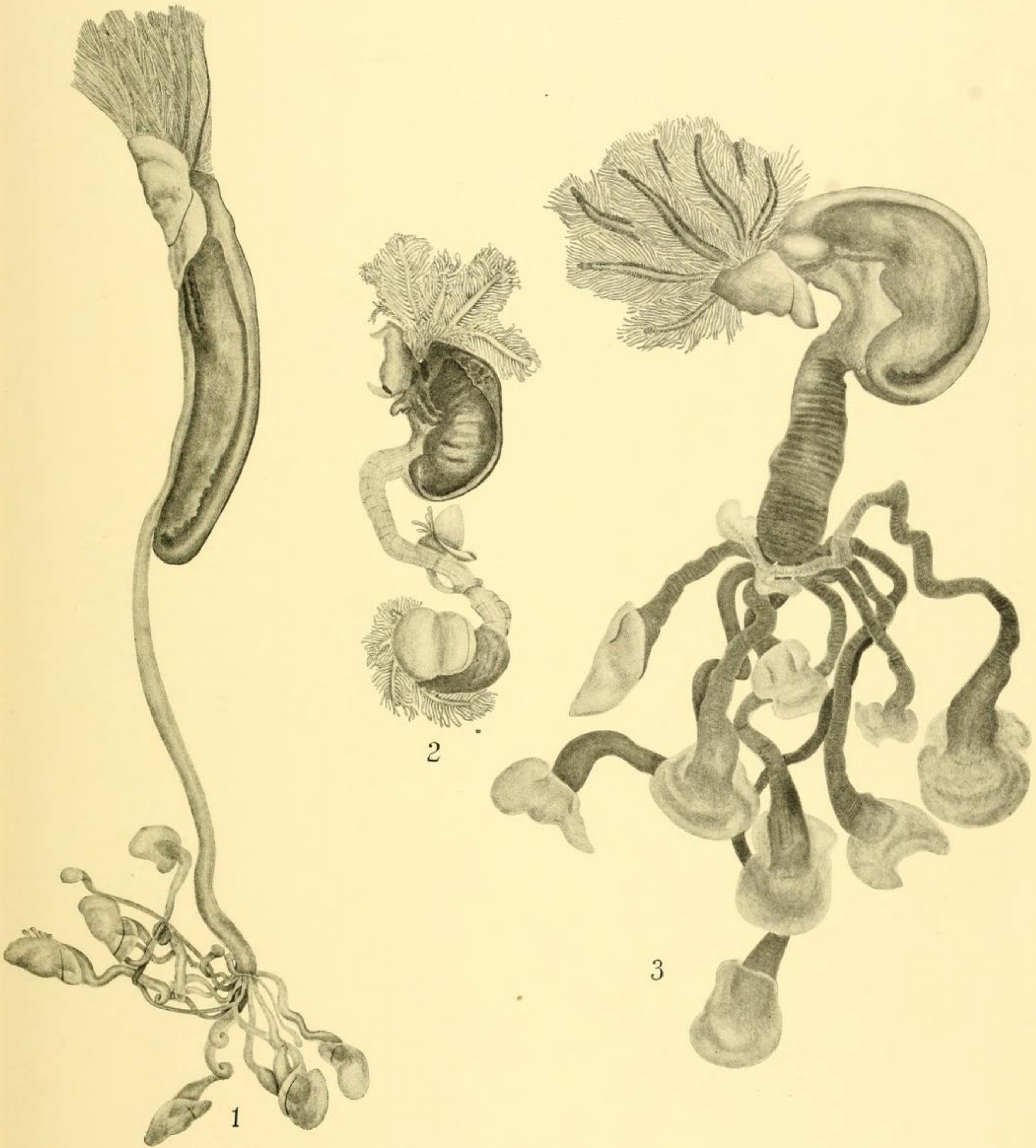


PLATE XXXV

Fig. 1. Zooid of *C. densus*, from St. 82.

Fig. 2. Zooid of *C. kempi*, from St. WS 97.

Fig. 3. Zooid of *C. fumosus*, from St. 170.



CEPHALODISCUS



PLATE XXXVI

a, proboscis; *c*, gonads; *cc*, collar cavity; *eg*, external gill slit; *f*, stomach; *g*, intestine; *gc*, gill cavity; *h*, pharynx; *i*, stolon; *ig*, internal gill slit; *m*, mouth; *pd*, dorsal wall of the proboscis; *r*, rectum; *rb*, dorsal wall of the arms with refractive beads.

Fig. 1. *C. fumosus*, sagittal section, showing the attachment of the stolon.

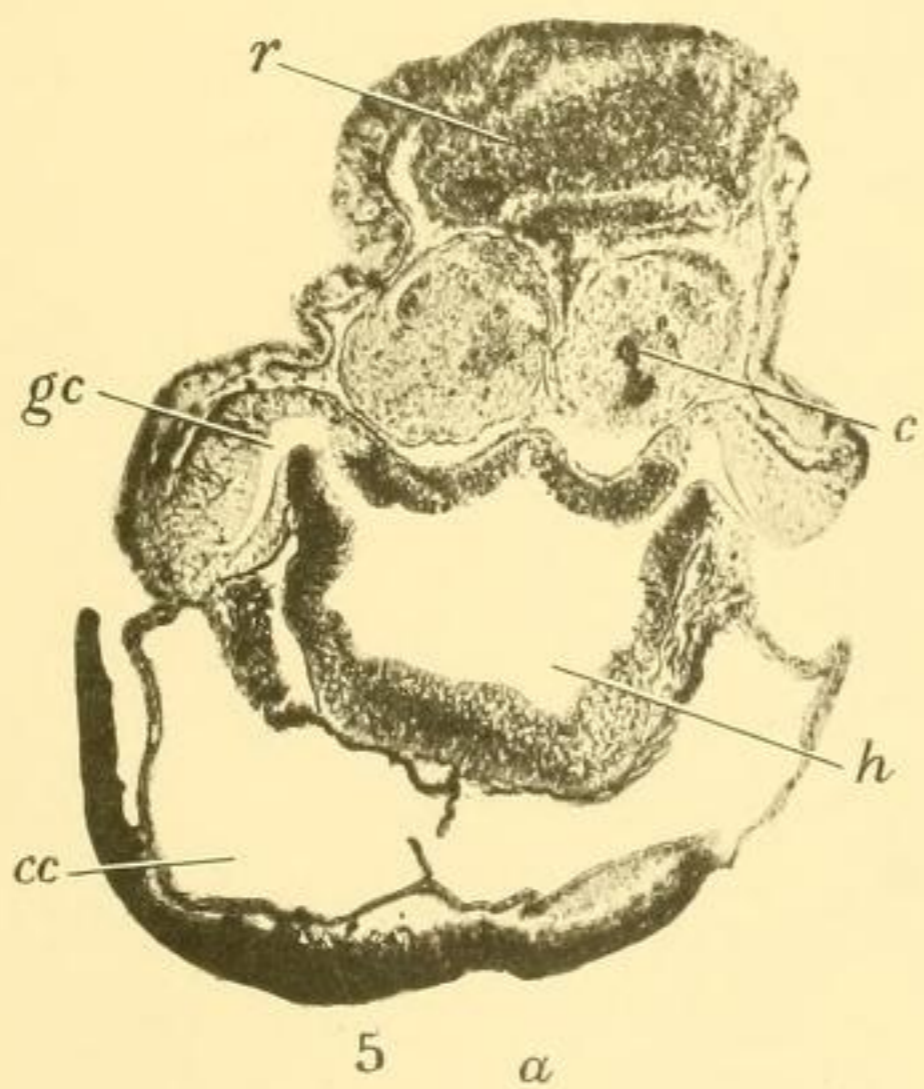
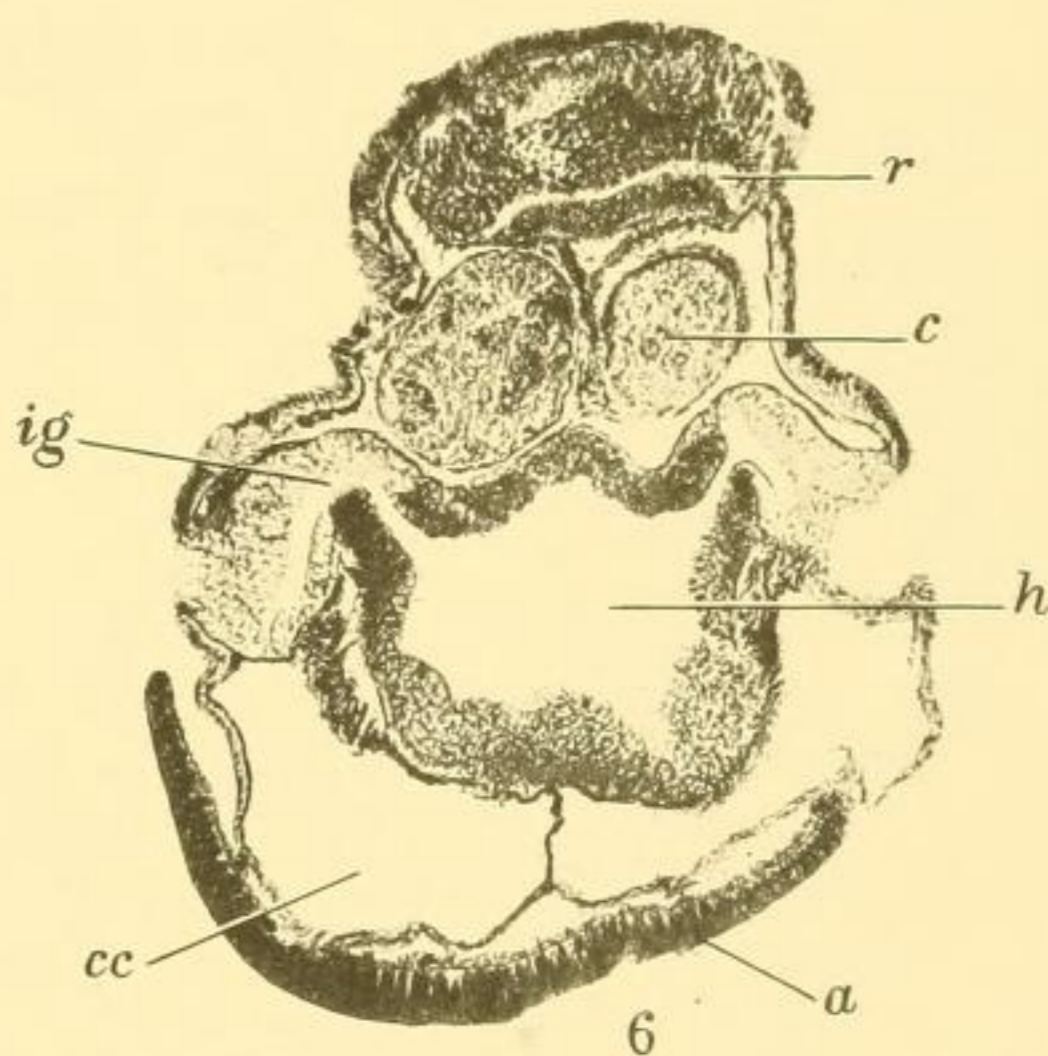
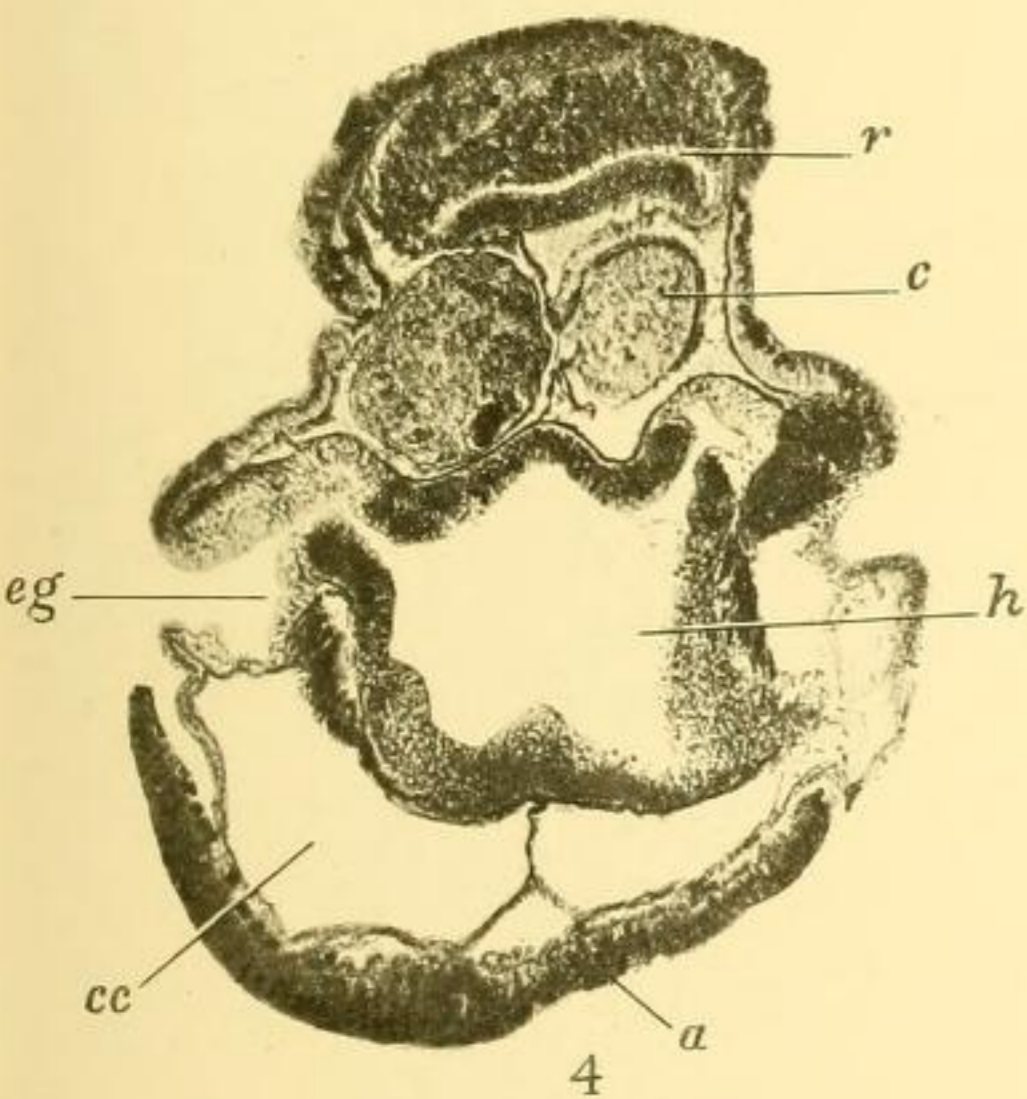
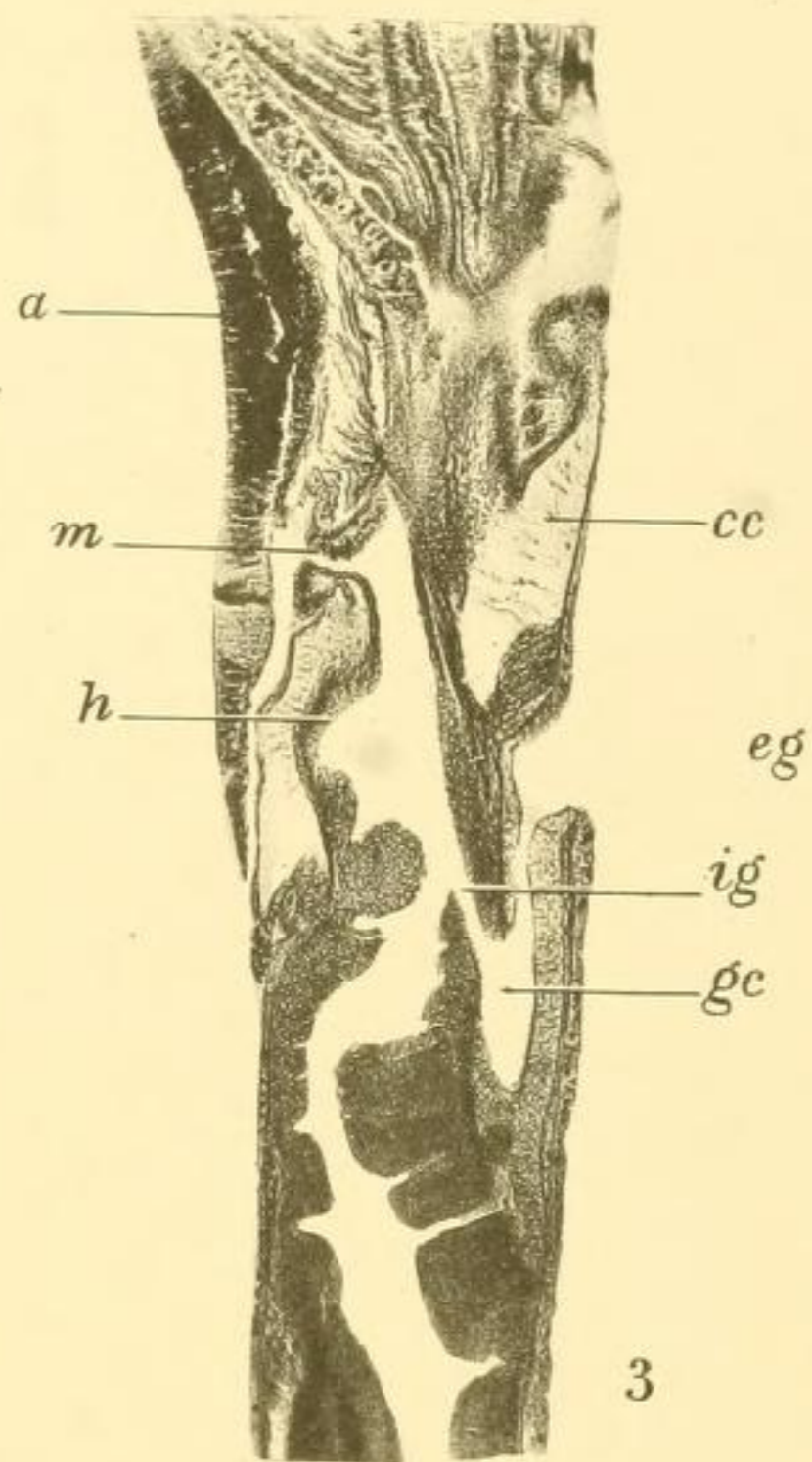
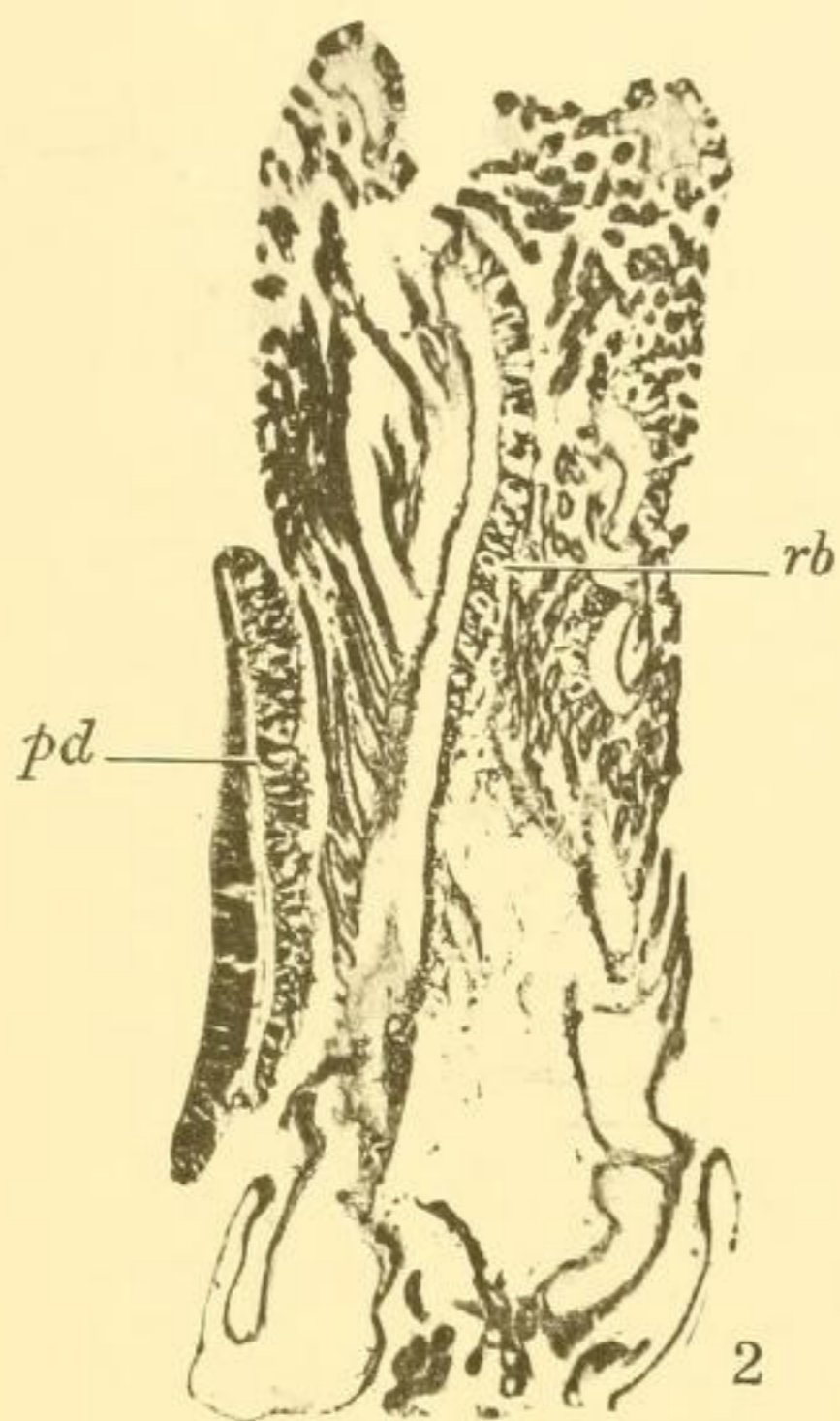
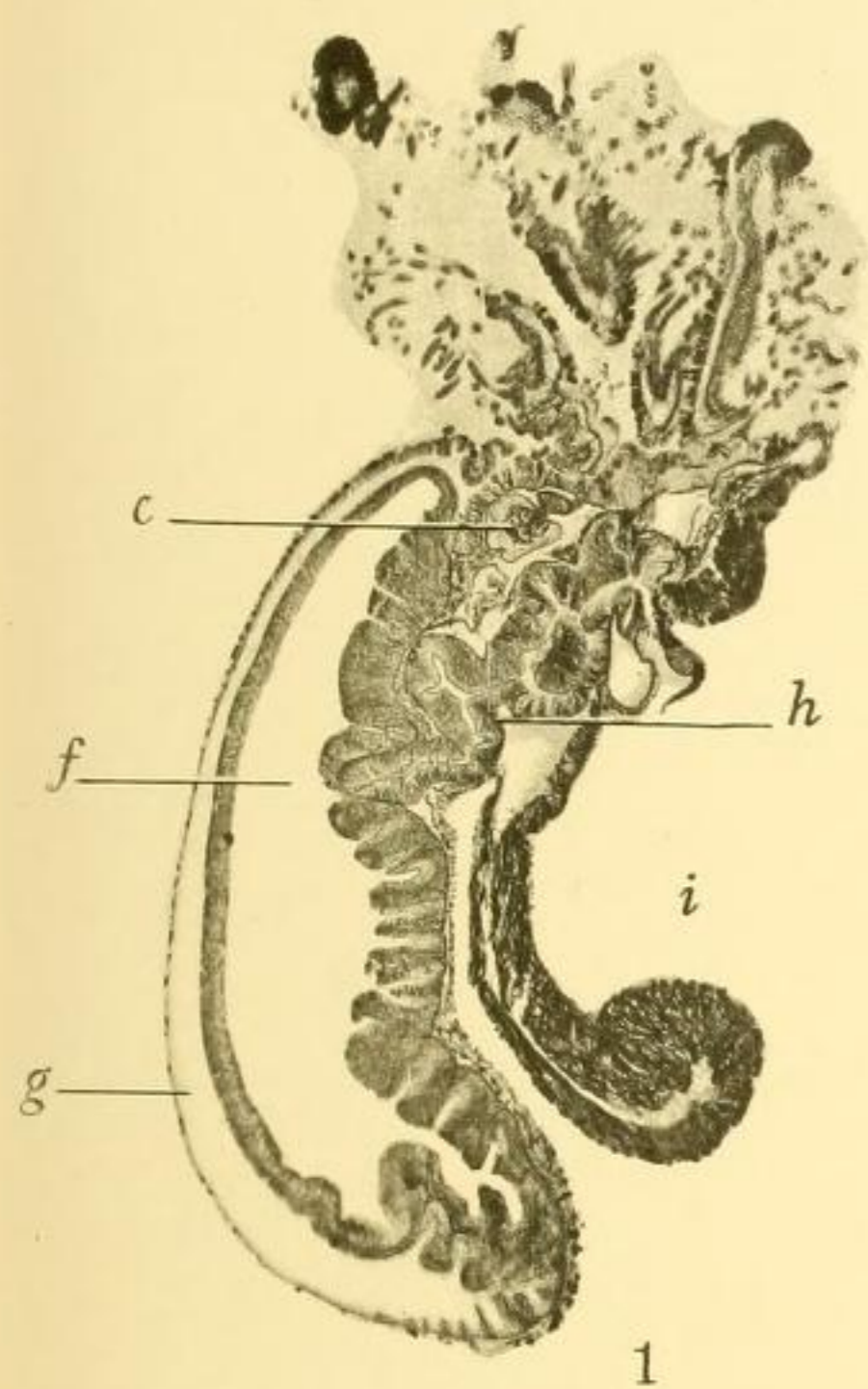
Fig. 2. *C. densus*, sagittal section, showing the refractive beads in the dorsal wall of the proboscis and arms.

Fig. 3. *C. densus*, sagittal section, showing the gill cavity and the external and internal gill openings.

Fig. 4. *C. densus*, transverse section, passing through the external gill slit.

Fig. 5. *C. densus*, transverse section passing through the gill cavity.

Fig. 6. *C. densus*, transverse section passing through the internal gill slit.



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PLATE XXXVII

a, proboscis; *b*, ganglion; *cc*, collar cavity; *ch*, cavity of heart; *cp*, collar pore; *d*, notochord; *dv*, dorsal blood vessel; *eg*, external gill-slit; *gr*, roof of gill slit; *h*, pharynx; *j*, pericardium; *jc*, pericardial cavity; *p*, *pc*, proboscis cavity; *pt*, problematic tissue; *pv*₁ and *pv*₂, pharyngeal blood vessels; *vv*, ventral blood vessel.

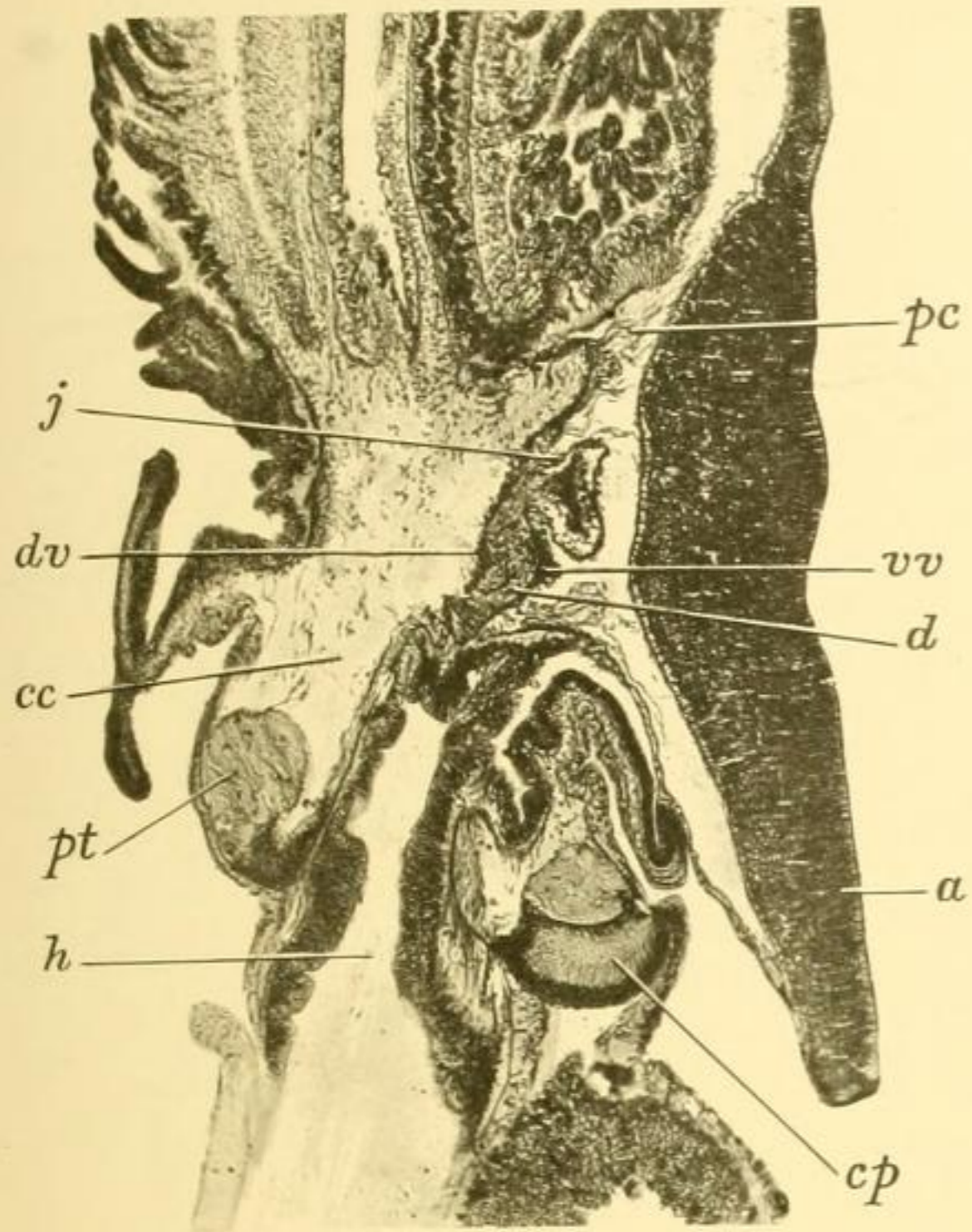
Fig. 1. *C. densus*, sagittal section through collar region.

Fig. 2. *C. densus*, sagittal section through collar region.

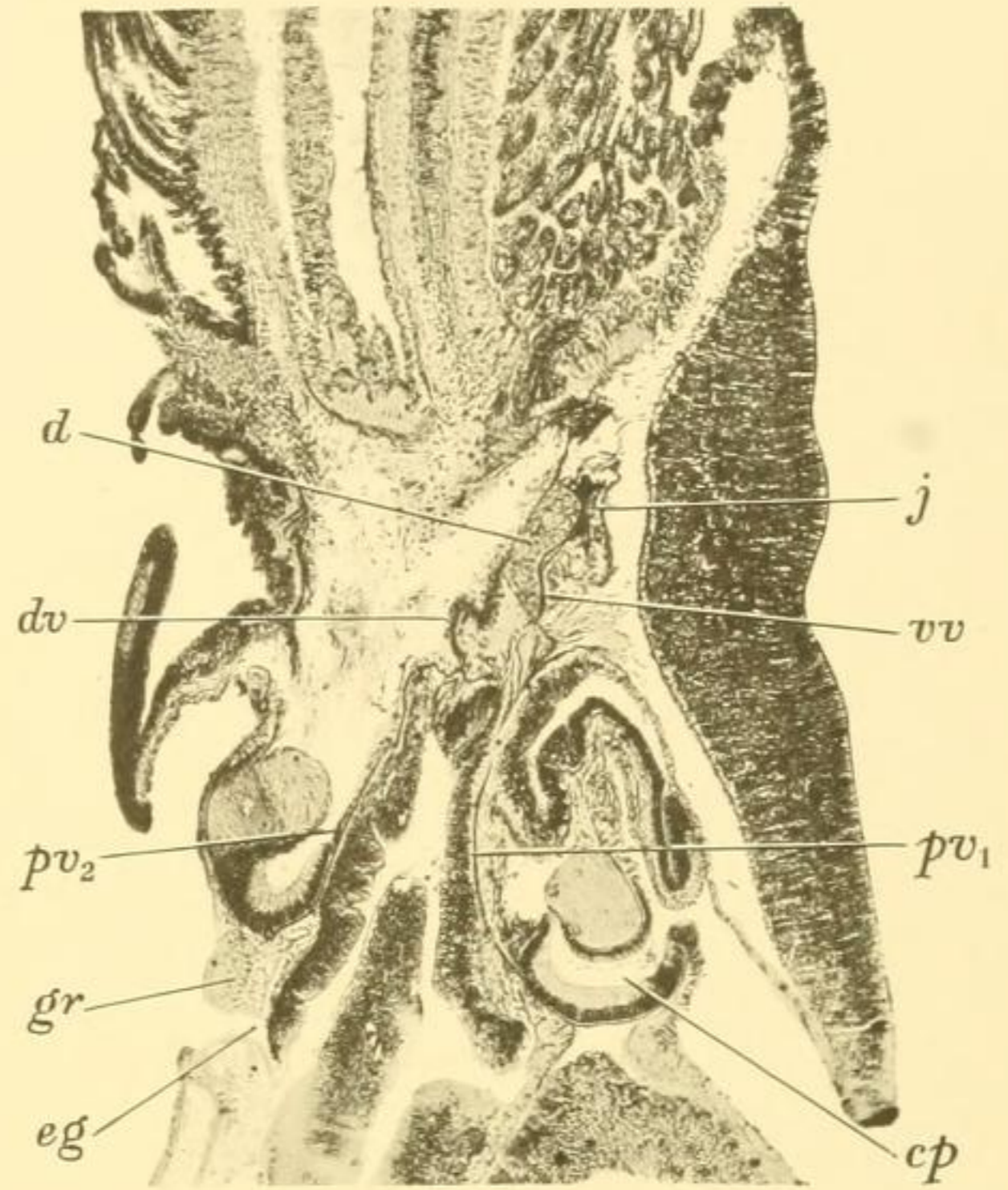
Fig. 3. *C. densus*, transverse section through the heart and pericardium.

Fig. 4. *C. densus*, transverse section of heart and pericardium.

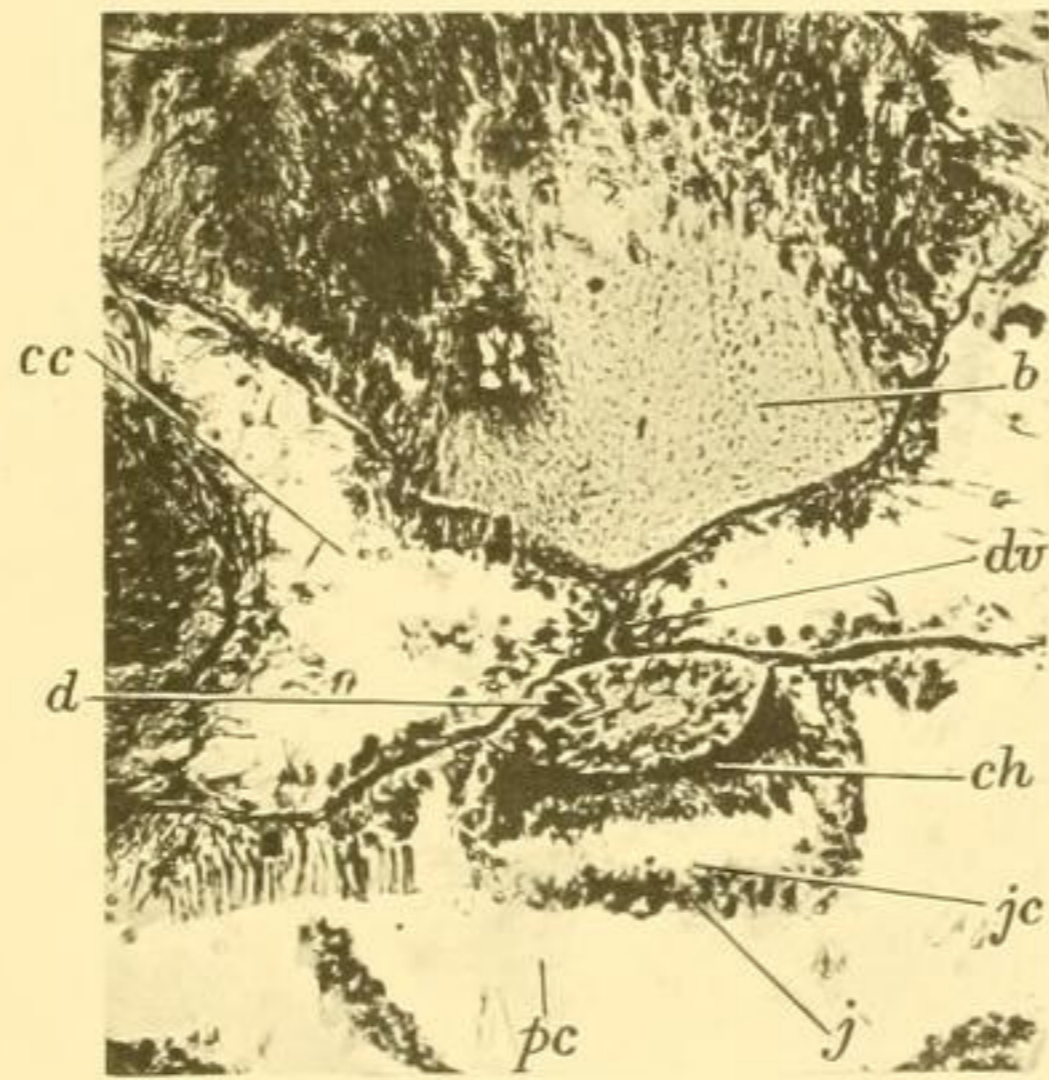
Fig. 5. *C. nigrescens*, transverse section passing through heart and pericardium.



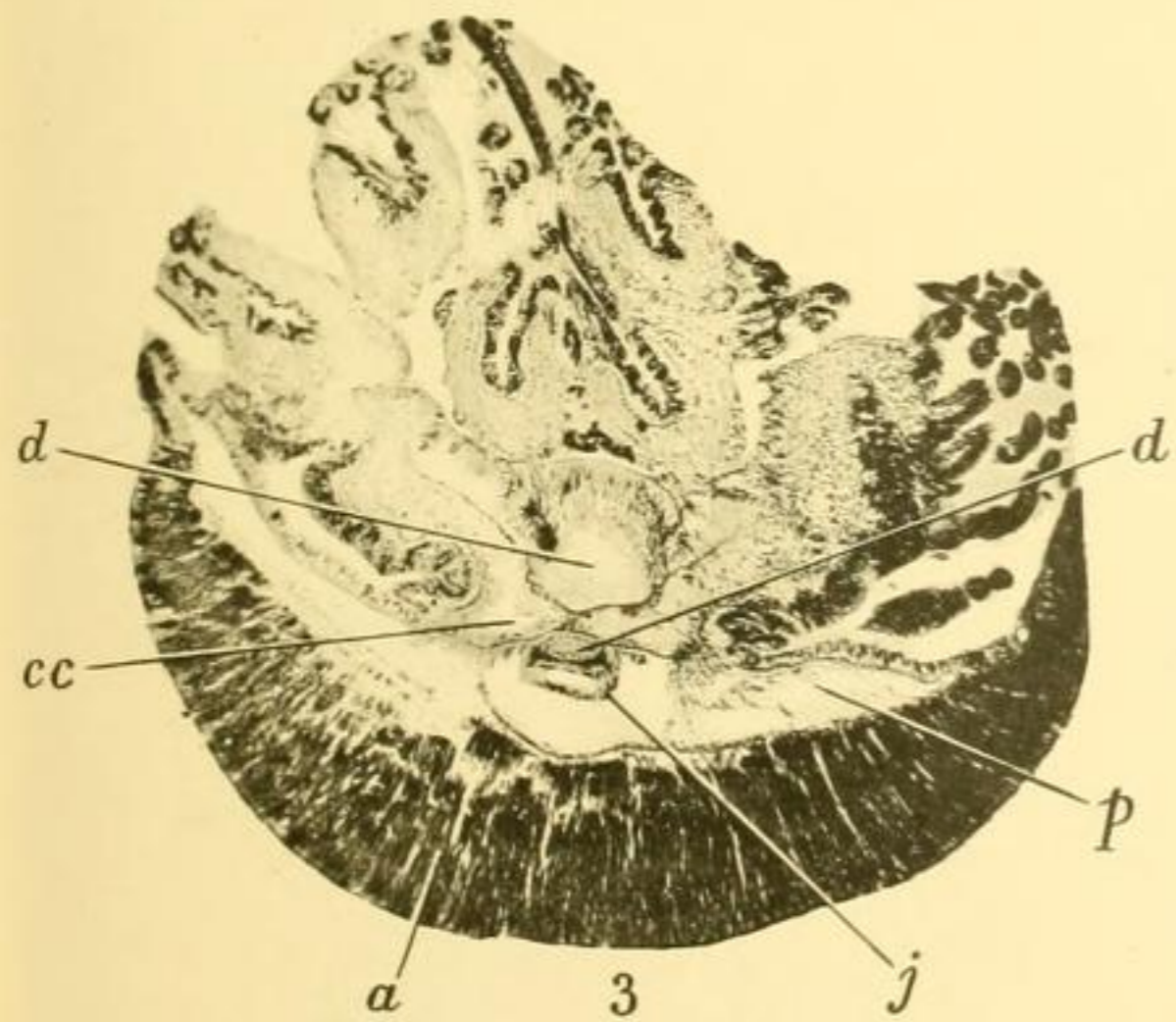
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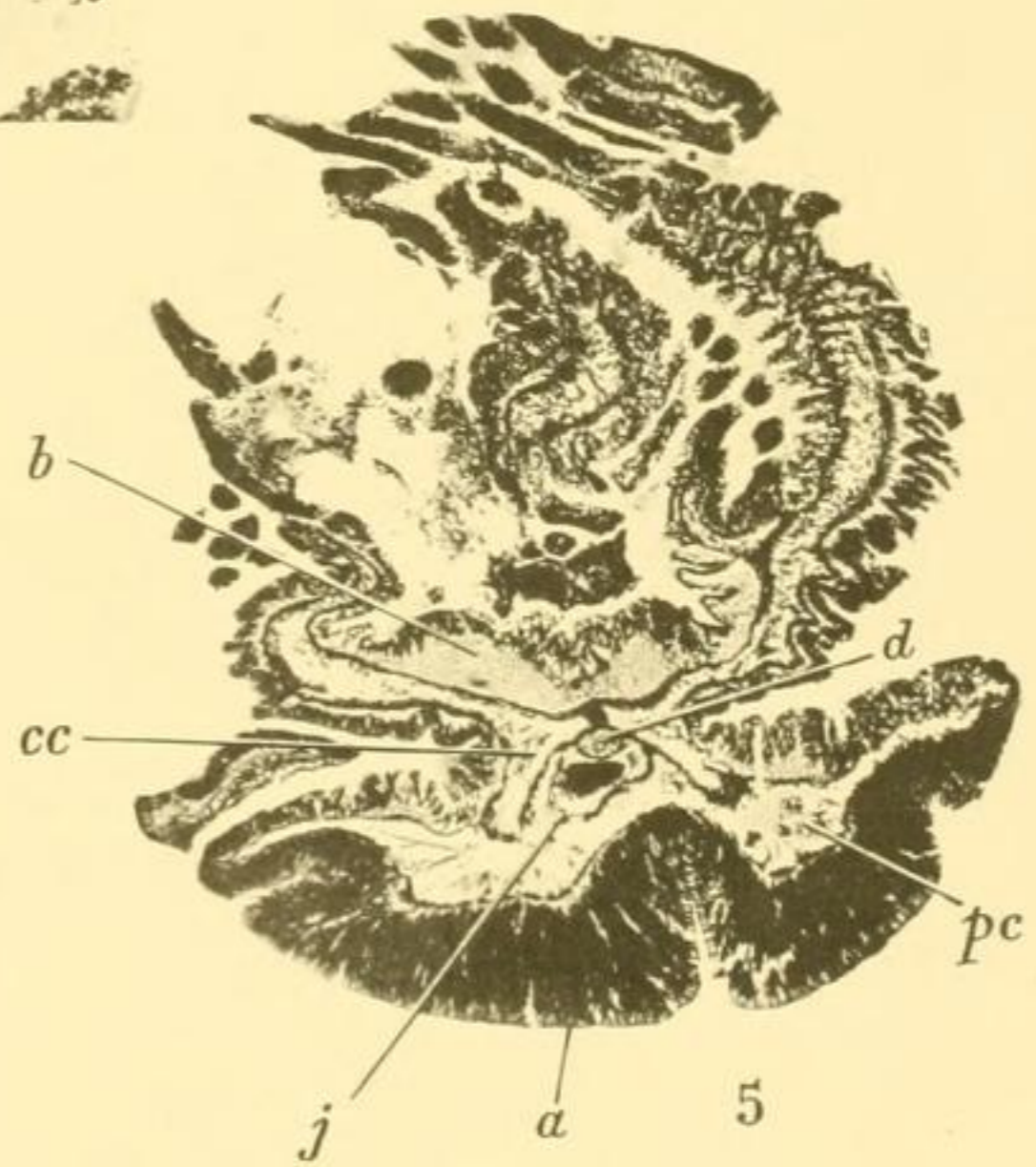
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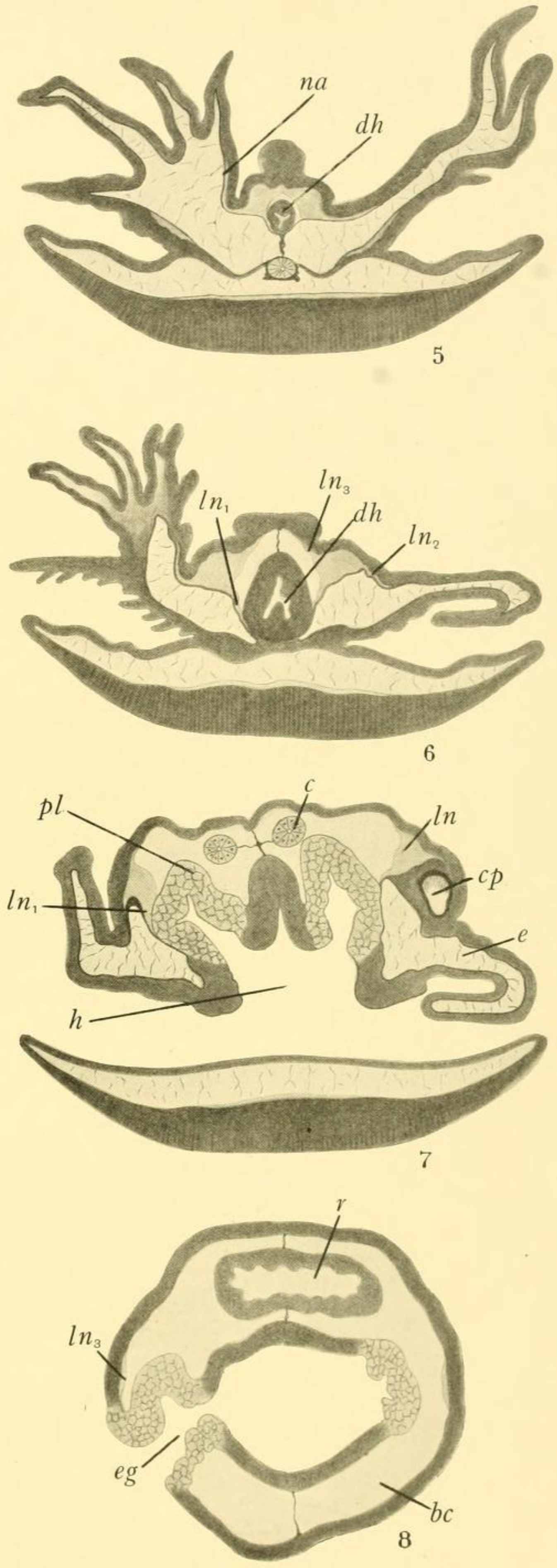
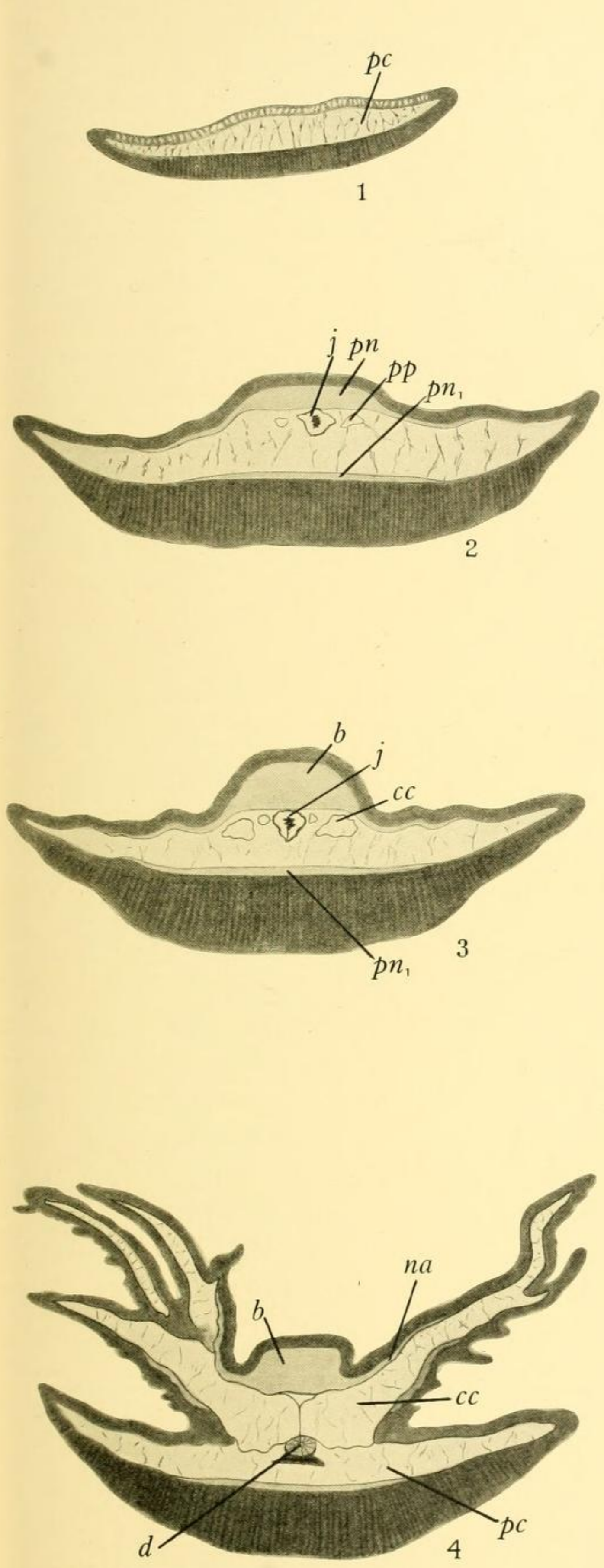
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PLATE XXXVIII

b, ganglion; *bc*, body cavity; *c*, gonad; *cc*, collar cavity; *cp*, collar-pore; *d*, notochord; *dh*, diverticulum of pharynx; *e*, post-oral lamella; *eg*, gill-slit; *h*, pharynx; *j*, heart and pericardium; *ln*, post-oral nerve; *ln*₁, nerve to pharynx; *ln*₂, nerve to post-oral lamella; *ln*₃, nerve to body wall; *na*, nerve to arms; *pc*, pericardial cavity; *pl*, pleurochord; *pn*, pre-oral nerve plexus; *pn*₁, nerve plexus in the ventral wall of proboscis; *pp*, proboscis pore canal; *r*, rectum.

Figs. 1 to 8. Series of transverse sections of *C. densus* showing the nervous system.



CEPHALODISCUS

