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ZOOLOGY

WILLIAM EMERSON RITTER

AND

CHARLES ATWOOD KOFOID

EDITORS

VOLUME 6

WITH 48 PLATES

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ZOOLOGY

Vol. 6, No. 1, pp. 1-10 October 15, 1908

CONTRIBUTIONS FROM THE LABORATORY
OF THE
MARINE BIOLOGICAL ASSOCIATION OF SAN DIEGO

XXIII

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BY
WM. E. RITTER AND SAMUEL E. BAILEY

PART I

THE POSSIBLE SIGNIFICANCE OF SUCH
INVESTIGATIONS

BY
WM. E. RITTER

PART II

PRACTICABILITY OF THE DETERMINATIONS

BY
SAMUEL E. BAILEY

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XXIII.

ON THE WEIGHT OF DEVELOPING EGGS.

BY

WM. E. RITTER AND SAMUEL E. BAILEY.

PART I

THE POSSIBLE SIGNIFICANCE OF SUCH
INVESTIGATIONS.

WM. E. RITTER.

The term senescence has been applied to widely diverse biological phenomena. Paleontologists in particular tell us about senescent species, physicians speak of conditions and diseases of senility or senescence, protozoölogists have recently had much to say about a weakening in the successive generations of pure cultures of unicellular animals; and the word also occurs not infrequently in connection with presumably normal tissues constituting the bodies of higher plants and animals. Is there any fact in all these different realms that deserves a common designation further than the fact that the longer organisms live the older they become? Are there really phenomena relating to the limitations and cessation of growth and development in departments of biology so remote from one another that may be reduced to one or a few common rules or principles?

With a view to pushing this inquiry a step further along the

course in which Professor C. S. Minot has followed it with such illumination, it has seemed to me that significant information might be obtained from weighing the same egg or a known number of eggs at different stages of development beginning with the earliest. It is probably always taken for granted that such eggs diminish in weight up to the time when extraneous food begins to be taken by the embryo. The well-known fact that the early growth processes are like physiological processes in the stricter sense, accompanied by a production of carbon dioxide, has, it would seem, generally been regarded as all the proof necessary to that effect. Since the loss from this source can tell nothing about the nitrogenous loss, this method of recognizing diminution in weight is inadequate for establishing quantitative relations between the total loss and rate of loss during a definite period of development.

I asked Mr. S. E. Bailey to see what he could do with the problem while at the San Diego Marine Station this last summer. The experiments are described in Mr. Bailey's own words. The results are meager since the time that could be devoted to the study was short. They are published not because they are regarded as of much value of themselves, but rather to show the practicability of such determinations and to give opportunity for a few reflections on the possible significance of this kind of investigations. These reflections I put in the form of questions.

Supposing the results obtained, namely, that eggs do diminish in weight from the very beginning of segmentation to the time when extraneous food is taken, to be correct, the following queries arise:

1. Since part of the loss is undoubtedly due to the consumption of energy in segmentation, is there reason to assume that any members of the egg-complex that divide automatically, *e.g.*, nucleus, chromosomes, centrosome, etc., do not share in the loss?
2. Is there reason to assume that any portion whatsoever of the egg in which the metabolic processes are going on, *i.e.*, any portion that can be counted as living, is exempt from a share in the loss?
3. If there is no good ground for making either of these assumptions, what becomes of the conception of a germ-plasm or

substance in the egg that passes on from one cell generation to the next "without break in continuity?"

4. In case it be held that one or both of the assumptions indicated in 1 and 2 are justifiable, is it not true that due regard for the principles of conservation of energy and matter puts such assumptions in the category of those hypotheses that are justified only by being made to be themselves tested, *i.e.*, that cannot be legitimately used as supports for other still wider hypotheses until they themselves shall have been proved?¹

5. Since the egg is surely a body of limited mass, must it not also be a body of limited potential energy? If this be so, and if development is from the outset an operation performed through the auto-consumption of both matter and energy that reaches to the fundamental metabolic processes, can there ever be complete restoration of the living material in the developing organism even after extraneous food is supplied?

6. If a diminution in weight up to the time of food-taking be an essential phenomenon in the development of the organism, what would be the form of curve that would represent the relation between the amount and rate of diminution? Would this curve be the same for all organisms? Would it have any necessary relation to the normal length of life of the particular organism?

There is apparently no end to the questions of this general tenor that might be asked, but beyond such as offer points of attack through observation and experiment, they are of doubtful profit. It would seem, however, that with those which do offer such points biologists might well occupy themselves.

From a methodological standpoint I would call particular attention to two facts in connection with such experimentation. (1) The nature of the problems aimed at demands that both the organisms and their conditions be kept as nearly normal as pos-

¹ Since preparing this manuscript it has been suggested by some of my biological friends to whom I have propounded these questions that I am "demanding too much" as regards the hypothesis of a continuous germplasm. My reply is that so far at least as this little paper is concerned I am in both letter and spirit, merely asking questions. There is only one "demand" even implied. That is that in biology we shall recognize *observation* and *generalization* to be bound together in a wedlock so sacred and indissoluble that no offense can in reality sever them.

sible throughout the experiments. So large a part of experimental work in biology, especially when developmental problems are concerned, is based first and foremost either on an initial mutilation of the organism or a radical disturbance of its natural surroundings, that it seems as though experimentation of the reverse sort ought to be attempted more than it is. Not that the interference type of experiment should be done away with; but the question of "fair play" would seem to come in. The organism ought to have a chance to reveal to us what it does habitually, that is, normally, as well as what it may do under exceptional circumstances. (2) The other fact to which special attention should be called comes out most conspicuously in the last question contained in number 6, *i.e.*, would there be any constant or necessary relation between the rate of loss of weight in the developing egg and the normal length of life of the organism? The special point here is the closeness with which the whole life-cycle of the organism would be linked together by such an inquiry. This seems to me important. For a number of years the conception of the "organism as a whole" appears to have been gaining a foothold in biology. So far, however, as I am aware, the idea has had sole reference to the organism at this particular moment or for a particular phase of its life; to particular equilibrational states, as one might say. It has been a *spatial* matter alone. Now the query is, Is there such a thing for scientific biology as a *life-cycle as a whole*? That is, are there qualitative and quantitative differentia within the same cycle, and as between different cycles, that one may get at by observation? Can the conception "organism as a whole" be extended to existence *in time* as well as to existence *in space*?

The problem certainly deserves wider and more rigid examination than it has had. Despite its obvious complexity it is not altogether unapproachable by experiment, as Minot's work in particular shows, and as does also this little contribution. The conception of a *continuous substance* known as *germ-plasm* and held to be "the carrier" of *heredity*, has undoubtedly been of great use to biology as a "working hypothesis." I am, however, of the opinion that its day of usefulness has passed and that it is now standing seriously in the way of sound progress. I be-

lieve it is inducing us either to overlook entirely or to view as insignificant vast multitudes of seemingly detached facts that might be measured by balance and rule, mathematically treated, and so reduced to "law and order" and thus shown to be significant facts in the life of the organism as a whole.

PART II.

PRACTICABILITY OF THE DETERMINATIONS.

BY

S. E. BAILEY.

The variation in the weight of eggs during segmentation and development has for some time been a subject of more or less interest and speculation. With a view to gaining more light on this subject, Professor Ritter asked me to try to make some direct determinations of this variation while I was at the San Diego laboratory this summer. As will be seen, my results are not in any way complete. I have simply made it obvious that experiments of this nature are practicable—that the technique of serial weighings of developing eggs is, for some kinds of eggs at least, a comparatively simple matter.

My problem was in substance this: 1. To find some hardy eggs which could be ensemated and allowed to develop under known conditions. 2. To find some method by which these eggs could be weighed accurately from time to time. To accomplish these objects various precautions were necessary. The eggs could not be dried before weighing and so had to be weighed in water. At first I experimented with the eggs of the ascidian *Ciona intestinalis*, and then with those of the starfish *Asterias tuberculata*. Great difficulty was encountered in handling them. They were too small and numerous to be counted easily and quickly, and one could never feel sure that some had not been lost from weighing to weighing. When kept in small silk nets, the eggs, net and all being weighed, other difficulties were encountered. The nets alone varied in weight from gradually soaking up water and accumulating dirt, and besides some eggs, not getting properly

aerated, died. At last I hit upon teleostian eggs that could be easily manipulated: Those of the California mud-fish, *Fundulus parvipinnis* were used.

It will not be too much of a digression to give a few notes on the breeding habits of the fish in the interest of future work with these eggs: *F. parvipinnis* exhibits marked sexual dimorphism. The males are apt to be slightly larger than the females though both sexually mature animals vary considerably in size (6.5-10.5 cm. for males, and 6.25-10.0 cm. for females). The females are of a silvery color with no dark bars, while the males are darker with brassy coloration on the fins and tail and several transverse black bars along the sides of the body. In captivity at least the males are cannibalistic and devour immediately any eggs laid by their consorts, so it was found best to keep the sexes separated. The fish are very hardy and may be kept indefinitely in aquaria without difficulty. Both males and females can be easily stripped and the eggs ensemminated either by the dry or wet method, although I got the best results with dry milt and believe this is the method generally used in large fish hatcheries.

The spawning season is evidently rather short. On July 8 I seined in Mission Bay and took over 200 fish. With a very few exceptions all were ripe and there was no difficulty in obtaining eggs and milt. On July 15 I seined again. Of the 262 animals taken (165 males and 97 females) with the exception of eight males, none were ripe.

The eggs are spherical, a light golden yellow in color and 0.28 cm. in diameter. In each egg there is a large oil drop which keeps constantly at the top of the egg. Just on the edge of this oil drop, or lying partially beneath it, is the germinal disc. When first stripped the eggs are soft and easily broken, the investing membrane being thin and readily ruptured. Ten to fifteen minutes after ensemmination the same eggs can be handled with a pipette or even lifted with forceps and are fairly resistant. As mentioned above I was unsuccessful in getting a second supply of eggs. The first lot obtained had developed until the heart had begun to beat and the eye and ear vesicles were noticeable before I mastered the technique of weighing. The blastodisc had spread over the whole yellow yolk mass, carrying with it droplets of the

large oil drop noted in fresh laid eggs. Of this first lot, moreover, a large percentage had died from the attacks of bacteria or other organisms. With the few remaining I carried on the experiment, so the results are in no way complete.

The method of weighing was as follows: The eggs were counted and each lot kept in a separate dish supplied with running sea-water which had been filtered through No. 20 silk bolting-cloth to remove dirt and small organisms. Each day the eggs were counted out into a beaker of filtered sea-water which had been warmed to 27 C. and allowed to cool to 25 C. After remaining here a few moments for the whole to come to constant temperature, the eggs were transferred to the weighing tubes by means of a large mouthed pipette.²

The tubes were immediately weighed to tenths of a milligram and the eggs at once returned to the hatching dishes. The tubes were thoroughly rinsed in distilled water and dried in a calcium chloride dessicator until the next weighing. Obviously the method of weighing in sea-water would show variation in weight only where the material lost or taken up had a specific gravity different from that of the water. The following is a table of the weighings made:

² I made these tubes by sealing a piece of thin glass tubing at one end and fastening it upright to a cover-glass with a bit of warmed paraffin. The open end of the tube was ground and provided with a small cover-glass. The eggs and sea-water were carefully introduced until the water came just to a level with the open end of the tube; then, by closing off with the cover-glass, a constant volume was obtained for each weighing.

TABLE I.
 Weighings made of Eggs plus water at Constant Volume at 25° C.

	SERIES A—55 eggs Enseminated July 10, 10 a.m.				SERIES B—28 eggs Enseminated July 8, 6 p.m.				SERIES C—10 eggs Enseminated July 9, 3 p.m.			
	Interval	Wgt. gms.	Loss	Gain	Interval	Wgt. gms.	Loss	Gain	Interval	Wgt. gms.	Loss	Gain
7/20 11:53 a.		8.3783		10:30 a.		8.0674		9:54 a.		5.6804		
3:15 p.	3½ hrs.	8.3729	.0054	4:40 p.	6 hrs.	8.0624	.0060	3:55 p.	6 hrs.	5.6793	.0011	
7/21 10:45 a.	19½ "	8.3726	.0003	10:25 a.	17½ "	8.0590	.0034	11:10 a.	19½ "	5.6779	.0014	
3:25 p.	4½ "	8.3718	.0008	2:20 p.	4 "	8.0663		3:35 p.	4½ "	5.6763	.0016	
7 22 5:20 p.	26 "	8.3701	.0017	5:30 p.	27 "	8.0610	.0053	5:45 p.	26 "	5.6720	.0043	
7/23 9:30 a.	16 "	8.3710		11:00 a.	17½ "	8.0609	.0001	10:10 a.	16½ "	5.6622	.0098	
4:30 p.	7 "	8.3735	.0025	4:55 p.	6 "	8.0558	.0051	4:40 p.	6½ "	5.6764	.0142	
7 24 3:30 p.	23 "	8.3710	.0025	4:15 p.	23½ "	8.0600		4:00 p.	23½ "	5.6761	.0003	
7/25 11:25 a.	20 "	8.3715	.0005	11:45 a.	19½ "	8.0632	.0032	12:00 m.	20 "	5.6789	.0028	
4:30 p.	5 "	8.3699	.0016	5:00 p.	5½ "	8.0621	.0011	5:10 p.	5½ "	5.6777	.0012	
7 27 9:45 a.	41½ "	8.3717	.0018	9:50 a.	41 "	8.0589	.0032	9:15 a.	40 "	5.6775	.0002	
7/28 9:20 a.	24½ "	8.3716	.0001	9:00 a.	23 "	8.0669	.0080	8:55 a.	23½ "	5.6740	.0035	

As is seen by the table, with few exceptions the eggs lost gradually in weight, and I believe these exceptions to be due to errors in manipulation and to dirt which got on the eggs in spite of the filtering and which could be seen even with the naked eye. (The sea-water was full of micro-organisms which clogged the filters and continually passed through onto the eggs.) When the weighings were brought to a close, the animals were still several weeks from hatching, and *their mouths had not yet opened*. The investing membrane was intact so no solid material could have gotten in from the exterior or passed out from the interior of the eggs. The loss in weight must have been due to carbon dioxide (CO₂) and organic salts representing the albuminoid loss, which had passed out through the egg-membrane and been washed away in the sea-water.

R. Pott³ gives some figures on the weight of hen's eggs at different hours of brooding. I reproduce a portion of one of his tables to show the general similarity of the results, *viz.*, a gradual loss of weight as a whole as development proceeds.

TABLE II.

Hours of Brooding	Wt. of Eggs
24	51.39
48	51.11
54	47.71
58	47.56
91	45.28
96	46.21
124	46.70
264	48.08

TABLE III.

Hours of Brooding	Wt. of Dry Substance	Wt. of Water
24	17.67	33.18
48	17.96	32.45
54	19.26	27.35
58	19.60	26.59
91	18.96	26.00
96	18.36	26.58
124	17.29	26.51
264	20.72	26.69

³ Untersuchungen über die chemischen Veränderungen im Hühnerei während der Bebrütung. Die landwirthsch. Versuch-Station, Bd. XXIII, 1879, pp. 203-247.

However he indicates an increase in the weight of dry substance, Table III. This may be explained by the fact that water taken up in the metabolism of development is probably chemically combined with the proteins, forming new chemical compounds of greater weight. However, *the discrepancy between Pott's results and those here recorded certainly needs further experimental examination.*

In conclusion, it is suggested that similar weighings of large holoblastic eggs, as for example those of amphibians, where the work done in cleavage must be considerable, might be especially interesting could these be quantitatively compared with similar weighings of eggs of rather closely related species but having meroblastic cleavage.

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THE LEPTOMEDUSAE OF THE
SAN DIEGO REGION

BY

HARRY BEAL TORREY

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BY

HARRY BEAL TORREY

The Leptomedusae of the San Diego region are represented in the collections of the Marine Biological Association of San Diego by eleven species which, with one exception, *Acquorea coeruleascens* (Br.), appear not to have been previously described. This unusual proportion of new species is to be accounted for largely by the fact that of the few papers concerned with Pacific Coast medusae none deal with the medusae of the San Diego region. Fewkes (1889) collected a few species at Santa Barbara, but no Leptomedusae. Chamisso (1821) collected but one medusa, *Aurelia labiata*, in California waters. Esehsholtz (1829) obtained two Leptomedusae, *Polyorchis penicillata* and *Acquorea ciliata*, on the Pacific Coast between 41° and 51° N. Lat. Agassiz (1865) found no Leptomedusae except *Polyorchis penicillata* south of the Gulf of Georgia. Murbaeh and Shearer (1903) described six Leptomedusae, namely, *Thaumantias cellularia*, *Polyorchis minuta*, *Proboscidactyla brevicirrata*, *Phialidium languidum*, *P. gregarium* and *Mesonema victoria*, from British Columbia. Maas (1897) recorded three Leptomedusae from the Gulf of Panama. Two of these are unknown here. The third,

Melicertum proboscifer Maas, may be identical with a Thaumantiid in the collection of the U. S. S. *Albatross* in 1904 on the California coast, to be considered in a later paper. The *Albatross* collected at the same time three species described in the present paper as *Scrippsia pacifica*, *Irene mollis* and *Tiaropsis* (*Tiaropsidium*) *kelseyi*, extending the range of the latter to Monterey, California. The type specimens of *A. coerulescens* (Brandt, 1838) were collected by Mertens in 1827, about 1600 miles west of San Diego. Brandt's paper describing and figuring Mertens' collections completes the list of papers dealing with Pacific Coast Leptomedusae.

Among the latter, those of the San Diego region form at present a well isolated group, whose relationships to other groups will be discussed later in connection with the other medusae of the region. Following is the list of species arranged by families:

- Thaumantiidae** *Ptychogena californica*, n. sp.
Polyorchidae *Scrippsia pacifica*, n. gen., n. sp.
Mitrocomidae *Mitrocoma discoidea*, n. sp.
Tiaropsis (*Tiaropsidium*) *kelseyi*, n. subgen.,
n. sp.
Eucopidae *Obelia purpurea*, n. sp.
Phialium bakeri, n. sp.
Phialidium loma, n. sp.
Phialopsis diegensis, n. gen., n. sp.
Eutimalphes brownei, n. sp.
Irene mollis, n. sp.
Aequoreidae *Aequorea coerulescens* (Brandt).

The hydroids for none of these species are definitely known.

LEPTOMEDUSAE Haeckel, 1866.

Craspedote medusae with gonads on radial canals, sense organs usually velar statocysts, in some forms ocelli and sensory clubs or cordyli. Non-sexual generation calyptoblastic hydroids.

Fam. THAUMANTHIDAE Gegenbaur, 1856.

Leptomedusae without statocysts; with numerous tentacles, usually bearing ocelli on their bases, cordyli (sensory clubs) between them; radial canals unbranched.

Gen. **Ptychogena** Agassiz, 1865.

Thaumantiidae with four radial canals which bear gonads in the form of transverse folds. Mouth central; no gastric peduncle. Tentacles without ocelli. Cirri absent.

Ptychogena californica, n. sp.

Figs. 1, 2.

Umbrella moderate, more than half as high as broad. Manubrium short, with thin walls; mouth large, without lobes. About 48 large tentacles with thickened, compressed bases and slender filaments. Between every two tentacles, 1-5 cordyli on prominences of varying size, resembling the bases of small tentacles.



Fig. 1.—*Ptychogena californica*. Camera drawing of a preserved specimen. $\times 4$.

Gonads with 12-14 folds in the proximal half of each canal.

Diameter 10 mm.

Distribution.—Off San Diego, May 31, 1904, in a vertical haul from 210 fathoms. Acc. No. 45.

Two specimens only have been collected; they are of the same size, with immature gonads. The cordyli resemble club-shaped filaments of tentacles in an arrested state of development (fig. 2). Each cordylus arises from a base of varying height somewhat within the row of tentacles, yet between the latter. Neither tentacles nor tentacle filaments are in good histological condition. The former, however, appear to be typical, with large, non-

pigmented endoderm cells and no nematocysts in the ectoderm, presenting a definite contrast with the tentacles in these respects. The cordylar bases grade in shape and structure into tentacle bases, and are grouped according to size like developing ten-

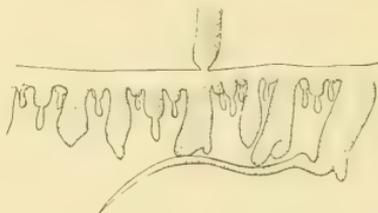


Fig. 2.—*P. californica*. Portion of the margin enlarged, showing tentacle bases and cordyli.

tales, the middle one of a group of three being the largest. The cordyli spring from the inner angle of their rather obtuse distal ends, like tentacle filaments. Structurally I have not been able to establish a transition between them and the latter.

The presence of raised bases for the cordyli in *P. californica* is exceptional among the species of *Ptychogena*. The resemblance of these bases to tentacle bases suggests a comparison with *Staurophora*, where, according to Hartlaub (1897), the cordyli develop into tentacles.

FAM. POLYORCHIDÆ A. Ag., 1862, *s. em.*

Leptomedusae with deep bells, four radial canals with numerous blind lateral branches, some or all of which may project as long tubular gonads into the subumbrellar cavity; tentacles numerous, hollow; ocelli present.

Gen. **Scrippsia**, n. gen.

Polyorchidæ with gastric peduncle, lateral branches of the radial canals in the form of numerous long tubular gonads from the peduncular portion of each radial canal; tentacles numerous in several cycles.

This genus may be distinguished from its nearest relative, *Polyorchis*, by the gastric peduncle and the absence of pinnately arranged branches of the radial canals distal to the gonads.

***Scrippisia pacifica*, n. sp.**

Fig. 3.

Umbrella deep, bell-shaped, with slight apical prominence, about as broad as high, broadest near margin. Gastric peduncle

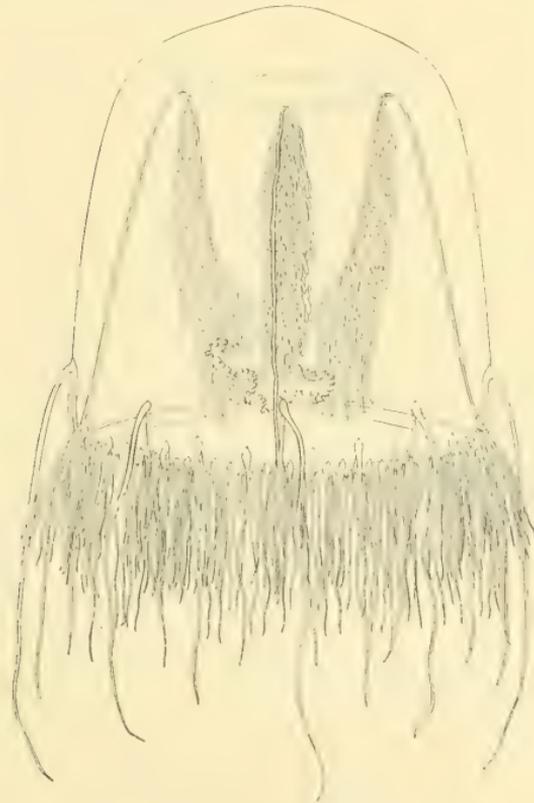


Fig. 3.—*Scrippisia pacifica*. $\times 1$.

moderate. Tentacles long, highly contractile, in 7 cycles: 4, 4, 8, 16, 32, 64, 128; those of first cycle leaving exumbrella about stout, broadly conical, more than half the height of the subumbrellar cavity. Manubrium short, with moderate, frilled lips. Gonads 30 to 60 on each radial canal, long, narrow. Velum

one-fifth the distance to apical pole from margin, other cycles successively nearer margin. Ocelli on bases of the tentacles of the last two cycles. Manubrium, gonads and tentacles pale yellow; canals yellow, occasionally carmine.

Full-grown individuals about 75 mm. high.

Distribution.—Surface at La Jolla, California. Acc. No. 1279. California coast to San Francisco.

This is one of the largest and most beautiful of the Hydro-medusae. The closeness of its relationship to *Polyorchis* is shown not only by the character of the gonads and occasional traces of lateral branches of the radial canals distal to the gonads, but by the presence of an individual in the collection with well-developed lateral branches on each radial canal between margin and gonads, showing that this *Polyorchis* character may be perfectly adopted by a sudden individual variation. Such a variation is, however, exceedingly rare. It may be interpreted as the appearance of a latent rather than a new character.

The gastric peduncle is well developed in the smallest individuals (8 mm. high) in the collection. There is, however, a gradual increase in its size with the growth of the individual and a corresponding shortening and thickening of the manubrium, which is long and slender in the 8 mm. individuals where it may project from the bell cavity. The general resemblance to *Polyorchis* is especially striking in these young forms.

In 1894, a single large individual was collected at the surface in the harbor of Oakland, California, where *Polyorchis penicillata* was formerly common. The U. S. S. *Albatross* obtained a considerable number of large specimens in 1904 from Monterey Bay, in dredge hauls from 19 to 86 fathoms.

Fam. MITROCOMIDAE Haeckel, 1880, *sens. em.*

sens. Lafoeidae Maas, 1905.

Leptomedusae with large open statocysts.

Metschnikoff (1886) obtained from the eggs of both *Laodice* and *Mitrocoma* very similar hydroids with the characters of *Cuspidella* Hincks. For this reason, he regarded both genera of medusae as Lafoeidae, the family in which, according to Hincks, *Cuspidella* should be placed. Owing to the striking differences

between their marginal sense organs, however, such an association of these genera appears to be rather artificial. Recognizing this fact, Maas has removed *Laodice* to the Thaumantiidae. He has retained the family Lafoeidae, but redefined it so as to include all Leptomedusae with large open statocysts, viz., *Mitrocoma* Haeckel, *Tiaropsis* Ag., *Phialis* Haeckel and *Halopsis* Ag.

This group of genera appears to be natural, but to refer it to the family Lafoeidae is open to objections. (1) That family is based on a genus of hydroids that produces no free medusae, hence does not possess the characters of the family as defined by Maas. (2) It is not clear that *Cuspidella* is as closely related to *Lafoca* as it is to *Calycella* and *Campanulina*, members of another family of hydroids; the discovery of its hydroid form, therefore, does not serve to place *Mitrocoma* definitely among the Lafoeidae. (3) Both *Laodice* and *Mitrocoma* produce generically identical hydroids. Yet they are placed in different families by Maas, as, in my judgment also, they should be.

In the light of these facts, a new family is needed for the four genera under discussion, with a genus of medusae, not hydroids that lack medusae, as type.

As such a genus, *Mitrocoma* appears to be unobjectionable, the family name becoming Mitrocomidae. Haeckel (1880) used this designation in a schema on p. 163 for all his Eucopidae without gastric peduncles, which artificial group contained *Tiaropsis*, *Phialis* and *Mitrocoma*. The existing term, then, removed from the Eucopidae with the genera just mentioned, seems, with a new characterization, to satisfy the present requirements.

Gen. **Mitrocoma** Haeckel, 1864.

Mitrocomidae with numerous open statocysts, numerous tentacles and marginal cirri, and four radial canals; no gastric peduncle.

Mitrocoma discoidea, n. sp.

Fig. 4.

Umbrella flat, three to four times as broad as high. Manubrium small and short, with four narrow, ruffled oral lobes. Tentacles 180-240, swollen at the base. Statocysts 20-60, scattered, with numerous statoliths in 2-3 rows. Marginal cirri

readily lost, may be as numerous as tentacles. Gonads narrow, almost entire length of radial canals from margin. Ring canal yellow-green; bases of tentacles purple; edges of lips with a single row of delicate purple spots.

Largest 45 mm. in diameter.

Distribution.—In numerous surface hauls off San Diego, May-July.

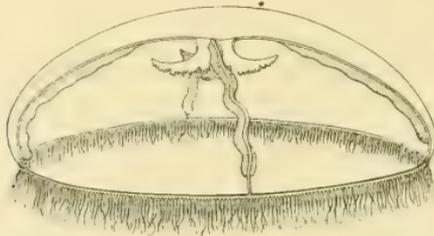


Fig. 4.—*Mitrocoma discoidea*. Slightly enlarged.

The cirri vary greatly in number, being rather more numerous in the young. Medusae with 32 tentacles may have two cirri between adjoining tentacles, though usually but one. In well-grown individuals they are usually fewer in number than the tentacles, and in many adults almost entirely wanting.

The statocysts vary much in number, but never exceed sixty and are usually nearer twenty. Occasionally two are found side by side, dividing between them the usual number of statocysts, apparently a result of fission.

Gen. **Tiaropsidium**, n. gen.

With 8 open statocysts, each with an ocellus at its base; with two kinds of tentacles; without marginal cirri and gastric peduncle.

Maas (1905) has called attention to the fact that the existing species of *Tiaropsis* are not of equal value. *T. diademata* Ag., *T. multicirrata* Sars and *T. Davisii* Browne are characterized by tentacles of but one kind. *T. mediterranea* Metseh., *T. punctata* Mayer, *T. rosca* Ag. & M., Maas' species (which he identifies provisionally with *T. rosca*) and the San Diego species are all characterized by tentacles of two kinds, four or eight large and a varying number of much smaller, more or less rudimentary tentacles between them.

I believe these clearly marked groups should be distinguished provisionally as genera. The first will then retain the name of the original genus. For the second, the name *Tiaropsidium* is proposed, *T. kelseyi* to be its type.

***Tiaropsidium kelseyi*,¹ n. sp.**

Fig. 5.

Umbrella moderate, about three times as broad as high. Manubrium small, short, with thin walls and slightly frilled lips. Four large perradial and 4 similar interradial tentacles with

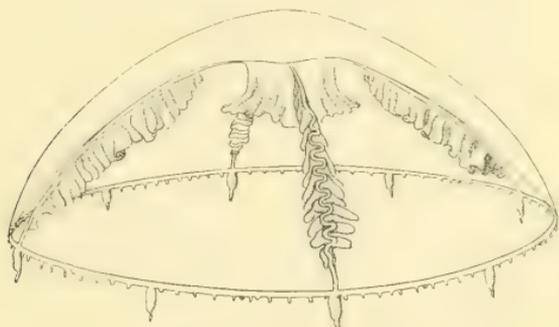


Fig. 5.—*Tiaropsidium kelseyi*. Slightly enlarged.

bulbous bases. Between each adradial sense-organ and the adjoining large tentacle on either side, 3-5 small tentacles. Gonads narrow, much folded in larger specimens, along entire length of radial canals. Umbrella colorless, transparent; manubrium, canals, gonads and tentacles a faint yellow.

Diameter 50 mm. in larger adults.

Distribution.—Single individual obtained in vertical haul from 200 fathoms, July 12, 1905, off San Diego. Acc. No. 1005, 30 mm. diam. A much damaged individual 45 mm. diam. obtained June 19, 1908, in trawl, from 50-100 fathoms. Many individuals, most of them badly damaged, obtained in numerous deep dredge hauls between San Diego and Monterey, California, by U. S. S. *Albatross* in 1904. The largest of these specimens are

¹ Named for Mr. F. W. Kelsey of San Diego, Secretary of the Marine Biological Association.

about 50 mm. in diameter. The gonads may fold transversely in a manner to suggest the gonads of *Ptychogena*.

Fam. EUCOPIDAE Gegenbaur, 1856.

Leptomedusae with closed statocysts and 4, rarely 5 or 6, unbranched radial canals.

Gen. *Obelia* Per. & Les., 1809.

Eucopidae with many short, non-contractile tentacles; eight statocysts on the inner side of the bases of adradial tentacles; gastric peduncle and marginal cirri wanting; velum rudimentary.

Obelia purpurea, n. sp.

Fig. 6.

Umbrella very thin and flat. Manubrium small, cylindrical or angular according to state of contraction, with four simple

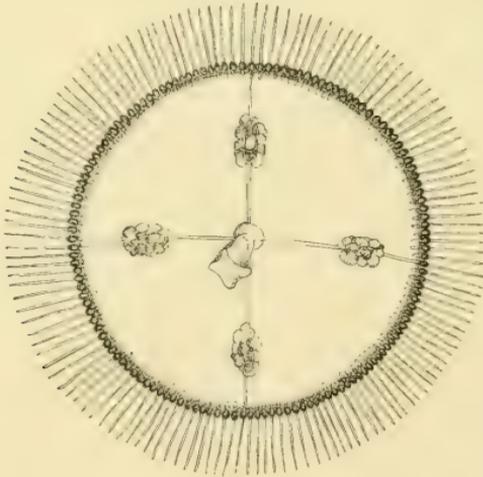


Fig. 6.—*Obelia purpurea*. $\times 18$.

oral lobes. Tentacles 110-160, one-fourth to one-third the diameter of the umbrella in length. Statocysts each with single otocyst. Gonads broadly ovate, one near middle of each radial canal, usually in distal half. Manubrium, canals and gonads yellow, bases of tentacles violet-purple.

Diameter 3-4 mm.

Distribution.—Off San Diego in winter and summer, at the surface and in vertical hauls from various depths to 160 fathoms.

This species resembles *O. dichotoma* and may prove to be the medusa from the hydroid in this region that I have identified with the European *O. dichotoma*.

Gen. **Phialium** Haeckel, 1880.

Eucopidae with 12 statocysts, 4 periradial tentacles with basal cirri, gastric peduncle wanting.

Phialium bakeri, n. sp.

Fig. 7.

In an earlier paper (1904, p. 16), I described from preserved material, under the name of *Clytia bakeri*, a hydroid whose gonophores within the gonangia were seen to possess two tentacles and the stumps of two more (though owing to an oversight in reading proof the gonophores were described as sporosacs). The next summer, colonies of this species discharged, in the laboratory, medusae of the following description:

Umbrella longer than broad, very thin, without gastric peduncle. Manubrium moderate, tapering, without oral lobes. Two tentacles 3-4 times the length of umbrella, with bulbous bases, at ends of opposite radial canals, each with a pair of long basal cirri; tentacular fundaments in connection with other radial canals. Four interradial statocysts, each with a single statolith. Broad velum. Ovate gonad from about the middle of each of the canals associated with the longer tentacles.

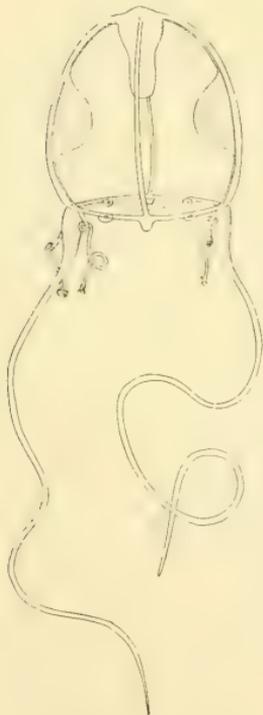


Fig. 7.—*Phialium bakeri*.
× 82.

I have not been able to connect this immature medusa definitely with any adult of these waters. It is almost identical with Fewkes' (1882) description and figures (19 and 20) of the young of *Phialium duodecimale* Haeckel. The chief difference consists in the presence of two gonads in the San Diego form. Specimens of adult *Phialium* have not yet been found near San Diego. The interradial position of the statocysts of the young prevents an easy transition to *Euchilota*, or the medusa suggested as a young *Phialopsis brownii*.

The hydroid is known from Oceano and San Diego, both on the coast of Southern California. It is found attached to the shells of mollusks, mainly clams (*Tivcla stultorum* at Oceano, *Donax laevigata* at San Diego), that inhabit flat, sandy, ocean beaches.

Gen. **Phialidium** Leuckart, 1856.

Eucopidae with numerous tentacles and at least as many statocysts lying between them; gastric peduncle and marginal cirri wanting.

Phialidium lomae,² n. sp.

Fig. 8.

Umbrella thin, about four times as broad as high. Manubrium short, with slightly frilled lips. Tentacles 28-34, rarely more.

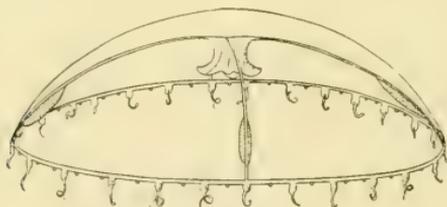


Fig. 8.—*Phialidium lomae*. $\times 6$.

One, occasionally two, statocysts with single statoliths between adjoining tentacles. Gonads narrow in adult, confined to distal half of radial canals. Gonads, canals, tentacles and manubrium faint yellow, umbrella very transparent.

² Named for Point Loma, San Diego.

Diameter 9-12 mm., rarely 14 mm.

Distribution.—Common in surface hauls off San Diego, during June and July.

This species is closely related to the species aggregated by Haeckel under the name *Phialidium variabile*. One specimen of 14 mm. diameter possessed 66 tentacles and about as many statocysts. Young forms are found with ovate gonads and 16-20 tentacles, *Epenthesis* stages.

Gen. **Phialopsis**, n. gen.

Eucopidae with a small number of long tentacles (16-32), numerous rudimentary tentacles (marginal papillae), and cirri; numerous large statocysts with several statoliths; gastric peduncle feebly developed.

This genus differs essentially from *Phialucium* Maas, recently defined as a subgenus under *Phialidium*, in possessing numerous marginal cirri. These organs are, however, readily lost (*vid. Mitrocoma discoidea* and *Eutimalphes diegensis*). And so closely does the San Diego species resemble in all other respects the East Indian *P. virans* (Bigelow) and *P. tenue* Browne, and the Fijian *Mitrocoma mbenga* Ag. & M., that a question is raised as to whether cirri may not ultimately be discovered in the latter species. In any case, the combination of two sorts of tentacles, marginal cirri and large statocysts with numerous statoliths seems to be adequate basis for a distinct genus, for which the name *Phialopsis* may be used until it becomes apparent that the type species of *Phialucium* Maas also possesses marginal cirri.

Phialopsis diegensis, n. sp.

Fig. 9.

Umbrella three to four times as broad as high, moderately thick, with a slight central swelling into the subumbrella cavity (rudimentary gastric peduncle). Manubrium short, with a cruciform base and broad fluted oral folds. Tentacles 16-28, well developed and regularly placed. Between adjoining tentacles, 5-9 rudimentary tentacles or marginal papillae, the largest always median in each group. Cirri, usually more numerous than the marginal papillae, scattered, 2-5 statocysts (usually 4 in

larger specimens) between adjoining tentacles, each with 2-6 statoliths. Velum moderately well developed. Gonads linear, on the outer three-fourths of the radial canals, reaching margin, sinus in contraction of bell.

Diameter of largest specimen 23 mm.

Distribution.—Taken, during May, June and July, in the vicinity of San Diego, at the surface and in vertical hauls to 160 fathoms. Acc. Nos. 6-11, 752, 959, 1382, 1398, 1402.

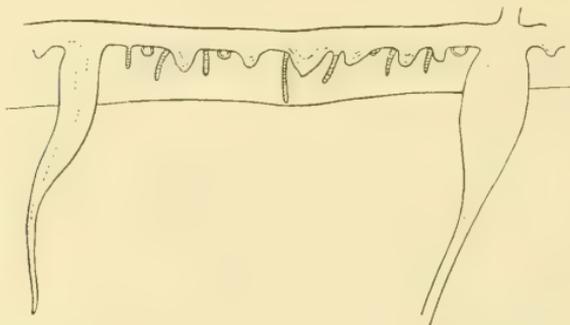


Fig. 9.—*Phialopsis diegensis*. Portion of margin. Much enlarged.

There is a tendency among the larger specimens to slight irregularities in the position of radial canals and gonads.

A single, small medusa that may prove to be an immature specimen of this species was obtained in a vertical haul from 100 fathoms, July 11, 1905, off San Diego; Acc. No. 995. The bell is hemispherical, as high as broad, without gastric peduncle, with well-developed manubrium of the *Phialopsis* type. Eight tentacles, 4 larger perradial and 4 smaller interradial, each flanked by 2 cirri. Between adjoining tentacles two marginal papillae, probably beginnings of tentacles. Between and adjoining these papillae a statocyst (8 in all) with 2 statoliths. Gonads immature, developing on the radial canals about three-fourths the length of the latter from the margin.

This individual resembles *Euchilota* more closely than it resembles *Phialopsis*. As no adults of the former genus have been obtained, it is placed provisionally under *Phialopsis*.

Gen. **Eutimalphes** Haeckel, 1880.

Eucopidae with 8 adradial statocysts and numerous tentacles, between which are numerous cirri; gastric peduncle well defined.

Eutimalphes browni, n. sp.³

Fig. 10.

Umbrella almost hemispherical, rather thick centrally and produced into a broad-based gastric peduncle about as long as the subumbrellar cavity is deep. Manubrium short and broad, hanging from a short, cruciform base, made by the junction of

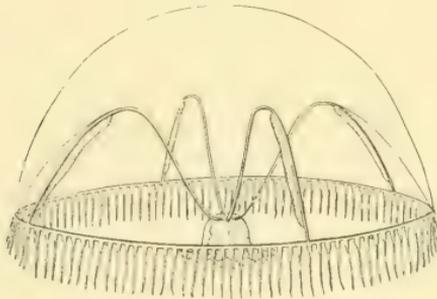


Fig. 10.—*Eutimalphes browni*. — 3.

the radial canals, and expanding distally into a wide and much frilled mouth. Tentacles short, with bulbous bases, about 130 in larger individuals, 1 to 3 pairs of long slender cirri flanking each tentacle. Marginal papillae wanting. Statocysts large, regularly placed between the tentacles, with 6 to 13 statoliths in each. Gonads narrow bands, hanging by one edge from the outer half of each radial canal, almost reaching the margin. The umbrella is colorless, the gonads with straw-yellow endoderm and turquoise-blue ectoderm, the tentacles with red-brown endoderm, turquoise-blue ectoderm.

The largest individuals are about 15 mm. in diameter.

Distribution.—Taken at the surface in the vicinity of San

³ Named for the well-known medusologist, Mr. E. T. Browne, of University College, London.

Diego, in June and July. Acc. Nos. 77 (type), 902, 959, 966, 1246, 1379, 1391, 1393, 1398, 1402.

Among 90 individuals, only 10 possessed cirri. In three of these (Acc. No. 77), the cirri are as described, in excellent condition. In the remaining seven (Acc. Nos. 1246, 1379) a few scattered stumps and rudiments are to be found. The 80 non-cirrate individuals are of all sizes and conditions of preservation. Assuming the cirrate form to be typical, it would appear that the absence of cirri may be due (1) to accidents of environment and (2) to spontaneous variation. The cirrate and non-cirrate forms might perhaps be regarded as distinct species—even genera, were the frequent practice of authors to be followed. Hartlaub (1897) distinguished *Eutonina* from *Eutimalphes* on essentially this basis, though he also considered the size of the stomach. For the present, however, this does not seem to me to be the wisest course to adopt with the San Diego material, as careful comparisons of cirrate and non-cirrate individuals has failed to reveal any other difference, even in the smallest details. Further, in the typically cirrate *Mitrocoma discoidea*, there is a large range of variation in the number of cirri.

The gonads arise as linear bodies along the radial canals, each with one end resting on the base of the gastric peduncle, the other half-way to the margin. The growth is therefore centrifugal.

Gen. **Irene** Eschscholtz, 1829.

Eucopidae with numerous tentacles, statocysts and marginal cirri; gastric peduncle short; gonads not occupying the entire length of the radial canals.

The following species has been placed here provisionally only, since the presence of cirri has not been demonstrated. In all other respects, however, it is a typical *Ircne*, and there is a strong probability that the cirri may have once been present (cf. *Mitrocoma discoidea* and *Eutimalphes brownei*).

Irene mollis, n. sp.

Fig. 11.

Umbrella about twice as broad as high, jelly thin and soft, gastric peduncle moderate. Manubrium short, with thin walls

folded into four prominent frilled lobes about a large mouth. Tentacles 150 to 180. Statocysts small, 1 (or 2) between adjacent tentacles, about 200 in all. Gonads narrow vertical bands along half the length of each radial canal from the margin. Gonads, canals and manubrium faint yellow; bulbs of tentacles brick-red.

Diameter of umbrella 15 to 20 mm.

Distribution.—At the surface in the vicinity of San Diego, during June and July. Acc. Nos. 77, 962, 966, 1379, 1382.

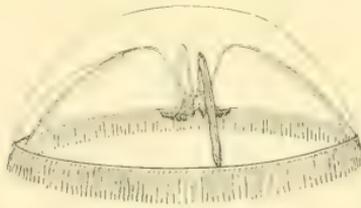


Fig. 11.—*Irenopsis mollis*. × 3.

This species is easily mistaken at first glance for *Eutimalphes brownei*, with which it occurs, but is less robust. It resembles in general *I. coerulca* Agassiz, from which it may be distinguished at once by the position of the gonads. Further, the gastric peduncle is not so tapering, the tentacles are more numerous, and the diameter is less than in the eastern species.

FAM. AEQUOREIDAE Eschscholtz, 1829.

Leptomedusae with numerous closed statocysts and numerous radial canals which bear the linear gonads; manubrium with broad base and thin walls.

Gen. *Aequorea* Per. & Les., 1809.

With the characters of the family.

Browne (1904) and Maas (1905) rely upon the form of the manubrium to distinguish between *Aequorea* and *Mesonema*. My observations on the living *Mesonema coerulescens* Brandt in the Northern Pacific confirm those of Claus (1883), and I agree with him that this character is of no practical value.

In a discussion in connection with *Mesonema pensile*, Browne (1904, p. 734) says: "The stomach is quite rudimentary and is practically absent, as its lower wall is only about 2 mm. in length, so that the mouth must always remain wide open." This is not a necessary conclusion. I have seen the lower wall of the manubrium of *M. coeruleescens* Br. contract to such a size and present every appearance of being then in its normal permanent condition: and I have also seen the same manubrium extend readily and the wide mouth narrow and completely close by a constriction above the oral fimbriations.

Since the character on which Eschscholtz based his separation of *Acquorea* and *Mesonema* is no longer considered adequate for the purpose, the foregoing facts, taken in connection with the admirable observations of Claus, would appear to argue conclusively for the abandonment of *Mesonema*, along with the no more happily conceived *Rhegmatodes* and *Polycanna*.

***Aequorea coeruleescens* (Brandt).**

- Mesonema (Zygodactyla) coeruleescens*, Brandt, 1835, p. 21;
Brandt, 1838, p. 360, pl. 5.
Zygodactyla coeruleescens, A. Agassiz, 1865, p. 108.
Mesonema coeruleescens, Haeckel, 1880, p. 228.

Umbrella thick, three times as broad as high, with a central, broad swelling into the gastric cavity. Manubrium with a very broad base and about 60 oral fimbriations; its wall highly contractile, mouth readily closed. Tentacles more numerous than the radial canals, which number about 120. Velum narrow. Gonads along nearly the entire length of the radial canals. Bases of tentacles a bright blue, umbrella faintly bluish.

Diameter may exceed 190 mm.

Distribution.—Taken at the surface, in June and July, in the vicinity of San Diego (Acc. Nos. 999, 1357, 1379). Mertens obtained the type specimens about 1600 miles to the west of San Diego. I met with it at Unalaska Island, in May, 1906.

The northern specimens were larger than those taken by Mertens. The San Diego individuals are much smaller, respectively 4 mm., 15 mm. and 55 mm. in diameter. In the last specimen there are but 90 radial canals, with indications of a some-

what larger number of tentacles on the damaged margin, and 30 oral fimbriations. There are signs of new canals and new tentacles. The gonads are immature.

In spite of the imperfect margin, which leaves undetermined the number of statocysts, and the absence in the preserved specimens of the blue color so characteristic of the species, I do not doubt that this San Diego form belongs with those taken by Mertens to the westward.

La Jolla, Cal.,

June, 1908.

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XXV

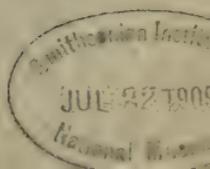
THE OPHIURANS OF THE SAN DIEGO
REGION

BY

J. F. McCLENDON

BERKELEY

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XXV.

THE OPHIURANS OF THE SAN DIEGO
REGION

BY
J. F. McCLENDON.

My interest in Ophiurans lies chiefly in the experimental side, and the present work was begun in June, 1907, with the hope that a taxonomic and biological study of the San Diego species might greatly facilitate work in which it was required to know breeding seasons and habitats of the different species. Unfortunately I left San Diego September 1, 1907, before much data on breeding seasons had been collected. I believe that the height of the breeding season for the majority of species is in the spring, although individuals full of eggs that were apparently not ripe were found during the summer. Owing to the confused state in which the taxonomy of the Ophiurans has been left, I found it impossible to complete the work without much aid from Dr. H. L. Clark, for which my sincere thanks are due him. I am also indebted to Miss Rathburn and Dr. Austin Clark of the National Museum; to the museum itself for the loan of specimens, and to the John Crerar Library and the Universities of Michigan and California for literature.

Although most of the species react negatively to light and hide under rocks and in sea-weed, sponges, etc., some of them

appear to be protectively colored. The abundance and ease of collection of the littoral species leads me to believe that hybridization experiments might be worth trying and that the eggs might also be favorable for many other problems in experimental embryology. It would be of interest in this connection to know what species are viviparous.

In giving the diameter of the disc the largest specimen at hand was always chosen. Most of the species have been described and figured elsewhere, but the following descriptions and figures have the advantage to the student at San Diego in all being made from the region where his material will be procured. No dissections are described; for example, *only the exposed part* of the radial shield is described.

Types or representatives of all are in the University of California museum, except *Ophiocnida hispida*, which is in the United States National Museum. The figures were drawn by the author, excepting 24 and 25, which were drawn by Mr. G. T. Kline.

Class OPHIUROIDEA Norm. 1865.

Order 1. ZYGOPHIURAE Bell 1892.

Ophiuroidea with well-developed parts in the skeleton of the arm segments. The arms are not branched and cannot be rolled up toward the mouth.

Suborder A. BRACHYOPHIURAE E. Perr, 1891.

Arm spines short, parallel to the arm axis.

Family 1. OPHIODERMATIDAE Ljg. 1867.

With numerous mouth papillae, no tooth papillae, 2-4 genital openings.

Genus *Ophioderma*.

Ophiura Lm. 1801 (*partim*).

Disc granulated. Teeth, and numerous, equal, close-set mouth papillae. No tooth papillae. Spines smooth, flat, shorter than arm joints, numerous (7-13). Two tentacle scales; only the upper one covers the base of the last arm spine. A notch in the

disc over base of arm. Four genital openings in each interbrachial space; the first pair begins at the outside of the mouth shield.

Ophioderma panamensis Ltk.

Fig. 1.

Additamenta ad Hist. Oph., II, p. 193.

Diameter of disc 25 mm. Length of arm about $3\frac{1}{2}$ -4 times diameter of disc. Disc granulated above and below so that only a minute portion of each radial shield is uncovered. Mouth papillae and teeth small. Mouth shields sub-triangular with the corners much rounded. Side mouth shields hidden by granules. Four genital openings in each interbrachial space. Tentacle scales flat and continuous with arm spines. Ventral arm plates about as broad as long, with corners rounded. Dorsal arm plates two to three times as broad as long with distal margin concave and corners rounded. Arm spines numerous, flattened, lying close to arm and shorter than arm joints. Color dark brown above, lighter below, the arms encircled by pale bands.

A common littoral species of the region. Panama to San Pedro and Catalina. San Diego M. B. L., La Jolla. Albatross stations 3588, 3589 and 3590, San Diego Bay. Smithsonian 5213, Catalina Id.; No. 1 San Diego (H. Hemphill). U. S. Nat. Mus. 12732 (*b*) Catalina Harbor 30-40 fathoms, (W. H. Dall c 6 1874).

Family 2. OPHIOLEPIDIDAE Ljg. 1867.

Three to four mouth papillae, of which the innermost is seldom below the teeth. No tooth papillae. Notch in disc above base of arm. Two genital openings in each interbrachial space.

Genus **Ophiomusium** Ly. 1869.

Teeth. No tooth papillae. Mouth papillae fused in a continuous row so that their former outlines are indistinct. Disc covered by plates and radial shields, all of which are fused. Upper and under arm plates minute, side arm plates meeting above and below, swollen and fused with neighboring plates. No tentacle pores beyond the basal arm joints. Small arm spines on outer edge of arm plates. Two genital openings in each interbrachial space.

Ophiomusium jolliensis sp. nov.

Figs. 2, 3.

Diameter of disc 12 mm. Length of arm $2\frac{1}{2}$ times diameter of disc. Disc covered with irregular plates, variable in size and shape, the marginal interbrachial ones very large. Five or six pairs of mouth papillae to each jaw. Teeth very acute. Mouth shields lanceolate, the point directed inward and sometimes separating the side mouth shields. Two genital openings in each interbrachial space. One tentacle scale small and flat. Only three pairs of tentacle pores on arm (3 basal segments). The three proximal ventral arm plates are pentagonal and bear tentacular openings. The remaining ones are sub-triangular or quadrangular with the inner margins convex. Dorsal arm plates lanceolate with the point directed proximally. Two or three short blunt arm spines. Color of preserved specimens cream or light grey.

San Diego M. B. L.: 1026 (Station 6, San Clemente), 215 fathoms. 972, four miles W.N.W. of La Jolla, 125 fathoms. 1038 (Station 13), 308 fathoms. 974, three-fourths mile N.N.W. of La Jolla, 85 fathoms. 1027 (Station 8, San Clemente), 330 fathoms. 1534. 1541.

Ophiomusium lymani W. Thos.

Figs. 4, 5.

"Depths of the Sea," p. 172, figs. 32, 33.

Diameter of disc 30 mm. Length of arm about 4-5 times diameter of disc. Disc covered with irregular polygonal fused scales. Radial shields very large and tuberculated, as is also the large marginal scale between them. Five to seven rectangular fused mouth papillae on each side. The outer ones may so fuse as to reduce the number. Mouth shields narrow and pointed at inner end. Side mouth shields large, meeting within, the outer ends much broader than the inner. Genital openings usually reaching only to the 2nd or 3rd arm joint, the inner ends curved. Tentacle scales small and flat. Tentacle pores in 1st and 2nd arm joints only. Under arm plates in 1st and 2nd arm joints only. Side arm plates meeting above and below. Upper arm

plates small and diamond shaped. Six to eight rudimentary arm spines. Color of preserved specimens grey.

This is a deep-sea cosmopolitan species. San Diego M. B. L., 1072 (La Jolla Sta. III, 600 fathoms).

Genus **Ophiura** Lm. 1816.

Ophiolepis M. & T. 1842 (*partim*).

Ophioglypha Ly. 1865.

Disc covered with plates or scales which are often swollen. Radial shields naked and swollen. Teeth. No tooth papillae. Mouth papillae long within, but small and short near outer end of the mouth slit and partly hidden by the scales of the mouth tentacles. Arm spines short and smooth, rarely exceeding the length of a joint. Tentacle scales numerous, the innermost pair of tentacle pores shaped like slits surrounded by numerous tentacle scales and opening diagonally into the mouth slit. In the disc, over the base of the arm, is a notch usually edged with papillae. Two genital openings starting from the sides of the mouth shield.

Ophiura lütkeni Ly.

Figs. 32, 33.

Proc. Bost. Soc. Nat. Hist., VII, p. 197, 1860.

Diameter of disc 8 mm. Length of arm about $5\frac{1}{2}$ times diameter of disc. Disc flattened, covered above with slightly swollen scales and radial shields. Each larger scale surrounded by smaller ones. Radial shields small, ovoid, pointed within. A notch above the base of arm. Interbrachial spaces below covered with slightly swollen scales. Eight pairs of mouth papillae, the inner ones spine-like and separated, the outer four broad and close together. Teeth. No tooth papillae. Mouth shields pentagonal, the inner angle acute, the others rounded, lateral edges emarginate. Side mouth shields long, narrow and meeting within. Genital openings beginning at the sides of the mouth shield. First and sometimes second tentacular openings, with two or three flat scales, succeeding four or five each with one flat scale and one minute spine-like scale, the remainder each with one flat scale. Ventral arm plates twice as broad as long, small

and well separated, proximal margin angular, distal margin convex. Side arm plates meeting below. Dorsal arm plates narrowed and truncated proximally, the distal margin produced into an obtuse rounded angle. Three tapering arm spines on the proximal joint, the dorsal one about as long as the arm joint. On the remaining joints the dorsal spine is a little shorter than the arm joint. The other two spines are shorter than the dorsal spine. Color of preserved specimen grey above and white below.

San Diego to Puget Sound, 22-600 fathoms. San Diego, M. B. L.: 1025, San Clemente, 60 fathoms. 1072, La Jolla Station III, 600 fathoms. 1112, 1288, $2\frac{1}{4}$ miles S.W. by S. of La Jolla, 50 fathoms. 1497. 1501. XII-2, June 5, '01, 30 fathoms. XIII-1, June 6, '01. XIV, 2, San Pedro, 100 fathoms. XIX, 2-5, San Pedro, 77 fathoms. XX, 1, San Pedro 77, fathoms. XXI-2, June 20, '01, 43 fathoms. XXVI-a. XXXI-a, near Potts Valley, San Pedro. L-1 and 2, off Pt. Loma, 25 fathoms. LV-1 and 2, San Diego, 25 fathoms. LXX-5, La Jolla, submerged valley, 100 fathoms. LXXII-1, off Pt. Loma, 30 fathoms. Smithsonian: 5214 Catalina.

***Ophiura kofoidi* sp. nov.**

Figs. 8, 9.

Diameter of disc $7\frac{1}{2}$ mm. Length of arm about four times diameter of disc. Disc thick but flat, pentagonal, covered with imbricated scales and radial shields. A large central scale. A notch over base of arm bordered by two rows of spines, one row being continued along genital opening. Five to six pairs of mouth papillae, the innermost sometimes spine-like. Teeth. No tooth papillae. Mouth shields large, pear shaped, the stem of the pear being a sharp angle pointing inward. Side mouth shields, narrow, meeting within. Genital openings starting between mouth shield and side mouth shields. First tentacle pore opening diagonally into mouth angle and surrounded by nine scales, second (in 1st arm joint) surrounded by six scales, the remainder each with two spine-like scales. Ventral arm plates short and well separated, convex distally, produced to a point proximally. Side arm plates meeting below. Dorsal arm plates broader than long in proximal part of arm, distal margin convex, narrowed proximally. Arm spines numerous, slender, acute, slightly curved, on the proximal joints the dorsal spines are $2\frac{1}{2}$ times length of arm joint, the ventral spines a little longer than

arm joint. Color of preserved specimen grey above, lighter below.

San Diego M. B. L.: 991, $1\frac{3}{4}$ miles N.W.N. of La Jolla, 80 fathoms.

Genus *Ophioplocus* Ly. 1861.

Disc closely and finely scaled above and below. Genital scales hidden. Teeth. No tooth papillae. Numerous even, close set mouth papillae. Side mouth shields wide and nearly or quite meeting within. Three short arm spines. Upper arm plates, near tip of arm, divided on midline into halves, which at base of arm are removed to outer lower corner of joint on each side and separated by a number of supplementary pieces. Two short genital openings in each interbrachial space, extending only half way to the margin of the disc and beginning outside the side mouth shields.

Ophioplocus esmarki Ly.

Figs. 6, 7.

Bull. Mus. Comp. Zool., III, pt. 10, p. 227, pl. V.

Diameter of disc, 30 mm. Length of arm $2\frac{4}{5}$ times diameter of disc. Disc and arms flattened. Radial shields nearly covered by scales. Scales irregular and swollen, giving the disc a pebbled appearance, the larger ones, above, being usually surrounded by smaller ones. The scales on the ventral side smaller than those on the dorsal and more uniform in size. Ten to twelve mouth papillae. Mouth shields sub-triangular, aboral margin rounded. Genital openings, two in each interbrachial space, beginning near the mouth shields, the edges granulated, and the granulation extending out to the margin of the disc. Tentacle scales usually 4-5 in number surrounding each tentacle pore. Ventral arm plates six-sided, narrowed behind, distal margin straight or slightly incurved. Dorsal arm plates broken into a large number of irregular pieces. Arm spines three in number, about two-thirds the length of the arm joints. Color of preserved specimens light or dark brown or bluish grey.

San Diego to Pacific Grove. Shore to 40 fathoms. San Diego M. B. L.: 1023, San Clemente, San Pedro, Sta. 5, 15 fathoms. Albatross: March 15, 1891, off Point Loma. U. S. N. M.: 12732 (a), Catalina Harbor, W. H. Dall

(c 6), 30-40 fathoms, 1874. No. 2 (Henry Hemphill), San Diego. Smithsonian: 12644, W. H. Dall (c 7), Catalina Harbor, 40 fathoms. 4290, Catalina.

Genus **Ophiocten** Ltk. 1854.

Disc thick and circular, partly covered by plates and radial shields between which are sometimes fine, close-set grains or small scales. Genital opening bordered by a row of papillae that often extends upward along the edge of the disc, over the arm base. Side arm plates come together below but not above. The broad mouth tentacle is enclosed between the first ventral arm plate and the outer edge of the side arm plate. Teeth. Mouth papillae. No tooth papillae. Two genital openings beginning at the sides of the mouth shield.

Ophiocten pacificum L. & M.

Figs. 14, 15.

Mem. Mus. Comp. Zool., XXIII, No. 2, 1899.

Diameter of disc 12 mm. Length of arm a little more than three times diameter of disc. Disc covered with separated plates and radial shields and the areas between them covered with imbricated scales. Radial shields narrowed within. Five to six pairs of mouth papillae in each jaw, the inner one spinous. Teeth. No tooth papillae. Mouth shield pentagonal, inner angle sharp, remaining ones rounded. Side mouth shields meeting within, narrowed without. Genital openings begin at sides of mouth shield, bordered with papillae that are continued up over arm. First pair of tentacle pores between basal arm plate and side mouth shields, each with two broad scales. Second pair of tentacle pores each with a bilobed scale. The remainder, each with one flat and one minute spinous tentacle scale. Ventral arm plates small and well separated. The first one trapezoidal, narrowed proximally. Side arm plates meeting below. Dorsal arm plates broader than long, narrowed proximally and convex distally; the proximal plates bearing minute spinous papillae on their distal margin. Three slender, slightly curved arm spines, the dorsal spine longer than two arm joints, the ventral spine a little longer than one arm joint.

From Galapagos Ids. and Gulf of Panama to San Diego; down to 1573 fathoms.

Sub-order B. **Nectophiuræ** E. Perr, 1891.

Spines on arms perpendicular to arm axis.

Section 1. **OLIGODONTIDA** Ludwig & Hamann, 1901.

Tooth papillae few or wanting.

Family 3. **AMPHIURIDÆ** Ljg. 1867.

One to five mouth papillae, the innermost often infradental. Arms arising from the ventral side. Two genital openings.

Genus **Ophiopholis** Müll. & Tr. 1842.

Disc more or less covered with grains or little spines. No tooth papillae. Mouth papillae on the sides of the mouth frames. Arm spines short, flat and stout. Upper arm plates surrounded by a rim of supplementary pieces. The lowest spine of the distal arm joints is a hook. General structure coarse and stout. Two genital openings beginning outside the mouth shields.

Ophiopholis bakeri sp. nov.

Figs. 26, 27.

Diameter of disc $6\frac{1}{2}$ mm. Length of arm four to five times diameter of disc. Disc (with exception of mouth parts) completely covered with short, thorny spines. Teeth sometimes divided in the middle and having rudiments of papillae. Five pairs of slender papillae. Mouth shields diamond-shaped, corners rounded, nearly twice as long as broad. One long, flat and narrow tentacle scale. Ventral arm plates octagonal, distal, lateral and proximo-lateral edges concave. Dorsal arm plates circular, each surrounded by a row of small, round supplementary pieces. Six arm spines in proximal portion of arm, decreasing to four in distal portion, minutely thorny. First spine (above) of variable length, second (longest) a little longer than arm joint, the remainder decreasing in length downward. Color of dried specimen pink or red.

San Diego M. B. L.: 1025, San Clemente, Station 5, 60 fathoms. 1026, San Clemente, Station 6, 215 fathoms. 1047, 4 miles N.W. by N. of La Jolla, 100 fathoms. 1155, $2\frac{1}{2}$ miles W.N.W. of La Jolla, 70 fathoms. XXVI-a. LXX-5, Soledad, submerged valley, Aug. 23, 1901, 100 fathoms. 1501. 1532. 1534. 1537. 1549.

Genus **Ophiaetis** Ltk. 1856.

Disc round and stout and covered with radial shields and imbricated scales, the latter usually bearing small spines. Teeth. No tooth papillae. Mouth angle short and narrow, with few (2-4) small mouth papillae. Arms somewhat depressed, in length 4-7 times the diameter of the disc. Arm spines short and smooth. Two genital openings, beginning outside the mouth shields.

Ophiaetis arenosa Ltk.

Fig. 16a. *Ophiaetis arenosa*, Ltk., partial view.

Fig. 16b. Partial ventral view of same.

Lütken, C. F. "Bidrag til Kundskab om Slagestjerne, III,"
Vidensk. Meddel. naturhist. Foren i Kjobenh. 1856.

Diameter of disc 6 mm. Length of arm about three and one-third times diameter of disc. Disc covered with radial shields and imbricated scales, the latter in interbrachial spaces and on edge of disc bear each a small spine on its outer edge. Teeth. No tooth papillae. One or two pairs of thin mouth papillae in each jaw. Mouth shield quadrilateral, inner angle sharp, the other angles rounded, outer edges convex. Side mouth shields meeting to form a continuous ring round the mouth. Genital openings beginning at mouth shield. One flat tentacle scale. Under arm plates about as broad as long. Upper arm plates broader than long, narrowed proximally. Five arm spines, upper one less than one arm joint, middle three each about one and one-half arm joints and lower one about one arm joint in length. Color of dried specimen cream with fuscous mottlings.

West coast of Central America. San Diego Bay near National City, in sponges, June, 1908, 15 specimens.

Genus **Amphiura** Forbes 1842.

Disc small and delicate, covered with overlapping scales and naked radial shields. Teeth. No tooth papillae. Mouth angle small and narrow with few (usually 4-6, seldom 8-10) small mouth papillae. Arm long, slender, even and more or less flattened. Arm spines short and regular. Two genital openings in each interbrachial space.

Sub-genus **Amphiura** Verrill 1899.

One apical or sub-apical mouth papilla. One (rarely 2) small, distal papilla (oral tentacle scale). Middle of jaw edge without papillae. Mouth slits gaping. Four to seven or more (rarely 3) arm spines. Radial shields divergent.

Amphiura verrilli sp. nov.

Figs. 10, 11.

Diameter of disc 8 mm. Length of arm five times diameter of disc. Disc above and below covered with imbricated scales. Radial shields naked, separated, and about twice as long as broad. Three pairs of mouth papillae. Teeth. No tooth papillae. Mouth shield diamond shaped, the edges next to the genital openings concave, corners rounded. Side mouth shields narrowed and meeting within, broad without. Genital openings beginning at mouth shields. One flat tentacle scale. Ventral arm plates concave on distal margin, narrowed proximally. Side arm plates meeting above, meeting below except at base of arm. Dorsal arm plates elliptical, about twice as broad as long. Four stout tapering arm spines, a little longer than arm joints. Color of dried specimen light grey.

San Diego, M. B. L.: San Diego, 100 fathoms. XXXI-a, near Potts Valley, San Pedro.

Sub-genus **Amphipholis** Ljg. 1867-71.

Two small lateral and one broad operculiform distal mouth papillae, forming a continuous series along the entire jaw and capable of nearly or quite closing the mouth slits. Radial shields in close contact. Disc covered with scales (usually naked).

Amphipholis pugetana Ly.

Figs. 12, 13.

Proc. Bos. Soc. Nat. Hist., VII, p. 193, 1868.

Diameter of disc $3\frac{1}{2}$ mm. Length of arm about five times diameter of disc. Disc covered with imbricated scales, the dorsal ones longer and meeting those on the edge in a distinct line. Radial shields naked, about twice as long as broad, meeting along their whole length. Three pairs of mouth papillae, the outer

ones very broad. Teeth. No tooth papillae. Mouth shield small, quadrangular, the inner angle the most acute. Side mouth shields narrowed within, where they meet. Genital openings beginning at mouth shield. Two flat tentacle scales. Ventral arm plates pointed behind (where the side arm plates meet for a very short distance), about twice as broad as long, distal edge slightly concave. Dorsal arm plates sub-triangular, distal margin convex, corners rounded. Disc light yellowish brown, lighter below, radial shields darker, shading into a sooty white at their outer ends. Mouth and ambulacral regions white. Arms at sides and above and arm spines a sooty white.

San Diego to Puget Sound. San Diego M. B. L.: 1026, San Clemente, Station 6, 213 fathoms. 1038, Station 13, 308 fathoms. 1166, N.E. from Long Beach (La Jolla) to 1st canyon, 30 fathoms. XLIII-3, San Diego, channel west of middle ground, Ballast Point, 5 fathoms. LXII-1, July 20, 1901, 18 fathoms. Shelters Cove, June 27, 1894. Wilson's Cove, June 11, 1896. Albatross: San Diego, March, 1898. Smithsonian 14182, Catalina, W. H. Dall. Smithsonian 12710, Catalina Harbor (c 6), 1873, 30-40 fathoms, sandy mud.

***Amphipholis puntarenae* Ltk.**

Figs. 20, 21.

Diameter of disc $7\frac{1}{2}$ mm. Length of arm about 7 times diameter of disc. Disc covered above by large imbricated scales and naked radial shields that meet along outer third. Inter-brachial space granulated. Three pairs of mouth papillae, outer one very broad, next narrower and inner one small and partly infradental. Mouth shield quadrangular, corners rounded, inner angle most acute. Side mouth shields, broad, meeting within, sub-triangular, corners rounded. Genital openings beginning at mouth shield. Two flat tentacle scales, the distal one larger. Ventral arm plates quadrangular, distal corners rounded, broader than long. There is a minute plate separating the outer ends of the side mouth shields that may be a vestige of the first ventral arm plate. Dorsal arm plates ellipsoidal, about twice as broad as long. Three stout sub-equal arm spines about the length of an arm joint. Color of preserved specimen grey.

San Diego M. B. L.: 1289-c, 4 miles S.W. by S. of La Jolla, 50 fathoms, 3 specimens. LXX-5, La Jolla, submerged valley, July 23, 1901, 100 fathoms, one specimen. Smithsonian: 12806, San Diego, H. Hemphill, 10 fathoms, 1 specimen.

Sub-genus **Amphiodia** Verrill 1899.

Three (rarely 4) small, subequal mouth papillae, none of them operculiform. They form a regular series attached mostly to the side jaw plate. No distinct oral tentacle scales. Three (rarely 4) arm spines. Radial shields often more or less joined.

Amphiodia barbarae Ly.

Figs. 22, 23.

Ill. Cat. Mus. Comp. Zoo. Harvard, VIII, pt. 2, p. 17, pl. III.

Diameter of disc 4 mm. Length of arm about 12 times diameter of disc. Disc covered with small imbricated scales. Radial shields naked, meeting along outer two-thirds of length, twice as long as broad. Three pairs of thick mouth papillae. Teeth. No tooth papillae. Mouth shield quadrangular, outer angle more obtuse, corners rounded. Side mouth shields very slender, meeting within, outer ends knobbed. Genital pores beginning at mouth shield. Two very short, flat tentacle scales. Ventral arm plates heart-shaped, with apex proximally. Side arm plates meeting below. Dorsal arm plates elliptical, about twice as broad as long. Three tapering arm spines, subequal, a little shorter than an arm joint. Color of dried specimen yellowish, disc sometimes greenish.

San Diego to Santa Barbara. San Diego M. B. L.: San Pedro, Station 1-1, May 22, 1901. San Pedro, Station (8), June 25, 1895. XXXI-a, June, 1901. XXXIV-a, up Little Harbor Valley, June 28, 1901. XXXVI-e, June, 1901. LXXIII-1, off Pt. Loma, July 25, 1901, 120 fathoms. 974, 1½ miles N.W. by N. of La Jolla, 85-100 fathoms. 1112.

Specimens from San Pedro (8) and XXXVI have more rectangular dorsal arm plates and some have more pointed mouth papillae. In young specimens from XXXIV-a the scales on edge of disc project as trifid spines.

Genus **Ophiocnida** Ly. 1865.

Disc small and delicate, furnished with naked radial shields and naked overlapping scales, the latter beset with small thorns or grains. Teeth. No tooth papillae. Mouth angles short and small, bearing a few (4-6) little mouth papillae. Arms long, slender, even, more or less flattened. Arm spines short and regular. Two genital openings in each interbrachial space.

Ophiocnida hispida Le Conte.

Figs. 34, 35.

Proc. Acad. N. Sc. Phila., V, p. 318, 1851.

Diameter of disc 7 mm. Length of arm about $8\frac{1}{2}$ times diameter of disc. Disc covered with small imbricated scales bearing pointed spines (not shown well in figure). Radial shields close together but not touching, 2-3 times as long as broad. Teeth. No tooth papillae. Three pairs of rounded mouth papillae, inner pair appearing like a split tooth, outer pair broader than the rest. Side mouth shields broad without, narrow within, meeting or nearly meeting within. Mouth shields varying in size, diamond shaped, elongate radially. Genital pores beginning at mouth shield. Two flat tentacle scales. Ventral arm plates rectangular, about $1\frac{2}{3}$ times as broad as long, with corners rounded. Dorsal arm plates elliptical, about three times as broad as long. Three arm spines, blunt, flattened, about $1\frac{1}{3}$ times as long as arm joint, subequal except on distal end of arm where the dorsal spine is smallest. Color in alcohol, pale yellow, with small fuscous spots on disc and a larger fuscous spot near middle of each radial shield. Arms brown, interrupted with pale yellow with a median discontinuous fuscous line above. Arm spines pale, tinged with brown. Tentacle scales pale. Mouth parts pale, tinged with fuscous.

From west coast of Central America to Catalina. Smithsonian: 4100, Catalina, W. H. Dall (c 32).

Ophiocnida amphacantha sp. nov.

Figs. 24, 25.

Diameter of disc $7\frac{1}{2}$ mm. Length of arm about 10 times diameter of disc. Disc covered with imbricated scales, some of which bear large, pointed spines. Radial shields narrow and touching without. Four pairs of mouth papillae on each jaw, besides a pair over the mouth tentacles. Teeth. No tooth papillae. Mouth shield pointed within, outer edge short and straight, edges next the side mouth shields convex, edges next the genital openings concave. Side mouth shields narrowed and touching within. Genital openings beginning very near the

mouth shield. Two very short, flat tentacle scales. Ventral arm plates rectangular with the corners cut off and the distal margin concave, longer than broad. Dorsal arm plates oval, and broader than long except at base of arm. Five to six stout, tapering arm spines, almost as long as arm joint. Color (preserved): arm yellowish, disc greenish.

San Diego M. B. L.: XXI-5, June 21, 1901, about 150 fathoms; XXXIV-a, up Little Harbor Valley, June 28, 1901. LXXIII-1, off Point Loma, July 25, 1901, 120 fathoms.

Genus *Ophionereis* Ltk. 1859.

Disc covered with fine, overlapping scales. Radial shields nearly hidden by scales. Large, oblong teeth. Mouth angle small and short and bearing 9-10 small, close-set papillae. A few (3-5) short, smooth arm spines. One large tentacle scale. Each upper arm plate has a supplementary piece on either side. Two genital openings beginning outside the mouth shield.

Ophionereis annulata Le Conte.

Figs. 36, 37.

Proc. Acad. N. Sc. Phila., V, p. 317, 1851.

Diameter of disc 13 mm. Length of arm about six times diameter of disc. Disc puffed in interbrachial spaces and covered with minute imbricated scales which nearly hide the radial shields. Mouth papillae, 5 pairs on each jaw and one pair in the mouth angle. Teeth. No tooth papillae. Mouth shields hexagonal. Side mouth shields narrowed and meeting within. Genital openings beginning at the mouth shield. One flat oval tentacle scale. Ventral arm plates square, corners rounded, distal margin concave. Dorsal arm plates rounded and narrowed distally. Three stout, flattened arm spines tapering distally, about $1\frac{1}{2}$ times the length of arm joint, dorsal spine shorter than the others.

West coast of Central America to San Pedro, shore to 35 fathoms. San Diego M. B. L.: VIII, San Pedro Harbor, May 29, 1901. XLIV-1, Quarantine Station to Beacon $3\frac{1}{2}$, San Diego, 5 fathoms. LXVI-1, Beacon 5 to $3\frac{1}{2}$, along north side of channel, San Diego, 8 fathoms. Whites Point, San Pedro, June 4, 1901. U. S. N. M.: No. 5, Henry Hemphill, San Diego. U. S. F. C.: San Diego. Albatross: Sta. 3620, San Diego Bay.

Family OPHIACANTHIDAE E. Perr. 1891.

Side arm plates well developed, usually meeting above and below. Numerous long spines. Mouth papillae usually numerous, forming a continuous row. First ventral arm plate usually concave within and bearing two papillae. Generally one median tooth papilla, sometimes several or a large cluster.

Genus *Ophiacantha* M. T. 1842.

Disc swollen and covered with a thin skin that obscures the underlying coat of fine imbricated scales, sometimes covers the radial shields and bears spines, thorns or rough grains. No tooth papillae. Mouth angle large and bearing 7-16 papillae. Four to eleven usually rough or thorny arm spines. Side arm plates nearly or quite meeting above and below. Two genital openings.

Ophiacantha normani Ly.

Figs. 18, 19.

Bull. Mus. Comp. Zoo. Harvard, VI, No. 2, p. 58, pl. XI.

Diameter of disc 27 mm. Length of arm about 6 times diameter of disc. Disc covered with imbricated scales bearing small sharp spines and partly covering the radial shields. One median and 4 pairs of mouth papillae on each jaw and one minute pair in corner of mouth. Mouth shield compressed radially, extended aborally into a blunt process. Side mouth shields narrow, meeting within. Genital pores beginning at mouth shield. One small sharp tentacle scale. Ventral arm plates ellipsoidal. Side arm plates meeting below. Dorsal arm plates triangular and bearing minute papillae on their convex distal margins. Four slender sharp arm spines, the upper one sometimes as long as three arm joints, the others decreasing in length downward. Color (preserved) muddy white.

Eastern and Western Pacific. San Diego M. B. L.: 1072, La Jolla Station, 600 fathoms.

SECTION 2. POLYDONTIDA, Ludwig & Hamann, 1901.

Tooth papillae numerous.

Family OPHIOCOMIDAE Ljg. 1867.

Mouth papillae. Teeth. Arms arise from ventral side of disc. Moderate or long spines perpendicular to arm. Disc, at least above, covered with granules on a soft skin, seldom with scales and naked radial shields. Mouth shields small or medium size, not extending into interbrachial space. Two genital pores.

Genus *Ophiopteris*, E. A. Smith, 1877.

Disc granulated. Radial shields covered. Mouth angle small and short and with small mouth papillae. Tooth papillae very numerous and arranged in a close, vertical lump. Four teeth. Arm spines smooth and solid, the upper one having one or two supplementary scale-like spines applied to its base. One tentacle scale. Two genital openings beginning outside the mouth shield.

Ophiopteris papillosa Ly.

Figs. 28, 29.

Ill. Cat. Mus. Comp. Zoo. Harvard, VIII, pt. 2, p. 11, 1875.

Diameter of disc 11 mm. Length of arm about $3\frac{1}{2}$ times diameter of disc. Disc completely covered above with stout cylindrical stumps. Interbrachial space covered with more slender stumps. Four to six pairs of small mouth papillae on each jaw and one small pair in the corner of the mouth (tentacle scales). Tooth papillae in four or five vertical rows, those in the middle being irregular. Mouth shields sub-triangular, with rounded corners. Side mouth shields narrow, meeting within. Genital openings beginning at mouth shield. One flat tentacle scale. First ventral arm plate small and sub-triangular with outer corners cut off and slightly broader than long. Dorsal arm plates hexagonal, about $1\frac{1}{2}$ times as broad as long. Five flat, blunt arm spines, the first (dorsal) and sometimes the second are reduced to scales, the third and sometimes the fourth about as long as three arm joints, the fifth usually shorter than two arm joints. The spines are very finely serrated toward their tips. Color, brown.

Lower California to San Diego. San Diego M. B. L.: XVIII-1, June 12, 1901, 30 fathoms. LI, off Pt. Loma, 25 fathoms. LXII-1, July 20, 1901, 17 fathoms. LXVIII-1, July 22, 1901, 30 fathoms. Albatross: March, 1898, San Diego.

Genus **Ophiothrix**, M. T. 1842.

Disc set with thorny grains or thorny spines. Radial shields large, triangular, swollen. Numerous crowded tooth papillae forming a vertical oval. Teeth. No mouth papillae. Five to ten arm spines often three times as long as the arm joints. Usually a small, spine-like tentacle scale. The base of the jaw pierced with a hole. Interbraachial spaces swollen. Two genital openings, beginning outside the mouth shield. Outer arm joints with hooks.

Ophiothrix spiculata Le Conte.

Figs. 38, 39.

Proc. Acad. N. Sc. Phila., V, p. 318, 1851.

Diameter of disc 15 mm. Length of arm about $5\frac{1}{2}$ times diameter of disc. Disc including radial shields covered with thorny spines. Radial shields nearly touching above base of arm. Tooth papillae in a linear vertical oval with a vertical row in the middle. No mouth papillae. Mouth shields compressed radially. Side mouth shields sub-triangular. Genital openings beginning at mouth shield. One small tentacle scale. Vertical arm plates a little broader than long. Dorsal arm plates pentagonal, $1\frac{1}{2}$ times as long as broad. Seven long, serrated arm spines, the 2nd or 3rd being longest and about $4\frac{1}{2}$ times the length of arm joint. Color, greenish brown, sometimes yellowish. Arms interrupted with orange bands. A cluster of orange spots near base of each arm on upper side of disc and internal to these the disc is speckled with orange (in one case the central area was white while the rest of the animal was colored normally). Mouth region whitish.

West coast of Central America to Pacific Grove. Shore to 100 fathoms. Very abundant. San Diego M. B. L., stations: VI, San Pedro, outer harbor, 11 fathoms. VIII, San Pedro, harbor, May 29, 1901. XIV-2, San Pedro, about 100 fathoms. XVI-2, 3, San Pedro, 9 and 13 fathoms. XVIII-1, June 12, 1901, 30 fathoms. XIX-5, about 77 fathoms. XXI-2,

June 20, 1901, 43 fathoms. XXIII-2, June 22, 1901. XXVII-b. XXVIII-a, off Isthmus Harbor, between White Rock and Fish Harbor, 12-30 fathoms. XXX, Potts Valley, San Pedro, 20 fathoms. XXXV-a, June 29, 1901, 30 fathoms. XXXVI-c. XXXVIII-a, 25 fathoms. XLVI-2, 56 fathoms. L-1 and 2, off Pt. Loma, 25 fathoms. LXII-1, 17 fathoms. LXVIII-1, San Diego Harbor. San Pedro, Sta. 3, June 21, 1895. San Pedro Sta. 15, June 29, 1895. Pacific Grove. On kelp roots from Portuguese Bend, June 1, 1901. San Clemente. Avalon, 1893. San Pedro Harbor, June 18, 1901.

Smithsonian: 7474, San Diego Bay, Rosa Smith. 12714, Catalina Harbor, W. H. Dall, January, 1874 (c 6), 40 fathoms. 12643, Catalina Harbor, W. H. Dall, January, 1874 (c 7), 40 fathoms. 12722, San Diego, Rosa Smith, ac. No. 14099. 12734, Catalina Harbor (c 32), U. S. N. M., 40-60 fathoms.

Albatross stations: 3576. 3620, San Diego Bay.

***Ophiothrix rudis* Ly.**

Figs. 30, 31.

Bull. Mus. Comp. Zool. Harvard, III, pt. 10, p. 239, pl. III, 1874.

Diameter of disc 11 mm. Length of arm about five times diameter of disc. Disc covered with cylindrical spines, which bear microscopic thorns. Radial shields bare. Almost touching without. Numerous tooth papillae. No mouth papillae. Mouth shields quadrilateral, the inner angle obtuse, outer angle right and lateral angles acute. Side mouth shields narrowed and separated within. Genital openings beginning outside mouth shield. Tentacle scale similar to a small arm spine. Ventral arm plates quadrangular with corners cut off. Dorsal arm plates fan shaped. Five to six minutely serrated arm spines (including tentacle scales), the first (dorsal) or second being the longest and about $3\frac{1}{2}$ times length of arm joint, the rest decreasing in length downward. The general moss green color and character of the spines makes the animal resemble seaweed. Disc above green, often with reddish or bluish tinge. Radial shields sometimes with a few red or orange spots. Arm green (often yellowish) above with narrow fuscous and broad red cross bands; almost white below with broad spines usually green. Mouth region pale. Females with ripe eggs in summer.

Along shore, La Jolla. Salinas Cove, June 5, 1901. San Diego Channel, June 18, 1901. Smithsonian: San Diego. (Henry Hemphill), No. 4. 7471, San Diego, C. R. Oreutt (U. S. N. M., ac. No. 14530). Albatross: March 15, 1890, Pt. Loma.

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EXPLANATION OF PLATES.

PLATE 1.

- Fig. 1. *Ophioderma panamensis* Ltk., partial dorsal view.
Fig. 2. *Ophiomusium jolliensis* sp. nov., partial dorsal view.
Fig. 3. Partial ventral view of same.
Fig. 4. *Ophiomusium lymani* W. Thos., partial dorsal view.
Fig. 5. Partial ventral view of same.
Fig. 6. *Ophioplocus esmarki* Ly., partial dorsal view.
Fig. 7. Partial ventral view of same.

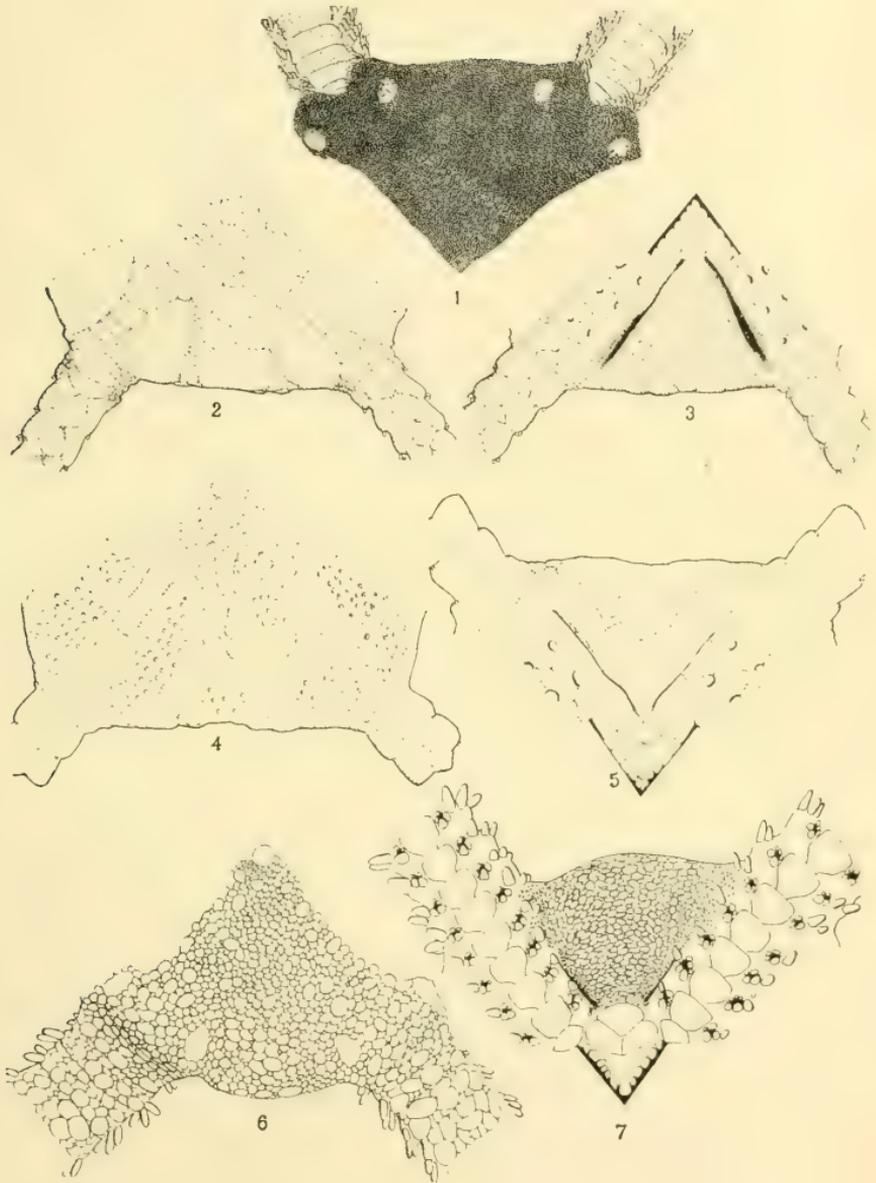


PLATE 2.

- Fig. 8. *Ophura kofoidi* sp. nov., partial dorsal view.
Fig. 9. Partial ventral view of same.
Fig. 10. *Amphiura verrilli*, sp. nov., partial dorsal view.
Fig. 11. Partial ventral view of same.
Fig. 12. *Amphipholis pugetana* Ly., partial dorsal view.
Fig. 13. Partial view of same.

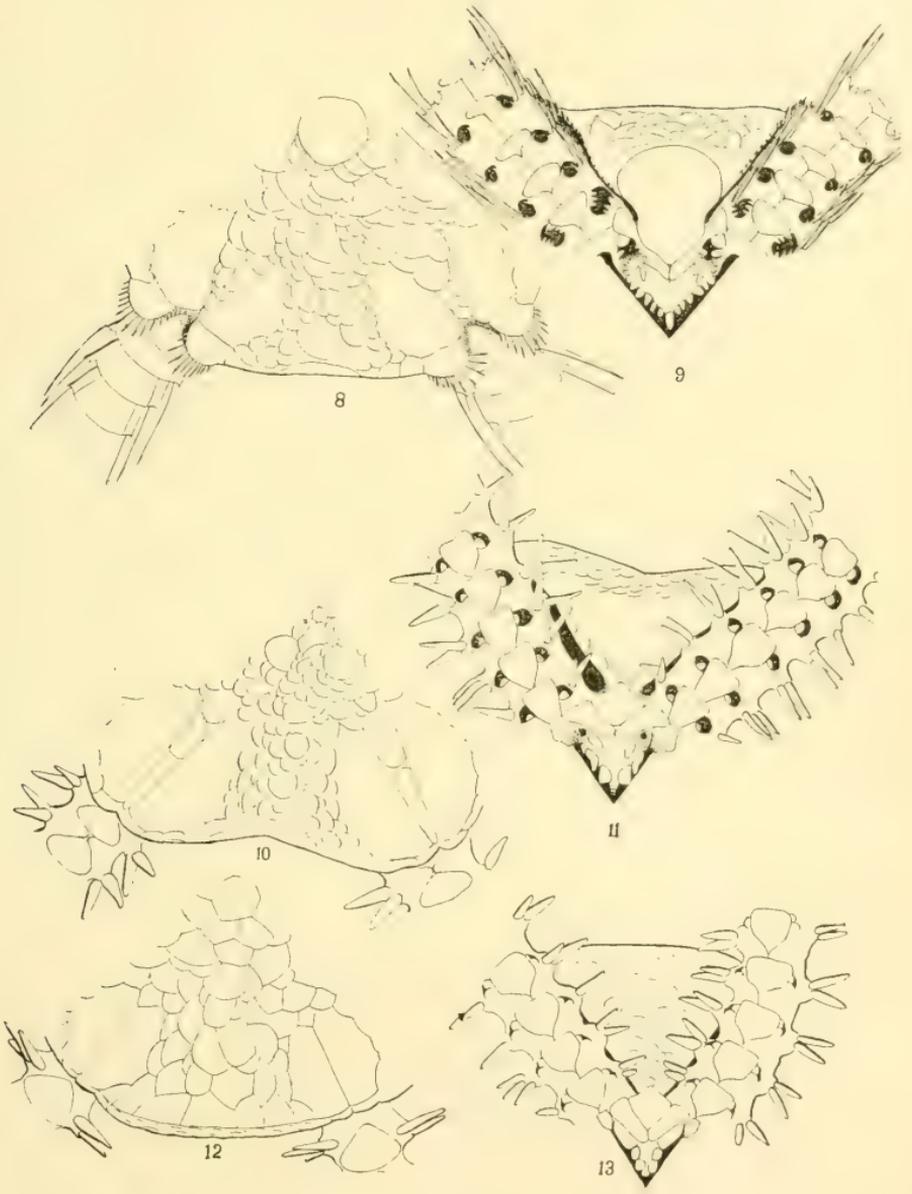




PLATE 3.

- Fig. 14. *Ophiocten pacificum* L. & M., partial dorsal view.
Fig. 15. Partial ventral view of same.
Fig. 16. *Ophiactis arenosa* Ltk., partial dorsal view.
Fig. 17. Partial ventral view of same.
Fig. 18. *Ophiacantha normani* Ly., partial dorsal view.
Fig. 19. Partial ventral view of same.

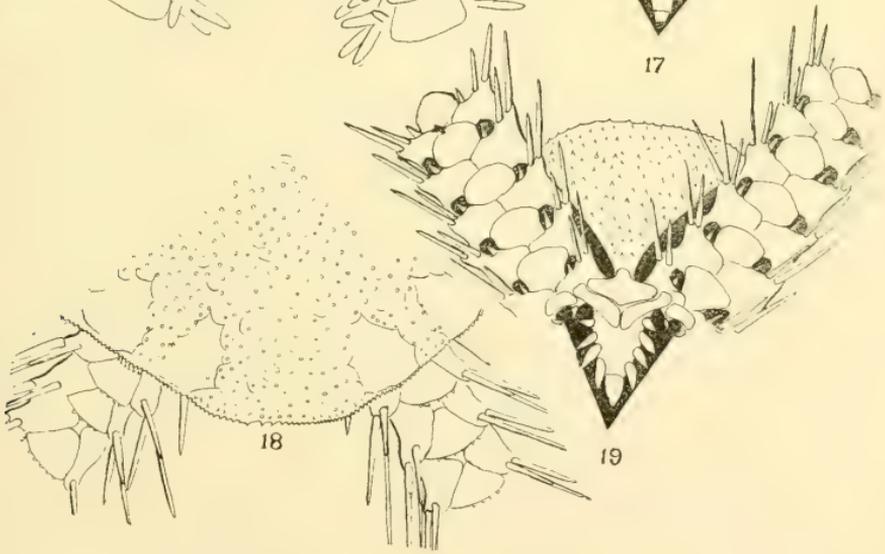
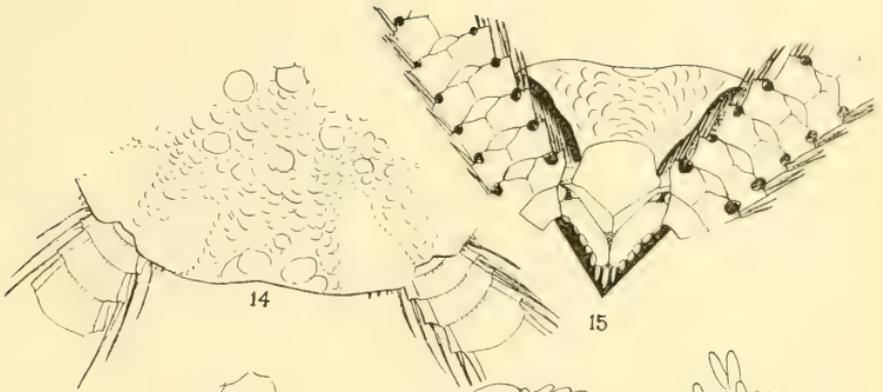
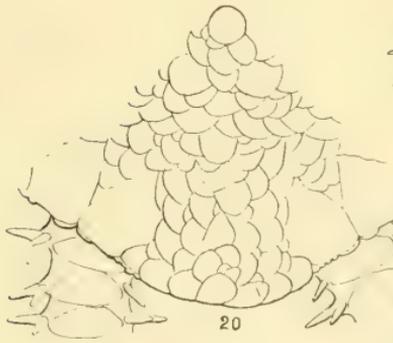
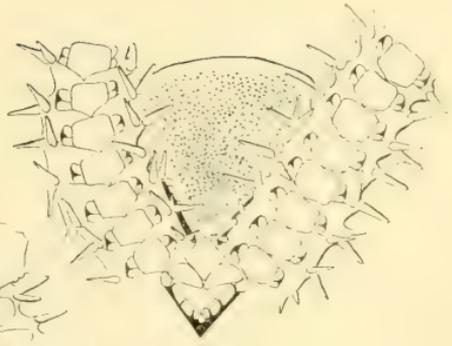


PLATE 4.

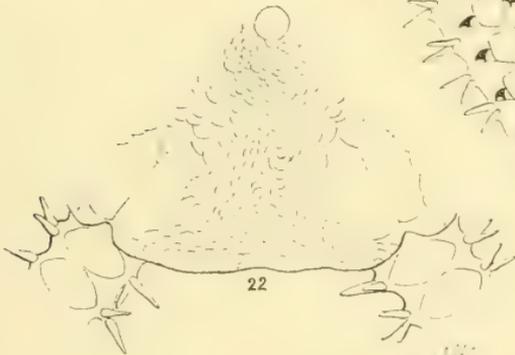
- Fig. 20. *Amphipholis puntarenæ*, partial dorsal view.
Fig. 21. Partial ventral view of same.
Fig. 22. *Amphiodia barbaræ* Ly., partial dorsal view.
Fig. 23. Partial ventral view of same.
Fig. 24. *Ophiocnida amphacantha*, sp. nov., partial dorsal view.
Fig. 25. Partial ventral view of same.



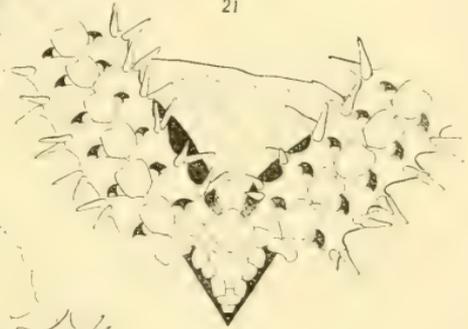
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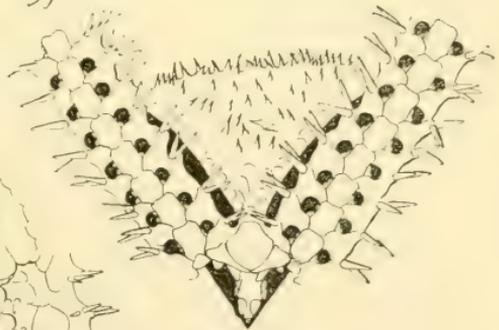
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PLATE 5.

- Fig. 26. *Ophiopholis baleri* sp. nov., partial dorsal view.
Fig. 27. Partial ventral view of same.
Fig. 28. *Ophiopteris papillosa* Ly., partial dorsal view.
Fig. 29. Partial ventral view of same.
Fig. 30. *Ophiothrix rudis* Ly., partial dorsal view.
Fig. 31. Partial ventral view of same.

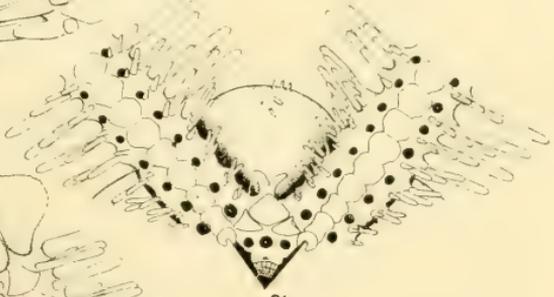
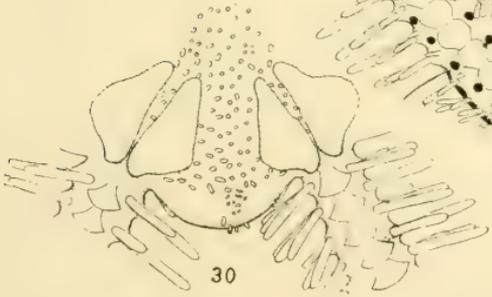
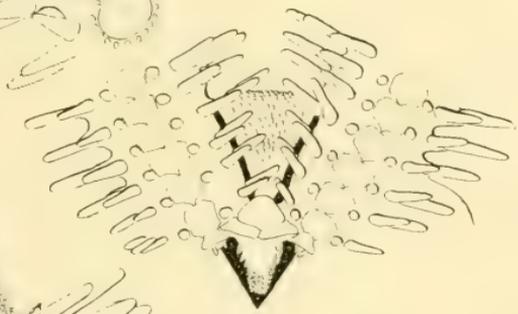
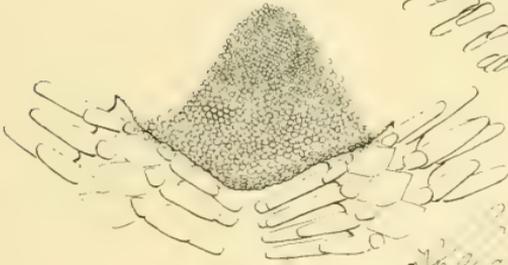
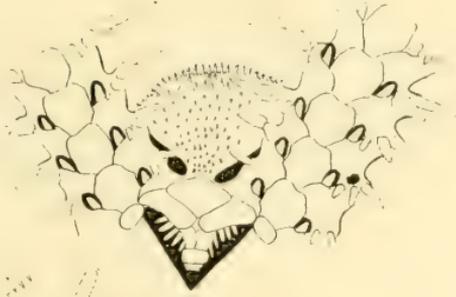
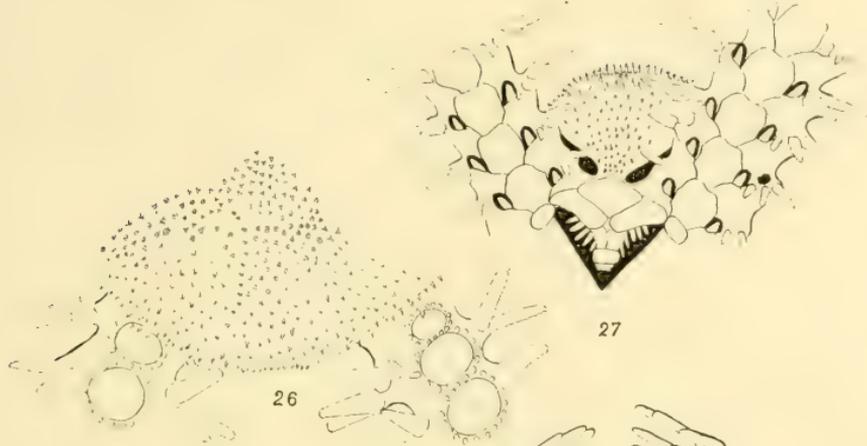
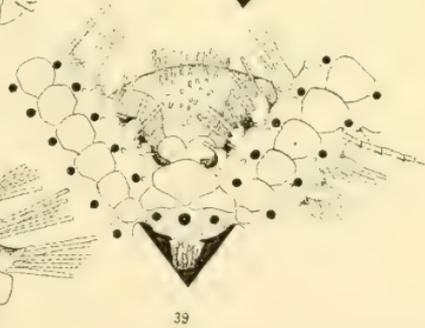
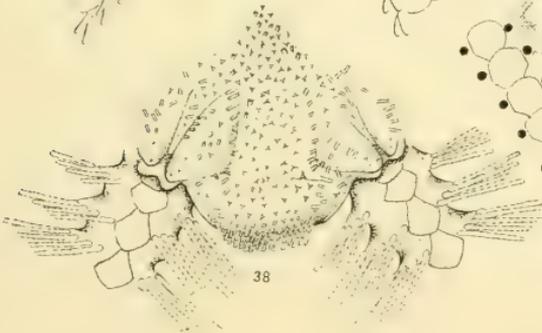
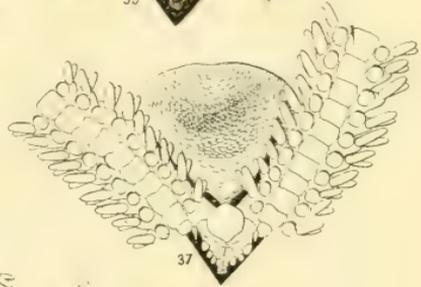
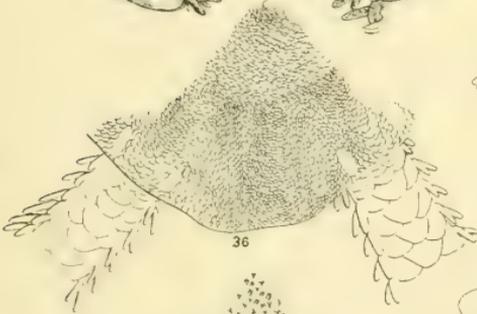
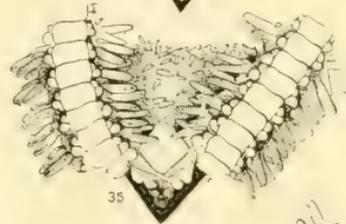
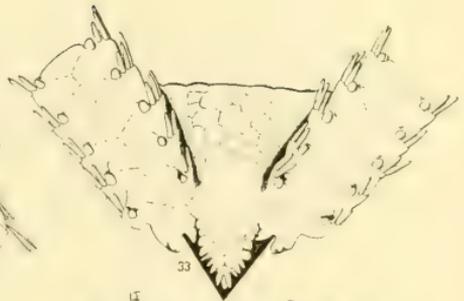
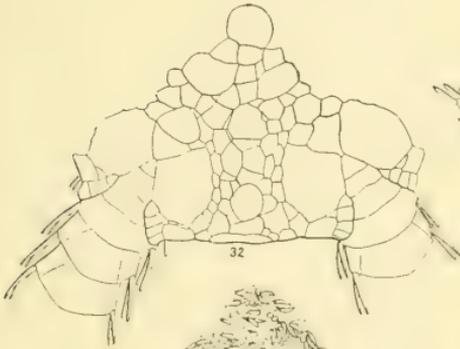


PLATE 6.

- Fig. 32. *Ophüira lütkeni* Ly., partial dorsal view.
Fig. 33. Partial ventral view of same.
Fig. 34. *Ophiocnida hispida* Le Conte, partial dorsal view.
Fig. 35. Partial ventral view of same.
Fig. 36. *Ophionereis annulata* Le Conte, partial dorsal view.
Fig. 37. Partial ventral view of same.
Fig. 38. *Ophiothrix spiculata* Le Conte, partial dorsal view.
Fig. 39. Partial ventral view of same.



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CONTRIBUTIONS FROM THE LABORATORY
OF THE
MARINE BIOLOGICAL ASSOCIATION OF SAN DIEGO

XXVI

HALOCYNTHIA JOHNSONI N. SP.
A COMPREHENSIVE INQUIRY AS TO THE EXTENT
OF LAW AND ORDER THAT PREVAILS IN
A SINGLE ANIMAL SPECIES

BY
WM. E. RITTER

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CORRECTION OF THE NAME OF AN
OPHIURAN.

In my paper "The Ophiurans of the San Diego Region" (*Univ. Calif. Publ. Zool.*, Vol. 6, No. 3) I named one species of doubtful affinities after Verrill. Later I transferred this species to the genus *Amphiura*, but overlooked the fact that there was an *Amphiura verrilli* previously described. To avoid possible confusion I now suggest the name *diastata* for this species.

***Amphiura diastata*, sp. nov.**

Amphiura verrilli McClendon. "The Ophiurans of the San Diego Region," *Univ. Calif. Publ. Zool.*, Vol. 6, No. 3, p. 43, figs. 10-11 (plate 2).

Diameter of disc 8 mm. Length of arm five times diameter of disc. Disc above and below covered with imbricated scales. Radial shields naked, separated, and about twice as long as broad. Three pairs of mouth papillae, two of which may be considered oral tentacle scales. Teeth. No tooth papillae. Mouth shield diamond shaped, the edges next to the genital openings concave, corners rounded. Side mouth shields narrowed and meeting within, broad without. Genital openings beginning at mouth shields. One flat tentacle scale. Ventral arm plates concave on distal margin, narrowed proximally. Side arm plates meeting above, meeting below except at base of arm. Dorsal arm plates elliptical, about twice as broad as long. Four stout tapering arm spines, a little longer than arm joints. Color of dried specimen light grey.

San Diego M. B. L.: San Diego, 100 fathoms. XXXI-a, near Potts Valley, San Pedro.

J. F. McCLENDON.

Woods Hole, Massachusetts.

September 14, 1909.

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1. INTRODUCTORY REMARKS.

Earlier English men of science were fond of speaking of their studies as "inquiries". The usage seems to me wholesome. Implying the interrogation point as the word clearly does, it is a good reminder that ascertained truths of nature are always footholds for further advance, quite as well as so much positively gained.

By "comprehensive" I do not mean that everything concerning this species is included in the study. It seemed desirable, though, to let the title indicate that the "inquiry" reaches in several directions. So strong is the tendency of exact biolog-

ical research to require the remark that such-and-such a conclusion holds "at least so far as concerns such-and-such an animal or plant", that it seems as if the taxonomic standpoint will sooner or later have to be taken seriously into account in all researches whatever.

Halocynthia (Cynthia) haustor Stimp. is one of the most abundant species of ascidian in Puget Sound. The original description of it by Stimpson ('64) being inadequate, von Drasche ('84) re-described and figured it in much greater detail. Herdman ('98) testified to the general accuracy of von Drasche's description and added some observations of his own. Examination of numerous specimens from the Sound carried on in connection with the preparation of this paper modifies somewhat the published descriptions, but in no wise impairs the validity of the species. *H. haustor* has consequently a secure place in science.

In San Diego Bay, in Wilmington, or San Pedro Bay, and at various other points on the coast of Southern California as far north at least as Point Conception, occurs abundantly an ascidian so closely resembling *H. haustor* that the innumerable specimens taken during the last ten years, particularly in San Diego and Wilmington bays, appear under labels bearing this specific name. However, recent thoroughgoing study of the southern animals, as also of the northerners, reveals the fact that they are sufficiently different to require different designations. The southern one I consequently name *Halocynthia johnsoni* after Miss Myrtle Johnson, one of my students, but for whose dissections and sketches no such extensive examination of the structure and variation of the species would have been practicable.

The great abundance and ready accessibility of the species along with its hardiness will, in all probability, make it a favorable subject for future special investigations. I have thought it desirable, partly on this account, to deal with the species considerably more fully than under prevailing conditions it is customary, or perhaps altogether convenient, to do in the original record of a new species.

The species undoubtedly flourishes best in shallow, land-locked waters. Nowhere has it been found in more than strag-

gling numbers excepting in San Diego and Wilmington bays. At San Diego it occurs abundantly on the piles of the city waterfront, but it also is a dweller on muddy bottoms at some places in the middle and upper bay. Just what characterizes the localities favored, I am unable to say. At San Pedro it has been taken scarcely anywhere else than in those portions of Wilmington lagoon, or bay where the water is so shallow as to be accessible to a small launch at high tide only. Here it was taken during the summers of 1901-02 in great numbers, mingled with rock-oysters and pectins. A few small specimens were the reward of careful search by myself on the defiant rocks of Point Conception at New Year's time, 1908. At no other outside points has the species been taken, though more extensive search would, without doubt, increase the range and number of places inhabited by it.

2. DIAGNOSIS OF THE SPECIES. *Halocynthia johnsoni* n. sp.

Superficial characters:—Variable in form, this largely dependent upon habitat; generally elongate antero-posteriorly, somewhat larger at the broadly attached posterior end; *siphons* varying in length but always evident, never widely separated at base; *color* generally dark brownish yellow, this usually obscured by mud and other foreign substances, inner surface of orifices bright red; *surface* more or less irregular and corrugated, but rarely or never presenting positive tubercles; *size*: length of largest specimens 6 to 8 cm. including siphons, thickness nearly always less, sometimes by one-half. (Pl. 7.)

Test:—Varying in thickness not infrequently reaching 4 to 5 mm., less frequently falling to 1 mm.; varying also in consistency from distinctly hard and firm to something approaching fleshiness; surface in general rather even, tubercles wanting, and ridges or other inequalities sparse, wide, and low; not well supplied with blood-vessels.

Mantle:—Bright red, particularly anteriorly, not transparent, rather thick. *Musculature* moderately strong on the siphons and anterior half of body; an external layer of fine, irregular, generally transverse fibers, and an inner layer of much stronger radial fibers grouped in distinct bundles (Pl. 8, fig. 2, *m. mus.*).

Branchial Apparatus:—*Siphons*, particularly as seen after removal of the test, typically, though by no means universally, of good length, frequently long and slender. (Pl. 7, figs. 1 and 1'.) Branchial generally broader at base and somewhat more terminal as to the long axis of the animal; orifices of both positively quadrangular, color of lobes with alternating red and white spots or areas. *Tentacles* varying in number from 17 to 62 (see tables), of very unequal size, compound. *Hypophysis*, typically horseshoe shaped, the two ends turned in more or less, but various deviations from the type. (Pl. 10, figs. 1 to 29, left column.) *Ganglion*, rather narrow, close behind the hypophysis.

Dorsal Langucts:—Generally rather long and slender, regular, varying in number from 43 to 187 (see table). *Branchial membrane* with six folds on each side, fourth from the endostyle usually largest, having maximum of 29 longitudinal vessels, the first from endostyle smallest with maximum of 24 vessels (see table). Transverse vessels also present, of different sizes, usually about six *stigmata* between each two longitudinal vessels: for purposes of description these designated as "long" and "short" (see table).

Intestinal Tract:—Situated on left side of the body, loop wide, the great bend reaching far forward, rectal limb with flexure, anus with a thickened edge, variously lobed and notched: (Pl. 10, figs. 1-29, right column). *Stomach* somewhat, though but little, greater in diameter than intestine, with typically three folds on inner aspect, the middle one largest (Pl. 8). *Liver* a brownish-yellow organ in the form of a bunch of grapes, opening by a short, wide duct into the distal end of the stomach, the gland itself lying between the stomach and the return limb of the intestine; some of the lobes closely adherent, probably by blood-vessels, to the outer surface of the branchial membrane. "*Lactal*" system presenting a number of irregular lobes projecting conspicuously along the great bend of the intestine (Pl. 8, fig. 3).

Reproductive Organs:—On both sides of the body, those of left in the intestinal loop, consisting of a double series of more or less regular, pear-shaped lobes placed close together along each side of the axial duct with which all communicate (Pl. 8,

figs. 2 and 3). the lobes adherent to the mantle on their outer surface, and the branchial membrane on their inner; many of the lobes containing both male and female elements.

3. SOME FURTHER ANATOMICAL POINTS.

The only points so far recognized which differentiate the California from the Washington species are in the structure of the test and the number of the tentacles. Test tubercles are prominent and hardly ever wanting in *H. haustor*. These are well shown in figures drawn from living specimens by Professor Bashford Dean (Ritter, 1900, Plate XVIII, figs. 8, 9, 10). Von Drasche speaks of the test as being very characteristic, and describes it as follows: "Sie wird von einem Netzwerk erhabener Rücken gebildet, welche von einander durch polygonal begrenzte Depressionen getrennt werden" (von Drasche, '84, p. 372). This characterizes admirably many old alcoholic specimens, but it is not adequate for living or even well-preserved formaldehyde material. In many cases the tubercles are quite wartlike, at times becoming almost pedunculate. At best a mere suggestion of these is present in *H. johnsoni*, and in a vast majority of the specimens nothing of the sort is visible. Examination of sections reveals the fact that the test of *haustor* is much more vascular than is that of *johnsoni*, and that the tubercles are the chief seat of the vessels. Plate 11, figs. 8, 9, 10, illustrate this. Figure 8 is from *H. johnsoni* and represents what seems to be a typical condition as regards vessels in this species. In all likelihood specimens and areas might be found more vascular than the piece here figured, but the individual selected was one in which the test was at about the maximum of fleshiness, it being assumed that such condition would present the highest degree of vascularity. Figure 9 presents what seems to be a typical condition of the *haustor* test in the areas between the ridges. Figure 10 is from a section of one of the tubercles. It tells its own story as to the vessels. The bulbous termination of many of them much resembles the corresponding structures in the common test of several compound ascidians, notably the Botrylids and Polystyelids.

Tentacles.

The tentacle number in twenty-five individuals of *H. johnsoni* varied, as the table shows, from 17 to 62, and averaged about 42. The average for the National City five, 39.2, cannot be regarded as enough less than the average for the others to be significant. In ten specimens of *H. haustor* the variation was from 12 to 29, with an average of 21.

The branching of the tentacles is rather diffuse for the genus, and is no haphazard, lawless matter. Plate 12, fig. 13, represents the whole of one of the largest tentacles of a specimen 1.25 x 1.5 x 1 cm. in size; *i. e.*, one of the smallest taken in ordinary collecting. Figure 11 shows the tip of one of the largest tentacles from a specimen measuring 5 x 3.5 x 3 cm.; *i. e.*, an individual of about maximum size. The smaller tentacle was 1.5 mm. long, the larger 7 mm. Both were drawn by Miss Johnson with as much faithfulness to detail as possible. It is obvious that new branches are added for a considerable portion of the animal's growth period. A little attention reveals several laws or rules according to which these additions are made. To discuss these a system of designation is necessary. The branches we may call primary (*b'*), secondary (*b''*), and tertiary (*b'''*). None of a higher grade have been observed. The axes of these may be designated as follows: *a* axis of the tentacle itself, *a'* axis of *b'*, *a''* axis of *b''*. Since *b'''* produces no branches, we need not be concerned with *a'''*. As each of these orders of branches appears in different sizes (ages), such of these as are referred to specifically have to be designated in some way. Those branches pertaining to any given axis may well be spoken of as generations. Thus all the *b*'s may be said to belong to the first generation (*g'*) of axis *a*. In the same way, all the *b''* would belong to the first generation of the axis *a'*. Inspection of figure 13 shows that in this particular tentacle only first and second generation branches of the first order, and only first generation branches of the second order, are yet present.

Not so with the large tentacle, a part of which is shown in figure 11. Here several other later generations are recognizable on the various orders of axes. Thus *g''*, *g'''*, *g''''*, also *g''''*, *g''''''* (all letters to the left), are seen pertaining to *a*. Also *g'* and *g''* of

b' (to the right in the figure) are recognizable on the particular b' specified by the lettering, and these two generations can readily be seen on most of the other b' 's. In several instances g'' is also recognizable on b' , as, for example, on the fourth from the base to the right. Furthermore g' and g'' may be recognized in several places on b'' , for example on b'' of b' at the base to the left.

But the orderliness of branch production recognizable to cursory inspection extends still further. Figure 13 illustrates especially well the points now to be noted. Although this figure is diagrammatic in a way, it is accurate as to numbers of branches. The positions, too, of all the branches and length of the primaries were determined by micrometer measurements, and the secondaries were drawn as accurately as possible. From this figure it is seen that the branches b' of the first generation are longest at a point on a somewhat distal to its middle, and that from these of maximum length the others become gradually shorter toward both the base and the apex of a . This undoubtedly means that new branches of this generation are added both distally and proximally¹ from the initial ones of the generation. A glance at any whole, full-grown tentacle reveals the general form scheme as unmistakably as does this young one. The specimen from which figure 11 was drawn, for example, shows it beautifully, but it was impracticable to draw the whole on a scale large enough to bring out the smaller details the illustration of which seemed of more importance. Again, inspection of the branches b' shows that the secondary branches b'' , without much doubt, follow in general the same scheme. Attention to the disposition of the b'' 's of figure 11 shows that the same rule holds in this presumably full-grown tentacle. At any rate, this much is obvious, that the largest b'' 's are never at either end of the axes of the b' 's. When it comes to the b'' 's, the prevalence of the rule is not so obvious, though in many instances intimations of it are seen. Attention should be called to the

¹Although allowing this statement to stand, I am now in considerable doubt about the addition of new branches proximalward. From observations made and information obtained touching somewhat similar series in other organisms, it seems not unlikely that new additions are here always distalward from those already existing.

fact that just as the largest b 's of a are somewhat nearer the distal than the basal end, so seemingly the largest b 's of a' are somewhat nearer the distal ends of these axes; and the same appears to be true for the other orders as well.

One other set of closely related facts is observable: the individual branches of any generation are arranged in the same plane but on opposite sides of the axis, and the new ones of the two sides come in in alternate fashion. This is well illustrated in figures 13 and 11. Figure 12 may seem to contradict this statement, but the contradiction is only apparent, it being due to the obliquity of the tentacle-axis to the line of vision.

Worthy of note finally is the fact that the branches of the several generations along the same side of any axis are in general in a line, this line being somewhat nearer the edge of the axis that looks toward the center of the tentacular circle.

Since the tentacle number is perhaps the most distinct differential character between the two species, it would be instructive to make a comparison of these organs in all the points shown above to be subject to rules of multiplication, to ascertain whether specific differences might not be found in some of these as well as in the number of the tentacles themselves.

There is little doubt that still more extended study of the two species with reference to other organ systems would bring out other specific differences. For the present, however, the test and tentacle differentials must stand as their identifying marks. But in addition to these two structural features of recognizable systematic value, there are a few others without such significance that still deserve particular attention.

Intestinal Tract.

In the intestinal tract (Pl. 8, fig. 3), the pronounced rectal bend, the obscurity of the differentiation of the stomach from the intestine proper, the circumscription of the liver, l , and its wide duct opening into the stomach, and the "lacteal" system, *lc. s.*, are noteworthy. The mantle adheres very closely to the viscera, especially to the intestinal tract. From this fact and the fragility of the intestinal wall, it is somewhat difficult to expose the organs uninjured. When this is accomplished one

still remains in doubt as to just where the stomach ends and the intestine begins. In figure 4 the distinctness has been exaggerated somewhat by the artist. It seems, however, that the "liver" empties into the stomach proper. Two of the three typical stomach folds are shown in the figure. It will be noted that the larger of these extends on beyond the mouth of the liver duct.

In no ascidian have I noticed so great a development of the alveolar lobes of the "lacteal" system as in this species. Their general distribution on the intestine is shown in Plate 8, fig. 3 (*lc. s.*), and a few of them somewhat more detailed, together with the ducts on the surface of the intestinal wall (*d. lc. s.*), in Plate 9, fig. 6. The anatomical conditions here presented suggest that this species would be favorable for a study of the physiology of both the "liver" and the "lacteal" system.

Reproductive System.

The reproductive organs are nearly symmetrically disposed on the two sides of the body, as figures 2 and 3 show. The combination of the female and male elements in the same gonadial pouches, a condition not uncommon in the genus *Halocynthia*, is also shown by these figures. In life the testis portions of the lobes (*gon. ♂*), always distal from the axial duct, are straw color, while the ovarian portions are a pinkish gray. The female parts are much the larger in amount, constituting the whole of the lobe in many cases, and rarely or never fail to constitute the major part of any particular lobe, though whether this proportion holds for the whole life of the animal I do not know. The sperm duct and oviduct are so closely united (fig. 2, *gon. d♂♀*) that I have not been able to distinguish them in *in toto* preparations except by the terminal papillae (Pl. 9, fig. 5) and the presence of sperm in the vas deferens. That the two ducts are distinct throughout has been shown particularly by Lacaze-Duthiers et Delage ('93), for *H. morus* of the European seas. Whether or not self-fertilization is ruled out in *H. johnsoni* is not known.

Decidedly worth noticing is the constancy in number of the gonadial lobes. By reference to the variation tables it will be

seen that there is less variation here than in either the number of branchial tentacles or dorsal languets.

The Branchial Sac.

The disposition and size of the dorsal languets is noteworthy. Plate 12, fig. 14, *d. l.*, shows the typical state of things for a small animal (1.25 x 1.5 x 1). The wide, bare area to the right (*A* indicates anterior, and the piece of sac is, of course, seen on its inner surface), between the series and the stigmata, and the entire absence of such an area to the left, attracts attention first. Although areas of this nature are not uncommon in the Cynthiidae, it is not often so broad as here. It is present, for example, in *H. superba* (Ritter '96). These two species, so very different in most respects, have another common point in connection with the languets, viz.: stragglers occur in both outside the line, *d. l.* These are more numerous in *superba* than in *johnsoni*. They are most apt to be on the bare area, but an occasional one is seen in other places. Only one is present in figure 14, but that is especially interesting since it is on the branchial membrane proper. I call particular attention to these stragglers, and raise the question, are they not, in essential nature, mutants?

In larger individuals the languets are longer and more slender than are those of the one shown in figure 14. I have taken some pains to determine whether the languets in this species correspond to the transverse vessels, or sinuses of the branchial membrane, as they undoubtedly do in some ascidians. Damas, (1900), for example, has established very beautifully such a relation in *Ciona intestinalis*. Figure 14 was drawn by Miss Johnson with this point especially in mind, and she has attempted to assign the different languets to particular sinuses. There is, however, so much departure from regularity even in so small a specimen that one cannot decide with great confidence that such a coincidence is the rule. I am inclined to believe that in still smaller individuals such a rule would be recognizable.

The investigations of Selys-Longchamps and Damas, which will be noticed more at length later, have put the transverse sinuses and stigmata in quite a different light both as to their

morphological and their taxonomic significance, from that in which they stood before. It is clear now that in probably all ascidians with a highly complicated branchial membrane this organ can be interpreted with confidence only by following its developmental stages back to at least the full set of protostigmata of the embryo, and further, that a reference to the number of stigmata and the different size-orders of transverse sinuses without taking into account the size of the individual, can have only a general value for species determination.

As the present study falls much short of the larval stage I am not prepared to discuss the sac makeup in any fullness. A few facts have, however, been ascertained that will be useful as a starting point for the study of earlier stages. Plate 13, fig. 15, is from a small individual, 1.25 cm. and fig. 16 is from an individual 5 cm. long. Both are intended to take in all the sizes of transverse sinuses present in the sacs concerned. It will be seen that *four* sizes occur in the smaller individual and *six* in the larger, and that in both the smallest are still incomplete. It will also be seen that the stigmata are fewer in number between the longitudinal vessels in fig. 15, and further that the ratio of breadth to length of the individual stigmata is greater in the former figure, *i.e.*, in the smaller individual. Although I have not studied in detail either sinus or stigmata production, I may say that nothing appears contrary to the conclusions reached by the authors above cited as well as by others, that new stigmata are always produced from old ones. In view of this apparently universal rule of stigmata production, it is interesting to inquire whether new sinuses are also produced from old ones. That such is not the case is almost certain, as the beginning sinuses in both the figures here referred to indicate.

4. SOME STATISTICS ON VARIATION.

Tables I and II present the quantitative results of the examination of twenty-five individuals of *H. johnsoni*. The series of outline figures, 1 to 29, Pl. 10, show the hypophysis mouth, and the anus respectively, of these same individuals.

TABLE II.

AVERAGE VALUES FROM TABLE I.

Tentacles		Dorsal Languets		Stigmata long		Stigmata short		Gonad lobes	
1st 13	2d 12	1st 13	2d 11	1st 13	2d 12	1st 13	2d 12	1st 8	2d 10
46.6	38	113	74.4	10	4	3	8	58.6	50.4

National City Five.

39.2	116.4	0	5	56.4
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Longitudinal Vessels <i>between folds</i>				Longitudinal Vessels <i>on the folds</i>	
1st 12.		2d 12.		1st 12.	2d 12.
No. 1	4.7	No. 13	2.57	19.8	20.
2	2.3	14	2.57	23.1	19.1
3	3.	15	3.15	24.	15.8
4	4.	16	2.4	22.5	17.7
5	3.7	17	4.	24.3	13.5
6	2.	18	2.3	20.	16.5
7	2.7	19	3.1	22.	15.6
8	3.7	20	2.3	20.3	17.1
9	2.59	21	4.	20.6	13.3
10	3.3	22	3.8	22.5	14.
11	3.	23	2.3	23.1	17.6
12	3.7	24	1.3	19.3	19.3
Av.	3.22	Av.	2.80	Av.	21.8
				Av.	16.6

National City Five.

I	3.1	24.3
II	2.7	20.
III	2.3	23.
IV	2.9	20.
V	2.4	16.6
	2.68	20.5

These tables and sketches make several interesting revelations concerning the variation of the species. Probably the most significant is the fact that in so many of the points examined the variation is clearly correlated with the size of the animal. The two particulars in which this is most positively seen, so far as the tables go, are the number of dorsal languets and the shape of the branchial stigmata. In table I the twenty-five specimens studied are arranged in order of size of the individuals, from largest to smallest. The gradual though very irregular increase

No. of Speci- men	Size			Thickness of Test
	L.	W	T.	
1	6.5	4.3	3.5	thick
2	5.4	4	3.4	"
3	5.3	3.5	3	"
4	4.7	3.7	3.4	"
5	4.8	4.6	2	"
6	4.7	3.2	1.7	thin
7	4.5	3.7	3.1	thick
8	4.5	3.5	2.8	"
9	3.7	3.4	2.6	"
10	3.6	2.6	2.5	"
11	3.4	4	2.2	"
12	3.5	2.7	2.1	thin
13	3	2.7	2.4	thick
14	3	2.5	2.1	"
15	3	2.6	1.8	medium
16	2.8	2.5	2	"
17	2.8	2.5	1.8	thick
18	2.7	2.8	1.7	thin
19	2.6	2.5	1	medium
20	2.3	2.5	1.4	thick
21	2.2	2	1.3	medium
22	2	1.8	1.3	"
23	1.9	2.2	1.4	thick
24	1.8	1.8	1.1	"
I	5	4	3	"
12'	3.2	2.5	2.2	"
II	5	3.5	3	"
III	5	3.5	2.5	"
IV	4.5	3.5	3	"
V	3.5	2.5	2	"

TABLE I.

No. of Specimen	Size			Thickness of Test	No. of Tent.	Longitud. Vessels (Upper Nos. = between Folds) (Lower Nos. = upon Folds)										Dorsal Lan-guets	Stig-mata	Locality	Station	Date	Preservation	Gonad Lobes			
	L.	W.	T.			1st	2d	3d	4th	5th	6th	7th	8th	9th	10th										
1	6.5	4.3	3.5	thick	56	4	1st 15	6	2d 15	6	3d 20	5	4th 26	3	5th 22	5	6th 21	4	153	long	S.P.	3 dredged	10/7/95	90% al.	57
2	5.4	4	3.4	"	62	2	18	3	22	3	26	2	25	2	22	3	27	1	86	"	"	19	27/7/95	2% form.	—
3	5.3	3.5	3	"	48	1	18	4	18	4	20	4	24	4	24	2	30	1	187	"	S.D.	Piles	1898	form.	57
4	4.7	3.7	3.4	"	54	3	17	4	21	5	22	5	24	4	25	4	26	4	120	"	"	?	20/1/00	"	55
5	4.8	4.6	2	"	51	2	18	3	19	4	22	3	29	3	26	6	22	5	113	"	S.P.	9 and 11	20/7/95	90% al.	34
6	4.7	3.2	1.7	thin	49	2	14	2	19	2	18	3	23	2	20	2	26	1	111	short	"	?	—/7/96	90 al.	60
7	4.5	3.7	3.1	thick	58	3	16	5	22	3	24	2	26	2	21	2	24	2	143	long	Coron.	?	10/7/95	2% form.	60
8	4.5	3.5	2.8	"	55	2	17	6	21	3	22	3	23	4	21	4	18	4	111	"	"	?	10/7/95	"	59
9	3.7	3.4	2.6	"	38	3	12	5	18	3	21	3	24	2	24	0	25	2	79	"	S.P.	19	29/7/95	"	41
10	3.6	2.6	2.5	"	30	1	16	5	22	4	22	3	25	4	24	3	26	5	112	"	S.D.	Piles	8/8/07	form.	—
11	3.4	4	2.2	"	39	2	22	3	20	3	23	4	24	4	26	3	24	2	86	short	S.P.	19	26/7/95	2% form.	—
12	3.5	2.7	2.1	thin	42	3	14	5	20	5	20	4	22	3	20	5	20	3	119	"	Coron.	?	10/7/95	90% al.	46
13	3	2.7	2.4	thick	52	2	15	4	21	4	21	3	21	2	18	1	24	2	98	long	S.D.	?	20/1/00	form.	58
14	3	2.5	2.1	"	29	2	14	4	17	3	20	4	21	2	20	1	23	2	73	"	S.P.	?	14/6/00	"	55
15	3	2.6	1.8	medium	56	2	11	3	13	3	18	3	18	3	17	3	17	4	56	short	"	8	30/6/95	90% al.	47
16	2.8	2.5	2	"	33	2	18	2	22	2	20	3	16	4	12	2	18	2	68	"	"	19	26/7/95	2% form.	35
17	2.8	2.5	1.8	thick	39	3	9	4	11	5	13	4	17	3	14	4	17	4	56	"	"	8	30/6/95	90% al.	47
18	2.7	2.8	1.7	thin	31	2	13	4	14	3	17	2	20	2	19	1	16	2	90	"	"	19	26/7/95	"	59
19	2.6	2.5	1	medium	60	2	13	5	14	3	18	3	18	3	15	2	16	4	43	"	"	8	30/6/95	"	58
20	2.3	2.5	1.4	thick	34	2	13	3	16	3	18	2	22	2	16	2	18	2	69	long	"	?	20/1/00	form.	54+
21	2.2	2	1.3	medium	43	3	12	4	11	6	14	5	16	4	14	3	13	3	44	short	"	8	30/6/95	90% al.	33
22	2	1.8	1.3	"	31	2	12	4	13	4	14	5	15	3	14	4	16	4	52	"	"	19	26/7/95	Cocaine 2% form.	58
23	1.9	2.2	1.4	thick	17	2	13	3	15	3	18	3	23	1	17	2	18	2	70	"	S.D.	Piles	—/8/07	form.	—
24	1.8	1.8	1.1	"	28	1	18	2	18	2	21	2	22	0	18	1	19	1	—	long	"	?	20/1/00	"	—
I	15	4	3	"	57	3	18	5	22	5	23	3	28	2	27	—	28	1	145	short	Nat. City	Piles	4/7/08	"	62 44
12'	3.2	2.5	2.2	"	24	3	21	2	22	2	24	3	20	3	19	2	16	2	57	long	S.D.	?	—/7/07	"	—
II	5	3.5	3	"	33	2	16	3	19	3	21	3	24	3	20	1	21	4	115	short	Nat. City	Piles	4/7/08	"	61 58
III	5	3.5	2.5	"	37	2	17	3	22	3	24	2	26	2	24	1	27	3	145	"	"	"	4/7/08	"	55 60
IV	4.5	3.5	3	"	45	2	16	4	20	4	19	3	24	2	22	2	19	3	106	"	"	"	4/7/08	"	52 40
V	3.5	2.5	2	"	21	3	13	3	14	3	17	3	20	3	17	1	19	1	71	"	"	"	4/7/08	"	52 40

in number of the languets with increase in size of the individual is undoubted, and the average number for the thirteen largest, 113, as compared with that of the eleven smallest, 74.4, is too pronounced to admit of any other interpretation than that *the number of dorsal languets increases with increase in size of the animals*. The data are not sufficient to prove whether the increase continues as long as there is increase of size of the individuals. So far however as the evidence goes it indicates such to be the case.

No effort was made to bring the change of shape of the stigmata to a numerical basis, though beyond the labor of making the measurements it would not be difficult to do. The change referred to consists in an increase of the ratio of length to breadth of the orifices. The classification into "long" and "short" can of course present the actual conditions only in a rough way. Nevertheless when all the branchial sacs are examined somewhat attentively by the same person (Miss Johnson did this), the line of separation between "long" and "short" is sure to be not far from the mean as this would be obtained by measurement. That the result reached was not subject to the bias which previous knowledge or supposition that length of stigmata and size of animal go together, is assured from the circumstance that this possibility was not thought of by Miss Johnson until the original laboratory notes had been tabulated. As a matter of fact the classification was made with the supposition of quite a different correlation. Figures 15, 16, and 17 illustrate the increase in length of stigmata with increase in size of animal, the individual from which fig. 15 was drawn being 1.25 cm. long, and that from which fig. 16 was drawn being 5 cm. long. The evidence that the longitudinal vessels of the branchial folds increase in number with size is little if any less convincing than is that of increase in number of dorsal languets, and in proportional length of stigmata.

The average for each individual is found by adding together all the vessels of all the folds of one individual and dividing by the number of folds. This does not regard the number on any particular fold, *i.e.*, the distribution of the vessels on the folds. I have little doubt that were the data sufficient it would be found

that the number on any particular fold in any particular animal increases with the size of the animal.

As table II shows, the average number of branchial tentacles in the first thirteen, *i.e.*, the thirteen largest individuals, is 46.6 while the average for the second twelve is only 38. Because of the difficulty of counting these structures the difference in the averages here is not large enough to make it sure that the results indicate what they seem to. The probability is however that they do.

Does this numerical increase of parts *with size* of animal mean increase *with age*? In other words, can we rely on size in this animal as an index to age? Of course this must be so within certain limits. Stated exactly the question is: Given two specimens, the one larger with a greater number of dorsal languets, for instance, does it follow that this one is older? The answer probably is that generally, though not invariably, this is true. The data are insufficient to enable us to speak more positively. From the taxonomic standpoint however, it seems that somewhat more account should be taken, in some groups of ascidians at least, than generally is of the possibility that numerical variations indicate age rather than specific difference. In some genera, as for example *Perophera*, it is certain that a limit of individual growth and a maximum number not only of stigmatic series, but also, within rather narrow bounds, of individual stigmata, is early reached.

5. TO WHAT EXTENT MIGHT THE DEVELOPMENT OF THIS ANIMAL BE REDUCED TO A REPETITIVE BASIS AND TREATED NUMERICALLY?

Asceidiologists do undoubtedly take it for granted that, within the same species at least, difference in size, and with this, difference in number of repetitive parts means difference in age. This assumption surely contains the truth, but the truth only in a general way, we say. Now the question comes, as it is bound to in every branch of science, how long are we justified in being content with procedure and hence with results based on what is true "in a general way"? Sooner or later any science, if it is really going ahead, is sure to look more closely at assumptions

which it has hitherto held as adequate and has used without particular questioning. It is sure to break up, so to speak, certain of its observations *en masse* into elements which must be examined more in particular. An excellent special instance of this general principle is afforded by the very matter of ascidian structure and classification here encountered. Recent studies by Selys-Longchamps (1899), by Longchamps et Damas (1900), and by Damas alone (1900), are even more strikingly to the point so far as actual observation goes, than are mine. For the present purpose I make reference to Damas's work chiefly. Concerning the multiplication of branchial stigmata Damas says: "C'est l'opinion ancienne sur le mode de formation des stigmates définitifs qu'un récent ouvrage théorique résume ainsi: 'Dans la branchie, le nombre des fentes stigmatiques et des trémas s'accroît, mais sans ordre'" (p. 20). By reference to the studies of Willey, Selys-Longchamps and others, he shows how erroneous the notion is that the production of new stigmata is 'sans ordre.' And he himself not only confirms the results of others as to the origin of new stigmata from those already existing, but goes a long step further by showing the extent to which the formation of various other elements of the branchial sac is correlated with the formation of new stigmata. Without entering into the details of his interesting study, the purport of it, so far as concerns this particular point, is contained in the following: "Les lois de nombre et de position qui régissent les différents ordres distingués plus haut de sinus transverses, de languettes dorsales et de muscles—lois de redoublement et d'alternance par intercalation—sont la conséquence immédiate et un autre mode d'expression du développement de ces différents éléments" (p. 29). The "development of the different elements" on which the "law of number and position" depends in *Ciona intestinalis*, the particular species studied by Damas, consists in the formation of six protostigmata in the larva, each of which gives rise to a primary series of *definitive stigmata*, these series being separated by five primary *interserial sinuses*, and then the division of each of these primary series by secondary sinuses, and so on. But as indicated in the law quoted, the multiplication of the dorsal languets and of the muscle bands is intimately correlated with the multiplication of the other branchial parts.

With attention focused upon the multiplication of parts in the branchial sac, as it is primarily by the studies of the French naturalists, and upon a similar process in tentacle development by the present study; and further upon the wide prevalence of a more or less distinct numerical order in the general make-up of the ascidian body clear to every zoologist, various far-reaching biological questions come easily to the front. 1. To what extent should the *individual ascidian be looked upon as a composite of more or less independent systems or parts, each growing and multiplying in its own way, i.e. in accordance with its own particular nature?* It is easy to give this general question objectivity in the case of such a species as *Halocynthia johnsoni*. See the systems, or parts that are describable, numerable and of course for some portion of the individual's lifetime are increasing in number by one means or another: the mantle musculature, particularly the radial siphonal muscles (fig. 2); the gonadial lobes (figs. 2 and 3), (to say nothing of the ovarian and testicular lobes proper contained in the larger lobes), and the lobes about the opening of the oviduct and sperm duct (fig. 5); in connection with the digestive tract the branched and alveolated liver (fig. 4), the lobulated lacteal system (figs. 3 and 6), and the anal lobes (fig. 7); in the branchial apparatus the circle of branchial tentacles each with its branches primary, secondary and tertiary (figs. 11-13); and finally the branchial folds, the stigmata, the branchial vessels or sinuses longitudinal and transverse, and the dorsal languets (figs. 14 and 16). In the face of such an array of repetitive structures, several of which have already revealed to cursory inspection a certain amount of "law and order," the question can hardly be avoided. Is it not likely that still closer, more detailed observation would discover still other repetitive parts whose production is also reducible to law? How does the problem before us differ from that of metamerism so much discussed a couple of decades ago? Is not that problem as it has usually been treated merely a special aspect of a much more general problem, *viz.*, that of the meristic constitution of the entire organism? If this question is entitled to an affirmative answer, as it seems to me it is, it would appear doubtful if there are any animals whatever, to say nothing of plants, that are not

in truth metameric to a high degree if not in fact essentially. Certain it is that under such a view the ascidians, which are usually regarded as non-metameric, at least in their adult stages, would change their status completely and would appear as meristic to a truly surprising extent.

To William Bateson seems to belong the credit of having perceived, more clearly than any other biologist of the recent period, that the problem of metamerism is really an aspect of a much larger problem. Although his recognition of *merism* and distinction between *meristic* and *substantive* variation are well known to biologists, it will not be superfluous to quote some of his words touching the point here being emphasized. "Under the term Merism," he says, "I have proposed to include all phenomena of Repetition and Division whenever found and in whatever form occurring, whether in the parts of a body or in the whole. The consequences of the admission of this proposition are considerable and should be fully realized; for on recognition of the unity of these phenomena it is possible to group together a number of facts whose association will lead to simplification of some morphological conceptions, and to other results of utility." (Bateson '94, p. 28.) Then after speaking of "segmentation" and "metamerism" as these terms are current in morphology, he continues: "By many morphologists the attempt has been made, either tacitly or in words, to separate such Metameric Segmentation from other phenomena of Repetition elsewhere occurring." Against such a course Bateson takes a strong stand. But even in doing this he reveals the seeming limitation to his relatively broad grasp of the truths involved. If my own conjectures touching the larger significance of merism be true, and if I read Bateson's book aright, the limitation to his grasp of the subject is marked by the fact that he viewed it primarily from the standpoint of variation. Following close upon the heels of what has just been quoted he writes: "In order to lay a sound foundation for the study of Meristic Variation these errors must be cleared away, and to do this it is necessary to break down the artificial distinction between the phenomena of Metameric Segmentation and other cases of Repetition of Parts, so that the whole may be seen in their true relations with each other. When this is done, the

mutual relations of the facts of Meristic Variation will also become more evident." The last part of this quotation undoubtedly indicates that Bateson recognized, in a general way at least, that the significance of merism reaches beyond the phenomena of variation alone. The implication in the last sentence especially is that meristic variation is itself only a part of the more general phenomena of merism. And this implication is still clearer in other statements, particularly those touching views of merism for the treatment of the problems of homology and phylogeny. Nevertheless it is worthy of note that not only did Bateson's immediate aims not call upon him to go into the subject from any other standpoint than that of variation, but that he was not, at any rate at the time of writing his book, quite clear as to what sort of a road one would be traveling who should attack the subject from the more commanding standpoint. "In introducing the method of the Study of Variation I have said that it can alone supply a solid foundation for inquiry into the manner by which one species arises from another. The facts of Variation must therefore be the test of the way in which organ arises from organ, and that thus Variation is the test of homology" (p. 30). To my mind this last sentence shows the author with compass and log out of true, and off the straight course on which he was sailing when he wrote the sentences about the identification of metameric segmentation with merism. It is impossible in this paper to give the grounds for my belief on this matter. Nor would I have my reference to Bateson's really monumental book misunderstood. My purpose is primarily not to criticize but to acknowledge and commend; not to show where Bateson fell short, but rather how far beyond accepted views he actually went.

This sally Batesonward I leave by calling attention to the fact that *resemblance* and not *difference* is in reality always the practical test of homology; and furthermore that Mendelian inheritance, the field in which Bateson himself has recently labored with so much brilliancy, furnishes one of the most convincing blocks of evidence to this effect. What in last analysis can we say about dominance but that as regards certain characters a particular individual plant or animal resembles one of its parents more than it does the other? We may, it is true, become

so absorbed in questions of how the germ can be so constituted as to make inheritance go as it does in these cases, that attention is diverted from the actual observations in which the questions are rooted. But this neither adds to nor subtracts from the facts themselves, either objective or subjective. There is a well worn maxim about not being able to "see the woods because the trees are so thick." The converse of this might be a useful maxim. It happens not infrequently that one becomes so intent upon the grandeur of a forest as to ignore the individual trees of which it is composed. The artist may legitimately do this. The scientist cannot. Mendelists need not of course spend all their time cogitating over the circumstance that dominance and recessiveness rest essentially on the observation that some of the offspring *resemble* one parent more than the other. They are, though, almost certain to go astray if they ever really ignore the fact.

My purpose in this inquiry is to see something of the outcome of attention to the trees as well as to the forest of merism. A goodly number of bald facts and some of the "law and order" as one species of ascidian exemplify them we have already seen. Now we may push inquiry concerning the still wider bearings of these somewhat further. Before doing so we must look at the mode of multiplication of stigmata a little more closely. For this we turn again to Damas's work. Referring to the three modes of stigmata formation recognized by his predecessors, he writes: "One sees that these three modes of multiplication of stigmata are only variations of the same process which may be characterized as follows:

1st. The stigmata are subdivided by triangular languets which cut the stigmata perpendicular to their long axes.

2nd. The essential (caractéristique) epithelium of the newly formed stigmata seems to be produced always from the epithelium of the pre-existing stigmata."

"A consequence of these facts is that typically all the epithelium bordering the definitive stigmata is derived from the epithelium of the six protostigmata" (p. 23). The group of epithelial cells in the stigmatje border which in many ascidians gives rise by division to the epithelium of the new stigmata is specially definitively set off in *Ciona intestinalis* (see Damas's figs. 7 and 8,

pl. I). One might almost speak of these cell masses in this species as "germs" of stigmata. One of the facts that I wish to call attention to is that the substantive basis of the stigmata is the border of epithelial cells around the orifice. Certainly as to origin and probably as to later development the stigmata can be adequately studied only by attending to these.

For the first step in our next general inquiry we return to the tentacles. In presenting the observations on the make-up and development of these it was pointed out that of the primary branches of the first generation, the earliest to appear probably, and certainly the longest, occupy a place somewhat distal to the middle point of the tentacle axis. (Fig. 13.) It was pointed out also that these longer, and presumably earlier primary branches remain throughout the lifetime of the individual longer and more elaborately branched than the later primary branches which arise both distally and proximally from them. Another way of expressing the fact is by saying that later formed primary branches of any generation never catch up in size with those coming on immediately before them. Attention was further called to the fact that in general the beginning and subsequent growth and development of secondary branches of one generation hold the same relation to their primary axes that the primary branches hold to the tentacular axes. And it was pointed out that typically the tertiary branches also have the same relation to the axes of the secondary branches. Now come several closely connected and exceedingly far-reaching questions about the multiplication of parts in these tentacles. The first may be put in the following form: Is there a rule or law according to which the branches of any given generation pertaining to any given axis diminish in length after their growth is completed? Almost certainly there is. Simple inspection of the primary branches of generation 1, for example, in the young tentacle shown in figure 13 seems to recognize such to be the case. If this be so, then there comes immediately another question, namely: Does the same rule hold for all the tentacles, and for all the orders of branches of all the tentacles? One should not fail to perceive that a law of diminution in length of branches for a

given axis and generation is a quite different matter from that of the validity of such a law for all tentacles and all branches.

So much for questions as to further "law and order" in the development of tentacles *in the same individual and in this one species*. Two questions, likewise unanswered for the present, touching these organs in other species, may now be asked: Because there is a definite scheme of tentacle techtonic recognizable in this species, does it follow that such would be the case for all other ascidians with branched tentacles? I should surely expect so, though an examination of published figures by various authors, myself with the rest, gives the impression that this is not so. The fact is significant. Is there a definite plan of branching in some ascidians and not in others, or have we been in the habit of simply ignoring the existence of such a plan; in other words of regarding the fact of tentacle branching "in a general way" only? The probabilities are clear. The facts can be easily ascertained by future observations.

The other question of inter-species scope that we may ask is: Presuming a plan of branching to prevail in all ascidians with compound tentacles, would specific characters be found in these schemes? Hitherto systematists have made little or no search for such characters in connection with these organs excepting as regards their number. As suggested in the section on tentacle structure, it is highly probable that such characters could be found in some cases at least, were a quantitative study of the tentacles made with reference to all accessible points in which rules of multiplication prevail.

Having swung into mid-stream in the quest after "law and order" in the development and structure of this ascidian, it is truly surprising to find how swiftly and smoothly we are borne along. To the recognition that rules *of some sort* do prevail in the enlargement and multiplication of parts there seems almost no limit. Exactly *what these rules are* is quite another matter. On this latter point I shall make a few remarks at the end of this section.

Only one other instance of probable orderliness will we look at in this study. Attention has been called to the fact that the

stigmata vary from "short" to "long." Figures 15, 16, and 17 illustrate this. It has also been shown that these form varieties are correlated with the size and at least to some extent with the age of the individual animals. Of course the individual stigmata develop. This latter fact is so obvious as to seem too trivial to mention. Yet from our present standpoint it is of real interest and demands special attention, for see what questions we may ask in consistency with the perceptions of multiplicative rules already reached. Recalling what has been noted about the material basis of the stigmata, namely, that this is the row of ciliated cells bordering the orifice, it will be seen that the development of the stigmata is dependent upon the multiplication of these cells. Is it not probable then that the various forms of the ellipse passed through by a particular stigma in the course of its development is determined by the rate of multiplication of the cells and the size of these in the different parts of the circumference, and is it not further probable that this rate of multiplication and cell-size are in turn dependent upon the distance in both time and locality of the cells from the initial "germ mass" of the stigmata to which attention was above called. Again, is it not probable that a diminishing rate of both cell-size and cell-multiplication occurs in the different time and locality parts of the border, so that, however long continued the development of the stigma, its sides would never become truly parallel; in other words, that its ellipsoid form would be retained throughout, though with ever increasing ratio of long to short axis?

Still further, is it not probable that the rule of diminution in multiplication and enlargement likewise holds as to the production of new stigmata so that in every branchial sac, to however vigorous and large-grown an animal it may belong, a definitely graded series of sizes and shapes of stigmata must theoretically and to some extent practically occur?

I conclude this section with the remark only incidental to the present "inquiries" though fundamental to possible future ones, that further mere inspectional study in the directions here blazed, if carefully prosecuted on this and other species of simple ascid-

ians, would almost certainly yield rich returns. But—and here is the cardinal point—the *exact nature* of these various meristic rules whose wide existence is revealed to simple inspection, can be found only by the most *exacting measurements* and the most *rigid mathematical treatment* of the data obtained by such measurements.

For the rest certain acknowledgments beyond the confines of ascidian literature are due. These I make with heartiness and pleasure, and regret that space limitations prevent particular mention of all but a few of the most pressing.

My indebtedness to Bateson for his expansive conception of merism has perhaps been sufficiently referred to already.

Professor Minot has, in my opinion, opened the door more widely than any other biologist to that vastly important subject, the diminution in multiplicative and incremental activity within the same organic system. Although I believe he will go astray if certain of the interpretations contained in his discussions on cytormorphosis are followed up consistently, his data-collecting and much of his presentation I regard as most admirable and of far-reaching import. (See particularly Minot '91 and '08.)

The well known work of Maupas ('83 and '89) and that by Calkins ('94) of more recent date, on the running-down phenomena in protozoan multiplication, bear almost, though not quite as weightily in the same direction.

Richard Hertwig's recent studies on nuclear and cytoplasmic proportion in cells belonging to the same line of descent, though carried on with the primary aim of gaining light on the problem of conjugation and sex are, it seems to me, of as much if not more significance for the problem of meristic organization and multiplicative activity. (Hertwig, '06.)

Finally in Dr. Raymond Pearl's conception of "intra-individual variation," and the "laws of growth," presented especially in his *Ceratophyllum* paper (Pearl '07) we have, I believe, the master stroke up to this time on the mathematical treatment of organic development. Although as to the mathematical soundness of such a work I am unfortunately utterly incompetent to speak, its general biological purport and sweep are unmistakable.

6. TO WHAT EXTENT ARE THE SPECIFIC DIFFERENCES BETWEEN
H. johnsoni AND ITS NEIGHBOR *H. haustor* ADAPTIVE?

That the animal is "in a general way" fitted to the conditions under which it lives is obvious. The proof of this is that in the ten years and more during which collections of it have been made and observations recorded, it has flourished luxuriantly. But the stand taken in these "inquiries" is that we will not be satisfied merely with what is true "in a general way."

Questioning further about the creature's adaptation, perhaps the thing we would most like to know is, how did it become fitted to its conditions? A moment's reflection makes it clear that any answers we may get to this question will have to be indirect,—will have to be inferential alone. This is obvious from the fact that such adaptations had already been acquired when the animals first came under observation. The acquirement is, in a word, a matter of the past, consequently irreclaimably beyond the reach of observation. We may indeed conjecture that acquirement of adaptation is still in progress, but the prospect of gaining any real satisfaction by pushing study on the basis of such a conjecture is practically nil, since all experience is to the effect that change of organic kinds goes on in nature either exceedingly slowly; or if suddenly, at rare intervals, the suddenness and rarity making the chance of witnessing it but slight.

Undoubtedly experimental work, particularly of recent years, has shown that under conditions that may be experimentally imposed, new organic kinds may come forth in a very brief time relatively, even though the coming be gradual. Undoubtedly, too, new organic kinds may come forth suddenly by sporting or mutation under natural conditions. But the myriad kinds which, uninterfered with by man, Nature herself presents, if the evidence of paleontology and ages-long observation are to be trusted, have in the vast majority of cases retained their identity during years and centuries, and even millenniums. And surely it is *nature as it is*, not *as it might be*, that science has to interpret. The biologist may sometimes be so carried away or dazzled by the startling results of experiments as to be neglectful of the fact that experiment can have no legitimate

scientific function other than to interpret nature itself. This becomes obvious the moment one reflects that the experimenter has always to go, finally, to nature unexperimented upon by man for the material with which to experiment.

Cabrillo's ships entered the bay now known as San Diego in 1542. Is there any likelihood based on observation that had that navigator collected some of these ascidians and could we today compare them with the specimens taken this summer, the two lots would present any recognizable difference? And does anyone doubt that the description here given of the species, provided it be accurate, will apply without modification to specimens that may be collected say five hundred years from now? But one bent first and foremost on inquiring how the animals came to be adapted to their conditions might say that if they have not changed since Cabrillo visited the locality and do not change in the next five hundred years, this means that the conditions have not changed and will not in the time specified. This expression of view would be made probably with the implication that change in environment and environed organism are wholly and inseparably linked together, and that at least so far adaptation can be accounted for. Let us accept this view provisionally. We can say then that sometime in the past (how many years before Cabrillo came, we have not the remotest idea) an ascidian species existed here or in some locality not remote that was not the same as *H. johnsoni*. In course of ages a gradual geological or other physical or biological change in the local conditions occurred and *pari passu* the ascidian underwent change and *H. johnsoni* was produced. Or, on the supposition that the ancestral form lived in some other locality slightly different from the San Diego bay region, we would presume that the new and different environment which caused the new adaptation was reached by gradual migration.

But even if this line of reasoning as to how the adaptation came about be accepted at its full face value, we are bound to admit that it is not very satisfactory, especially when the attempt is made to apply it in a specific instance like this. What exactly was the nature of the geological or other change in the locality? Change of level within comparatively recent geolog-

ical times the region has certainly undergone, but how much and what effect on the water and bottom conditions this might have had, we can surmise only in the vaguest way. Or, assuming migration instead of local change to account for the altered environment, where was this original home and in exactly what way did it differ from the newly-reached home? At best, answers to these questions must fall far short of proof.

Again, what were the characters of the ancestral species which through linkage with the assumed changing environment were transformed into the characters of *H. johnsoni*? Really, is it not well-nigh certain that we are forever shut away from anything even approaching proof as to how *this particular species* with which we are now occupied came to be what it is? Is there, then, any line of inquiry concerning the clear though complex fact of adaptation in *H. johnsoni* that promises a more satisfactory issue than the inquiry as to how the adaptations arose?

Some paragraphs back we agreed to accept "provisionally" the view that "change of environment and of environed organism are wholly and inseparably linked together." Suppose we fix attention on this proposition for a little. If we do this, are we not at once compelled to say that "only in a general way" are we prepared to maintain the truth of the proposition? One of the cardinal positions in these inquiries is that we are not to rest satisfied with what is true in a general way only. We are, in spirit at least, committed to the resolution of these general truths into their more special parts. Is there not, then, some way of getting a firmer hold upon the problem of how closely the species is linked to its environment other than by attempting to follow it and its environment into a past that is forever beyond the reach of observation, or into a future so remote that only generations yet unborn may lay hold upon it?

The space-range of the species affords an approach to the problem that has at least the advantage of being far more accessible to present observation than does the time-range. It is, therefore, surely desirable to travel this way as far as possible. Let us, then, take to it in earnest. First, let us look at the conditions under which the species lives *within its own range*. The questions that would seem to reach the supposition of close

linkage between organism and environment may be put in this way: Are there recognizable physical or biological differences of condition within the habitat of the species, and if so are there structural differences in the animals exactly corresponding to these environmental differences? Obviously, it would require an extensive examination of both animals and external conditions to answer these questions fully, but it is also obvious that the facts for such an examination are in the main accessible. They may be many, they may, some of them, seem trivial, they may be complex, their ascertainment may require much time and labor, but at least they are not clearly and from the outset wholly beyond the reach of observation.

A few of the more easily accessible facts in the case I am able to present. In San Diego Bay the animals are obtained most readily from the piles of the extensive wharves constituting the city's main waterfront. Here they live intermingled with great quantities of sponge, hydroids, tubicolous and other annelids, mussels, barnacles, and other ascidians, and may be gathered at any season of the year in almost countless numbers. But they are by no means restricted to this part of the bay. For example, during the summer just past, a number of specimens were secured, through Miss Johnson's efforts, from the few remaining piles of an old wharf at National City situated on the bay four miles farther towards its head than are the main city wharves. Since San Diego Bay is long and narrow, and has but a single communication with the sea, it is highly probable that two points, one of which is four miles nearer the mouth than the other, will present considerable differences as regards temperature and density of the water, and completeness of change during each ebb and flow of the tide.

In order to test this, I asked Mr. G. F. McEwen, the physicist of the Biological Station, who has in hand the study of the physical conditions of the water, to make temperature and density determinations of water samples from the several points in the bay at which *H. johnsoni* occurs. I will here consider only the results for the two points already mentioned. These may be presented in tabular form:

TABLE III.

WATER SAMPLES FROM NATIONAL CITY (UPPER BAY).							
Sample No.	Date and Time		State of tide	Temp.	$d_{15.56}^1$	d_t^2	
1.	July 14,	1:15-5:45	p.m. rising	27.9° C.	1.02698	1.2359	
2.	"	"	"	27.4° C.	1.02704	1.02378	
3.	"	"	"	26.9° C.	1.02672	1.02363	
4.	"	"	"	26.4° C.	1.02694	1.02400	
5.	"	"	" flood	25.2° C.	1.02661	1.02404	
SPRECKLES' WHARF SAMPLES (LOWER BAY).							
1.	July 18,	8:30	a.m. low-rising	21.2° C.	1.02568	1.02426	
2.	"	12:45	p.m. flood	18.4° C.	1.02518	1.02449	
PUGET SOUND SAMPLE (ELLIOT BAY).							
1.	July 3			?	?	1.01365	?

¹ $d_{15.56}$ = density reduced to standard temperature.

² d_t = density at observed temperature.

This table shows that the temperature of the locality farthest from the mouth of the bay was on the dates (near midsummer) approximately 6° C. higher during the entire flow of a tide than that of the locality nearer the mouth. This is a difference of about 30 per cent. It also shows that while the *observed* density of the lower station water is a little higher than that of the upper, the density of the upper station water considered *in relation to the difference in temperature* is greater by a value clearly recognizable in the third decimal place.

This comparison of temperatures and densities is of course far from complete. It should at least be extended to a mid-winter period. Almost certainly, should this be done, the upper station water will be found to be then colder instead of warmer than the lower station water. It is quite certain, too, that determinations made at the seasons when evaporation and precipitation are at their maxima, say in late August or early September for evaporation, and February or March for precipitation, the density differences of the two localities will be found still greater. There can, therefore, be no doubt that these two localities constitute two environments with rather large and readily measurable differences. Are there corresponding differences in

the individuals of *H. johnsoni* living in these environments? Inspection of the tabulated results of Miss Johnson's examination of the specimens from the two localities given in Table I reveals the fact that such differences do not appear within the range of the observations made. If they exist at all, our studies must be more searching to find them. We are consequently obliged to conclude that so far as the facts ascertained go, there are environmental differences within the natural habitat of this species that are without corresponding differences in the animals subjected to them.

We are not, of course, justified by the facts ascertained in extending this conclusion to a general denial of such correspondence. Since, however, we have examined these animals with at least the usual fullness and care upon which prevailing conceptions rest about species in this group of animals, it would seem that we are not justified in standing by a general hypothesis that environmental differences must register themselves fully and exactly in the structure and function of the organisms subject to them, unless we are prepared to push our study of the organisms to the point of recognition of such organic differences for all the environmental differences which we can detect.

Now suppose we accept this limitation—and, really, I do not see how we can escape it. As soon as we do so, trouble of another order comes in sight. Suppose we should examine a long series of specimens of *H. johnsoni* from the two localities here considered in far greater detail than we have the ones recorded, and suppose we should find certain mean or average differences between the two lots, could we be sure that the differences between the organisms were actually a register of the differences of the two environments? But should we not have to do that in order to sustain the hypothesis? It would seem so.

This phase of the problem can be approached from another direction. We have seen that *H. johnsoni* resembles rather closely *H. haustor* of Puget Sound, the two being distinguishable so far as at present known only by certain testicular characters and the number of branchial tentacles. Since we have found no differential characters as between specimens of *H. johnsoni* living in different environments, we have no ground for an answer

to the question of how closely and in exactly what respects the animals are adapted to their environment beyond the fact that they must be generally so adapted, else they would not flourish.

By turning, however, to another closely related species living in a still different environment, we are enabled to push the inquiry farther, since we have then a differential *between the organisms* as well as *between the environments*. The new advantage is in the circumstance that the question of linkage between organism and environment is so much narrowed down and made so much more definite. It now stands obviously this way: Do the differences between *H. haustor* and *H. johnsoni* correspond to, and are they inseparably linked with, differences between conditions of life in Puget Sound and San Diego Bay? Unfortunately, imperfect as our information is about the water of San Diego Bay, it is far more imperfect about the water of Puget Sound. However, through the kindness of Mr. H. C. Stevens of the University of Washington, Seattle, Mr. McEwen was able to determine for me the specific gravity of one sample of water from Elliot Bay, Puget Sound. This is shown in Table III.

One question can now be asked in very specific terms: Do the tuberculated, highly vascular test and the larger number of tentacles of *H. johnsoni* correspond to, in the sense of being dependent upon, the higher density and temperature of water in San Diego Bay? Undoubtedly one may conjecture such to be the case. However, since there is no proof that higher temperature does generally cause an increase in tentacle number, such a conjecture would be a hypothesis; but again, since some hypothesis of quite another character, for instance, that increased tentacle number is an expression of general physiological or growth tendency, has as much evidence to support it as has the other, neither hypothesis would, it would seem, be justified except for the purpose of being itself tested. It could not, that is, be justifiably used as a support of some other broader, more general hypothesis.

The results arrived at in this last section are so largely negative and skeptical as to contain little of promise or encouragement, at least so far as the questions of phylogenetic relationships and causes of adaptive modifications are concerned. But just

these questions have furnished much of the motive in biology for a generation.

On the other hand, the questions of rule, or scheme, in development and final arrangement of parts, as considered in section 5, and of the extent and character of adaptations, considered in section 6, seem to be open doors for gaining much information about these animals. But such questions have been very little the motive of recent biology.

It looks as though biological motive has been strong in directions where it could not get much positive knowledge and weak in directions where it might.

To want what is unattainable, and not to care much for what is close at hand, is said to be a trait of human nature, and possibly the traits of human nature have reached to some extent even to biological science.

7. SUMMARY OF RESULTS.

The procedure in this inquiry has followed strictly the analytical order. That is, the phenomena given by observation, the data, have been held strictly as the starting point in every section. These data have been the individual animals of a particular lot, treated together from the outset because of their unmistakable resemblance to one another and their having been found living together in a particular region, *viz.*, on the sea-coast of southern California.

A summary of the results may now be advantageously presented in the reverse or synthetic order.

1. An approximately exhaustive study of one of these animals finds it to contain a manifolding of similar parts to an extent that is surprising in view of the slight prevalence of such parts recognized by cursory observation.

2. Comparison of many individuals of various sizes and ages with reference to the details of structure reveals the fact that to a large extent, the measure of which is not known, these manifolded parts have arisen (*a*) as lineally genetic series (the branchial stigmata), from a few initial ancestral organs; while others have arisen (*b*) as repeated productions from common original

substrata or menstrua (the tentacles, the branches of the tentacles, the transverse blood sinuses of the branchial sac, etc.).

3. Attention to these repetitive series makes it quite certain that many of them, both of the genetic and of the simultaneous series, not only are subject to definite schemes as to positional arrangement and time of origin, but also as to mass relations. Otherwise stated, the repetitive series which obviously constitute so large a part of the whole animal are to a great extent subject to mathematically treatable order.

4. A fairly extensive comparison of animals from the coast of southern California with others very like them living in Puget Sound, State of Washington, discovers certain considerable and constant differences between them (difference in character of test and number of tentacles). Those living on the California coast need a group name to distinguish them from those living on the Washington coast. As such name *Halocynthia johnsoni* may be used, the Washington animals being called *H. haustor*. These two groups may be conveniently spoken of as species.

5. So far as the present inquiry has gone, the attempt to find a causal relation, or a necessary correlation, between the character differentials of the two species and their environmental differentials, has produced negative results. In other words, the results do not enable us to affirm anything more definite about the adaptation of *H. johnsoni* to its environment than that in a general way it is so adapted; that is, that it is sufficiently adapted to enable the individual animals to live and maintain their specific identity in a considerable range of environmental conditions.

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ABBREVIATIONS USED IN THE PLATES.

- a, a', a''*—axes of tentacle and primary and secondary branches, respectively.
a. l. s.—ampulae of lacteal system.
at.—atrial chamber.
b', b'', b'''—primary, secondary, and tertiary tentacle branches.
br. f.—branchial folds.
br. s.—branchial sac.
d. l.—dorsal languets.
d. l'.—supernumerary languets.
e.—esophagus.
end.—endostyle.
g', g'', g'''—primary, secondary, tertiary generations of tentacle branches.
- gon.* ♂ and ♀—male and female gonads.
int.—intestine.
l.—liver.
l. s.—lacteal system.
l. d.—liver duct.
long. s.—longitudinal sinuses of branchial sac.
m. mus.—mantle musculature.
o. l.—opening of liver duct.
st.—stomach.
st. f.—stomach fold.
s¹, s², s³, s⁴, s⁵, s⁶—transverse sinuses of the several orders.

EXPLANATION OF THE PLATES.

PLATE 7.

Figs. 1 and 1'. -Two specimens, natural size, of *Halocynthia johnsoni*.



Fig. 1

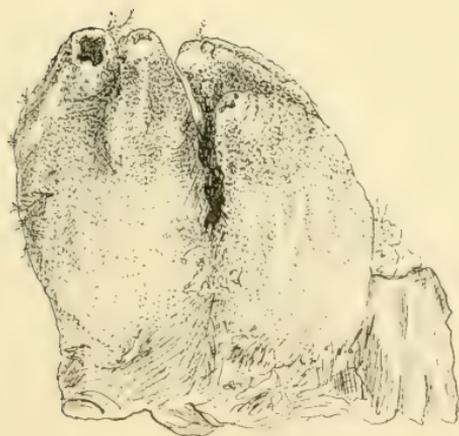


Fig. 1'

PLATE 8.

Fig. 2.—Right side, dissected to show mantle musculature, reproductive organs, and external surface of the branchial membrane.

Fig. 3.—Left side, showing especially the intestinal tract with its adnexa, the “liver” and “lacteal system”, and the reproductive organs.

Fig 2

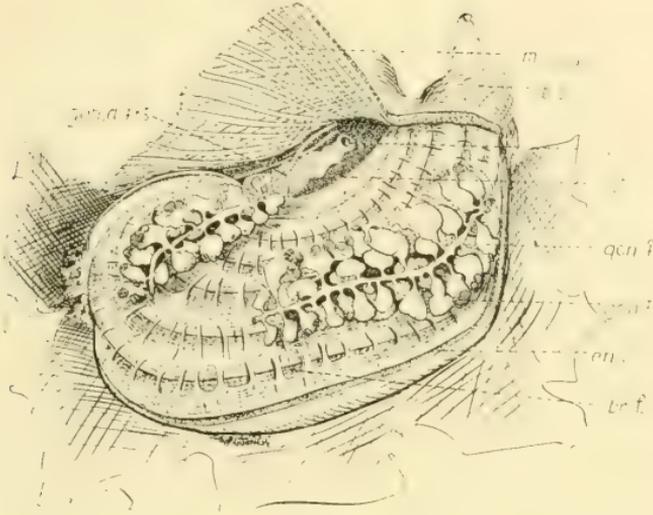


Fig 3

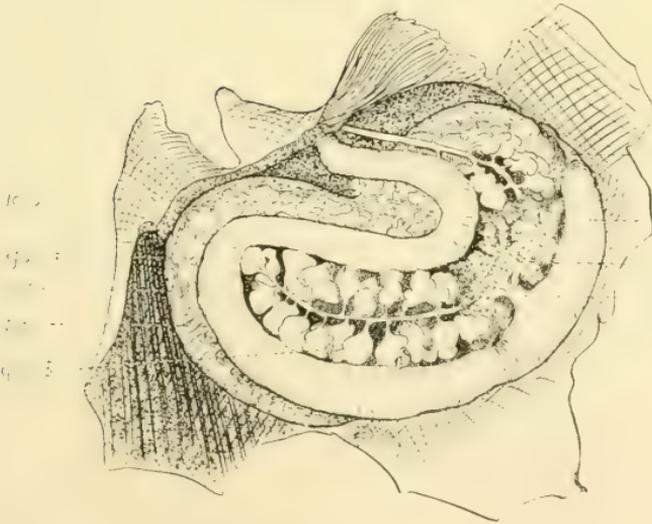


PLATE 9.

Fig. 4.—The stomach with the “liver.”

Fig. 5.—Terminals of the two genital ducts of one side.

Fig. 6.—A small piece of the intestine to show the character of the “lacteal system.”

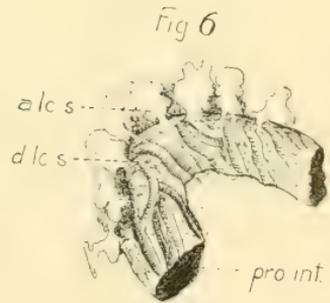
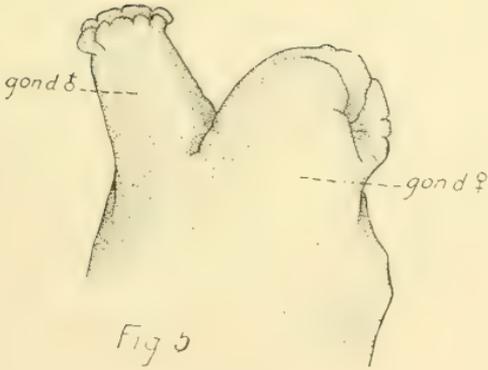
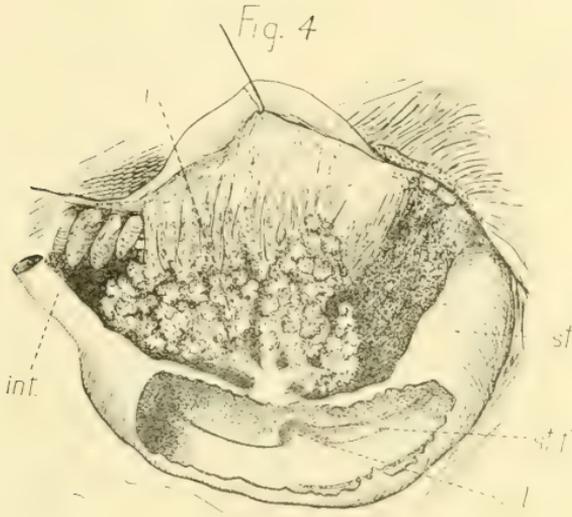


PLATE 10.

Fig. 7.—The hypophysis and anal rim of 29 specimens. Presented for the purpose of showing the variation of these parts. The numbers correspond to the numbers of the specimens tabulated in table I. The number in each pair stands next to the hypophysis.

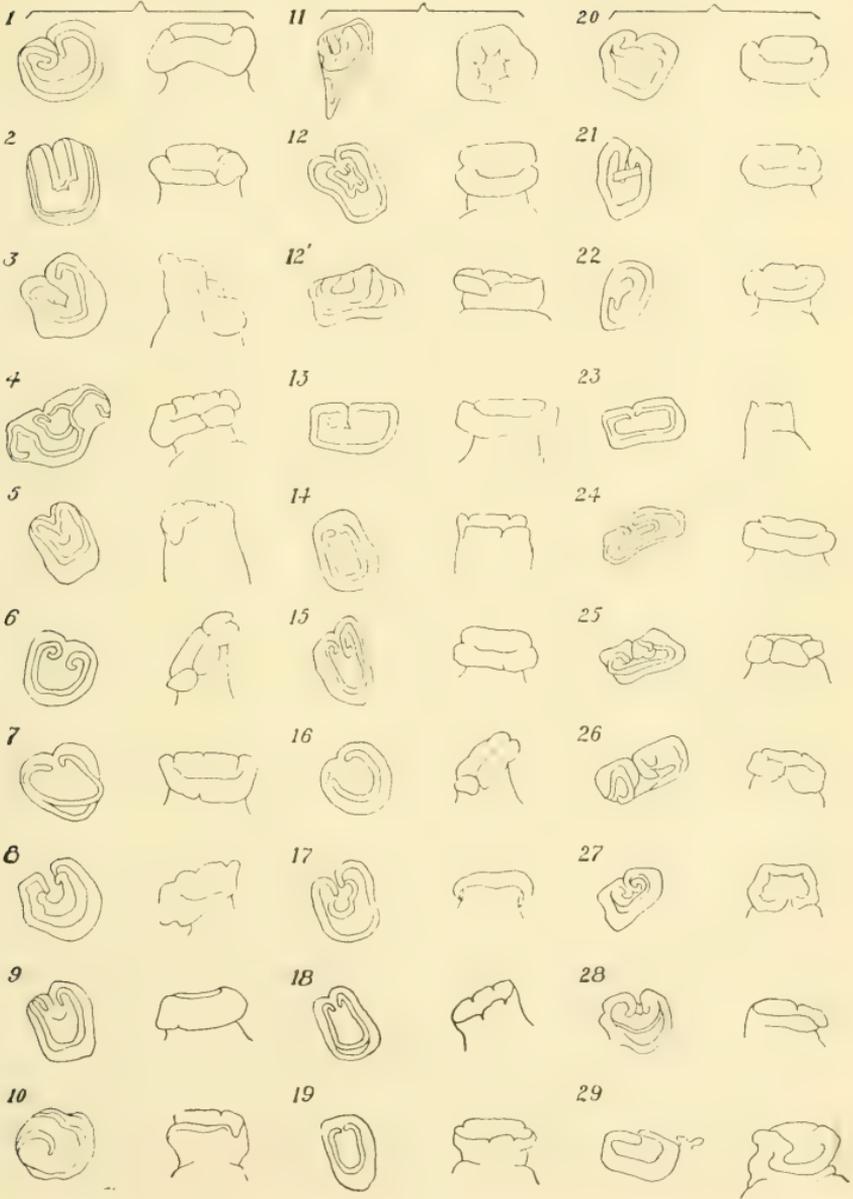


PLATE 11.

Fig. 8.—Section of the “thick test” of *H. johnsoni*, showing the absence of blood vessels.

Fig. 9.—Section of the test of *H. haustor* between the tubercles, showing the comparative rarity of blood vessels.

Fig. 10.—Section of the test of *H. haustor* on one of the tubercles, showing the abundance of vessels with the club-shaped terminals.



PLATE 12.

Fig. 11.—The tip of a full-grown tentacle that was 7 mm. long.

Fig. 12.—Entire tentacle of a small specimen. This tentacle was 1.5 mm. long.

Fig. 13.—Entire tentacle from the same individual from which fig. 12 was taken. In the figures of tentacles all the details were drawn with as much accuracy as possible. Fig. 13 was drawn to scale from micrometer measurements.

Fig. 14.—A fragment of the branchial membrane seen on its inner surface. Drawn especially to show the relation of the dorsal languets to the transverse blood sinuses. This is from a small individual 1.5 mm. long.



Fig 11

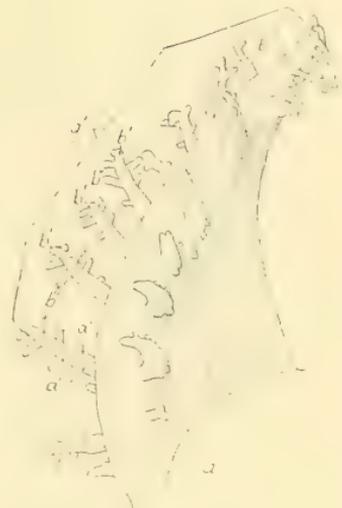


Fig 12

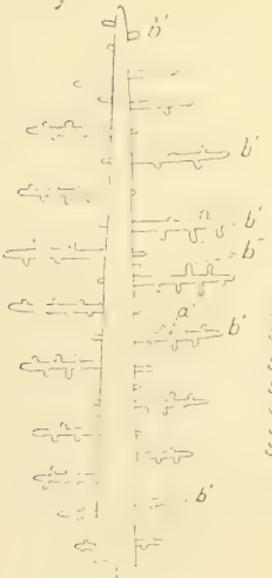


Fig 13

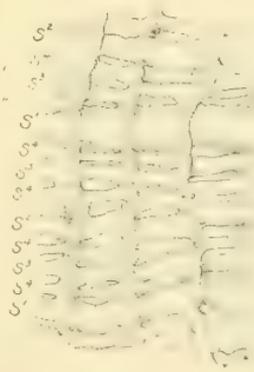


Fig 14



Fig 15

PLATE 13.

Fig. 15.—A piece of branchial membrane from a small specimen (1.5 mm. by 1.25 mm.), from the space between two folds and near the endostyle. All details of this and of figs. 16 and 17 were drawn with the greatest possible accuracy.

Fig. 16.—See Plate 14.

Fig. 17.—A membrane in which the stigmata are on the whole not quite so long as those of fig. 16, though the difference is hardly recognizable in the figure. The more incomplete state of S^6 in this membrane than in the one shown in 16 will be noticed.

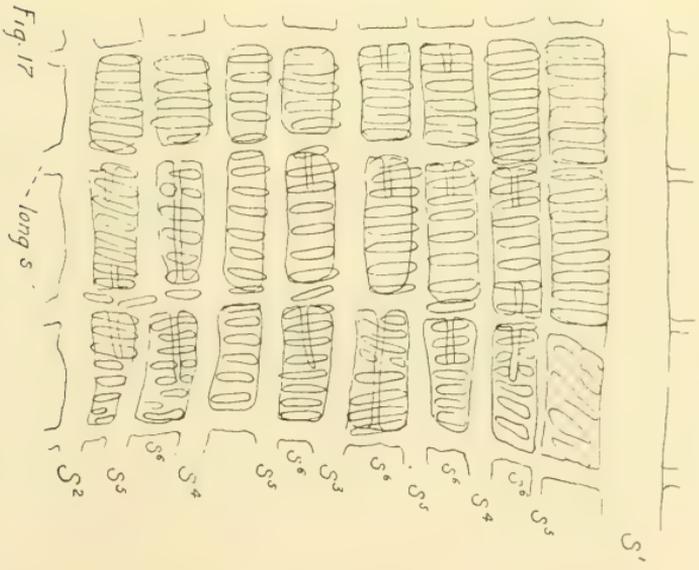
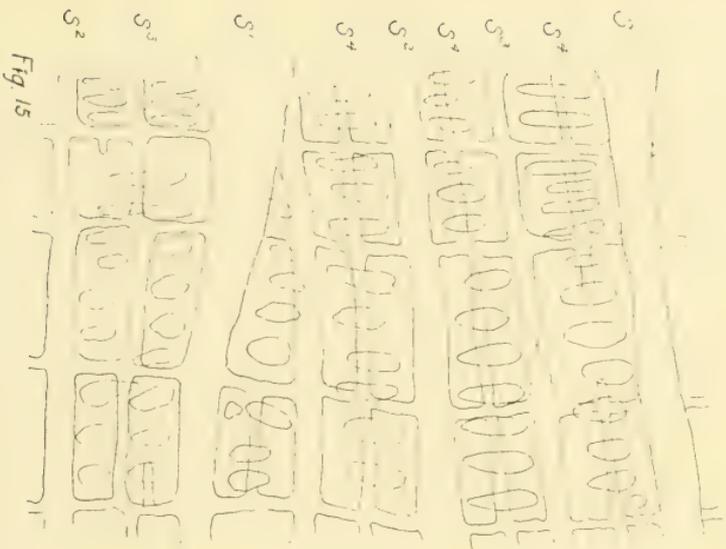


PLATE 14.

Fig. 16.—Branchial membrane from a large, seemingly full-grown specimen. This is the style of sac designated as “stigmata long” in the tables.

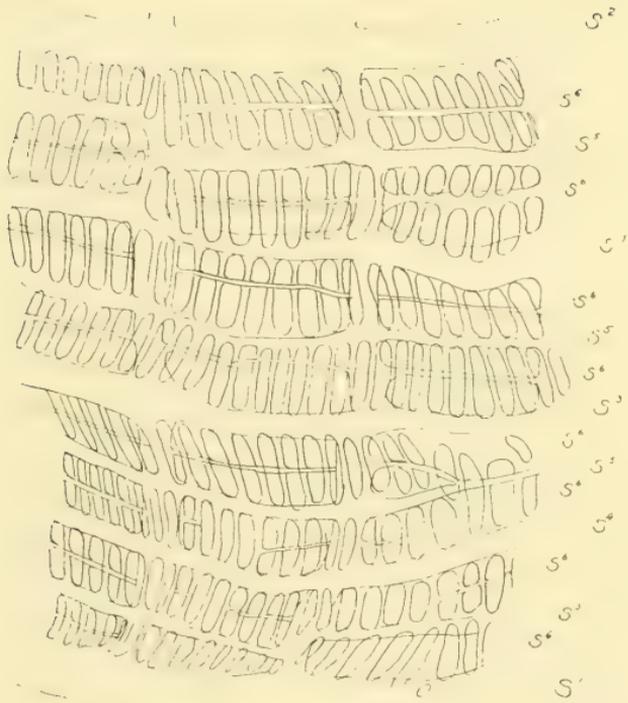


Fig 16 long s

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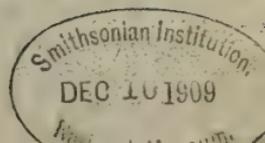
XXVII

THREE SPECIES OF CERIANTHUS FROM
SOUTHERN CALIFORNIA

BY

H. B. TORREY AND F. L. KLEEBERGER

BERKELEY
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CONTRIBUTIONS FROM THE LABORATORY
OF THE
MARINE BIOLOGICAL ASSOCIATION OF SAN DIEGO.

XXVII.

THREE SPECIES OF CERIANTHUS FROM
SOUTHERN CALIFORNIA

BY

H. B. TORREY AND F. L. KLEEBERGER.

In 1893, McMurrich¹ described, from a single imperfect specimen dredged in forty-four fathoms off the coast of Southern California, the problematical *C. vas*. Nine years later, Gravier² described a pelagic Cerianthid, sexually mature, which was found in abundance at the surface in the Gulf of California. These appear to be the only published references to the Cerianthids of the waters of Pacific America.

To this meager record we wish to add the following account of three other species, all from Southern California. The first, which we have called *C. aequatori*, is well marked by the small number of tentacles of each kind—never more than thirty-four—and the number and character of the mesenteries. The second, to which the name *C. benedeni*³ has been given, resembles externally *C. americanus*⁴ and *C. membranaceus*,⁵ but differs from these

¹Proc. U. S. Nat. Mus. XVI, p. 119.

²Comptes Rendus Acad. Sc. Paris, T. 135, p. 591, 1902.

³For Professor Edouard van Beneden.

⁴See especially McMurrich: Journal of Morphology, IV, p. 131, 1891.

⁵See von Heider: Sitzungsber. k. k. Akad. Wien, LXXIX, p. 204, 1879; Andres: Fauna und Flora des Golfes von Neapel, IX. Die Actinien.

and all other adult Cerianthids, so far as known, in possessing structures which resemble in all essential respects the *botrucnides* found by van Beneden⁶ in three genera of pelagic Cerianthid larvae. The third species resembles very closely the European *C. membranaccus* in structure, differing only in the arrangement of the mesenteries in the region of the siphonoglyph and possibly also in color, concerning which no notes are at hand. Provisionally, we have named this species *C. johnsoni*.⁷

Fam. CERIANTHIDAE.

Actiniaria with long cylindrical bodies, without foot disk, invested by non-adherent tube formed largely of discharged nematocysts; with tentacles of two orders, marginal and labial, approximately one of each to each intermesenterial space; with numerous unpaired mesenteries, developing, after first eight, in the median intermesenterial space opposite the single siphonoglyph; with strong ectodermal musculature in body wall.

Gen. **Cerianthus** Delle Chiaje,⁸ 1832.

With the characters of the family.

C. aestuari, n. sp.

This species is abundant on the sandy mud flats, between tides, in False Bay, a shallow, narrow-mouthed inlet cut off by a neck of beach and sand dunes from the sea just north of San Diego, California. Here it is associated with another burrowing anemone, *Harenactis attenuata*,⁹ and the hydroid *Corymorpha palma*,¹⁰ all are apparently restricted to Southern California.

Projecting shortly beyond the level of the sand, from a tube whose mouth measures about 8 mm. in diameter, *C. aestuari* spreads its outer tentacles in quiet pools to the extent of 10 or 12 cm. The number of these tentacles, which are in a single cycle, is small, never more than 34, usually about 30. They

⁶Les Anthozoaires de la Plankton Expedition. Kiel und Leipzig, 1898.

⁷For Dr. H. P. Johnson, formerly connected with the University of California, by whom our material was collected.

⁸Istitutioni d'Anatomia comparata. Edit. 1, con tavole, Napoli, 1832.

⁹See Torrey: Proc. Wash. Ac. Sc. IV, p. 373, 1902.

¹⁰See Torrey: Univ. of Cal. Publ. Zoology, I, p. 1, 1902; *ibid.*, II, p. 1, 1904; *ibid.*, III, p. 253, 1907; Jour. Exp. Zool., I, p. 395, 1904.

are banded with numerous broad stripes of delicate brown, the ground being a faint pink or colorless. In about twenty per cent. of the individuals, two tentacles, symmetrically placed, on either side of the median plane, but not quite diametrically opposed, are banded or solidly colored in a conspicuous manner with deep red brown. The inner or labial tentacles, agreeing in number with the outer, are but faintly tinted and without bands.

In full extension, the column may exceed 20 cm. in length, with an average diameter of something less than 1 cm. Thus it is about the size of *C. lloydi*,¹¹ but differs from the latter in the constantly smaller number of tentacles, as well as in coloration. The column is thickly streaked and mottled with reddish brown, lightening orally. At the bases of the outer tentacles are delicate markings in red brown.

The column, thin walled, is highly contractile, as are also the tentacles. The marginals may, in fact, be reduced to nothing, may disappear completely on the way from the collecting ground to the laboratory, and only gradually reappear and resume their normal size after many hours in aquaria. Such occurrences imitate closely the more obvious facts of loss and restoration by regenerative processes. Yet the disappearance and reappearance are to be explained otherwise, namely, by variation in the internal pressure of the water in the hollow tentacles and coelenteron.¹²

There is little to be said of the sheath with which the animal readily surrounds itself. It serves as a lining for the burrow, is composed of a feltwork of nematocysts and is easily torn.

Aborally, the body wall is pierced by a terminal pore.

The long oesophagus is characterized by an unusually broad siphonoglyph. The latter, indicated by the oblique shading in fig. 1, does not reach the lips of the mouth, and extends into the middle third of the column in contracted individuals, in connection with a triangular prolongation of the oesophagus. Opposite the siphonoglyph is a very narrow and faint depression in the

¹¹See Gosse: *The British Sea Anemones*, 1680; also Andres: *Fauna und Flora des Golfes von Neapel*. IX. Die Actinien.

¹²For the role of this internal pressure in the regeneration of tentacles, see a series of papers by Child, in the *Biological Bulletin* from October, 1903, to April, 1905. See also the same author for an experimental study on *C. acstuari*, in the *Biological Bulletin* for June, 1908.

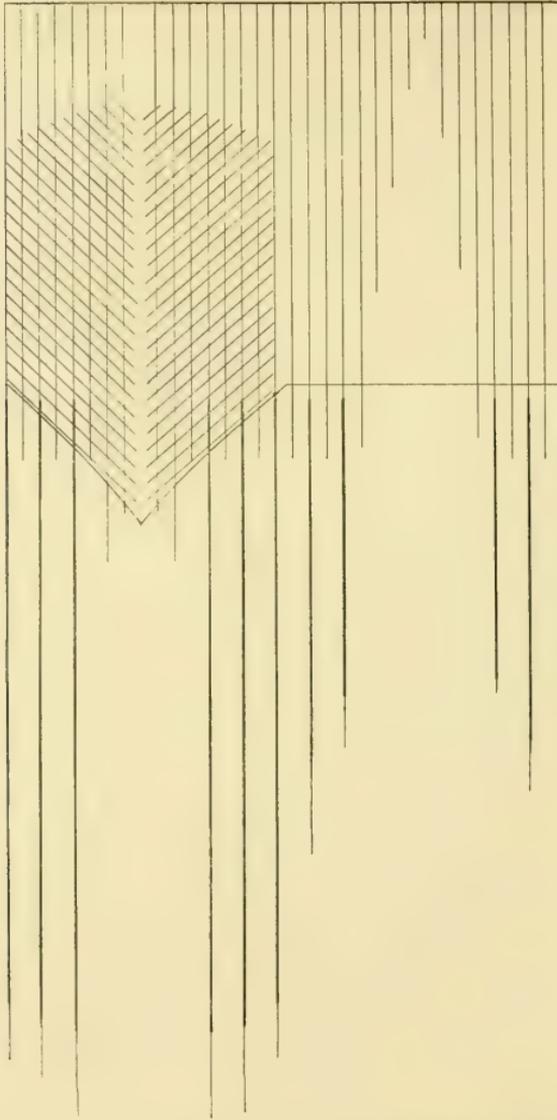


Fig. 1.—*C. aestuarii*. Semi-diagrammatic figure of its internal anatomy, the column wall and oesophagus having been cut longitudinally on one side, exposing mesenteries and siphonoglyph; the oesophagus is represented as transparent.

oesophageal lining, in the position of, but not to be regarded as, a second siphonoglyph.

The mesenteries correspond in number to each set of tentacles. Their arrangement is shown semi-diagrammatically in fig. 1. The longest six are in reality longer in proportion to the others than they appear to be in the figure. Four commonly reach the neighborhood of the terminal pore. The longest ten alone bear gonads, as indicated by the heavier lines. Alternating for the most part with them are much shorter mesenteries which bear much-coiled mesenterial filaments along their free edges. The directives extend little or not at all beyond the lower edge of the siphonoglyph. In the growing zone, opposite the siphonoglyph, are several short mesenteries that do not reach below the lower edge of the oesophagus, but are readily seen in serial sections and show by their length the order of their development. There is no sign of the arrangement of the mesenteries into the groups of four characteristic of *C. membranaceus*,¹³ *C. borealis* Verrill¹⁴ and *C. johnsoni*. In this respect, *C. aestuari* is especially simple.

True acontia are wanting, as well as the filamentous processes of the mesenterial filaments found in *C. benedini* and *C. johnsoni*.

The species is hermaphroditic. Each gonad contains, side by side, in separate follicles, developing ova and sperm.

The essential characters of *C. aestuari* are:

1. Coloration: column streaked and mottled with brown; tentacles delicately banded, with frequently a single pair more deeply and conspicuously colored.
2. Small number—not more than 34 each—of marginal and labial tentacles.
3. Thin column wall.
4. Long oesophagus with broad siphonoglyph that does not reach lips.
5. Essentially but two orders of mesenteries, corresponding in number to each set of tentacles.
6. Absence of acontia, true or false.

¹³Faurot: Arch. Zool. Exp. et Gen. (3), III, p. 43, 1895.

¹⁴Kingsley: Tufts' College Studies, No. 8, June, 1904.

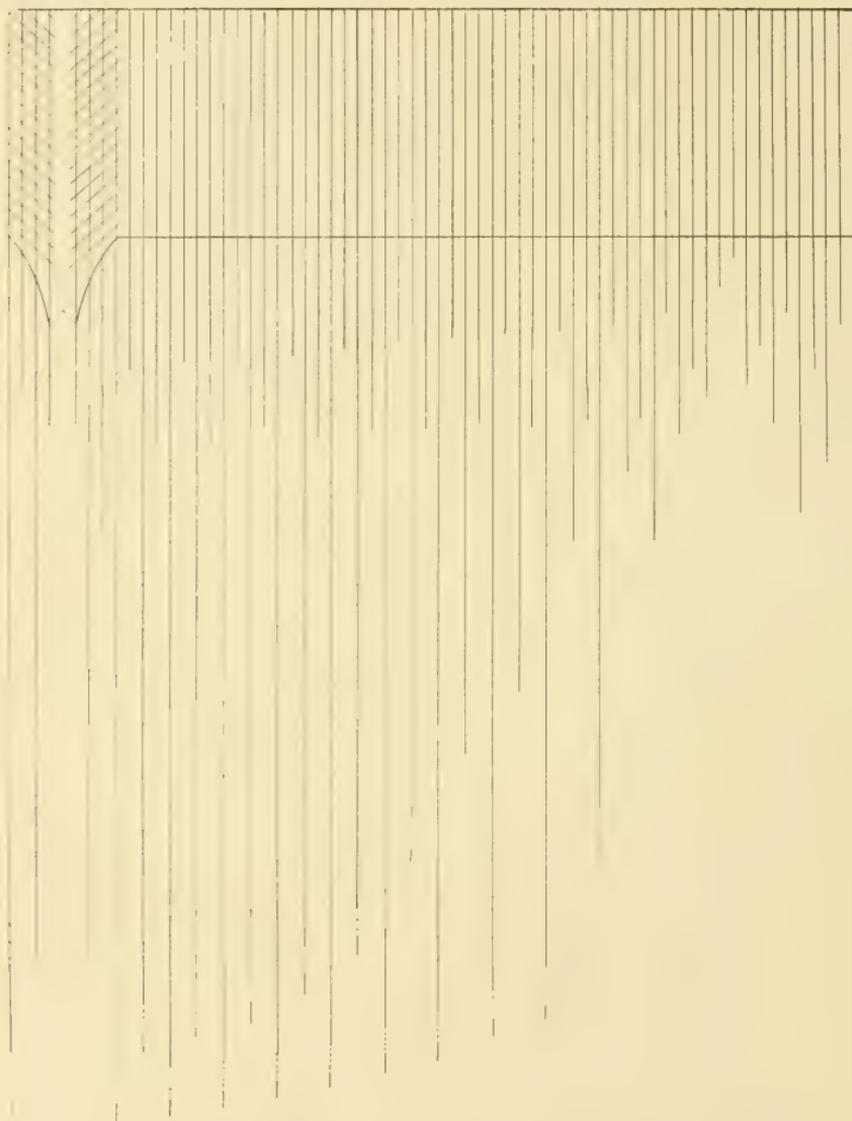


Fig. 2.—*C. benedeni*. Similar to Fig. 1. Certain mesenteries are greatly shortened, as indicated by the dotted lines, and but little more than half the lateral extent of the column wall is shown, the animal being essentially symmetrical.

C. benedeni, n. sp.

This specimen is described from preserved material; color notes are lacking. So far as our information at present extends, it is a resident exclusively of San Diego Bay. There it has been found on the sandy shoals bordering the channel.

C. benedeni is readily distinguishable from its relative of False Bay by the much larger number of tenacles: 90 to 100 marginals arranged in three cycles; the labials agree in number with the marginals. The body is also larger and its wall much thicker and more muscular.

In fig. 2, the internal characters of the species are represented semi-diagrammatically.

There is a single true siphonoglyph—with a narrow seam-like groove opposite, as in *C. aestuari*—running the full length of the oesophagus. Compared with the siphonoglyph of *C. aestuari*, it is relatively narrow, involving fewer mesenteries.

The mesenteries belong to four orders of differing length, arranged in the "quatreseptes" of Faurot (1895). Approximately eighteen—belonging to the first order—reach the vicinity of the terminal pore, several of the second order reaching almost as far. The directives extend a short distance below the oesophagus, but are furnished neither with mesenterial filaments nor gonads. Mesenterial filaments are tightly coiled on the shorter mesenteries—of the third and fourth orders.

Gonads are confined to the longer mesenteries—of the first and second orders, and are hermaphroditic, as in *C. aestuari*.

In the foregoing structural characters, *C. benedeni* resembles *C. borealis* Verrill closely, differing mainly in the larger number of mesenteries which approach the terminal pore. We come now to the consideration of a difference which distinguishes *C. benedeni* from all other adults, so far as existing descriptions go.

C. benedeni possesses no true acontia, of the type found in the *Sagartiidae*. It is well furnished, however, with the more or less branching, flattened filamentous processes of the mesenterial filaments which have been figured in some detail by von Heider (1879) for *C. membranaceus*. They occur on all mesenteries except the directives. On the mesenteries of the third and fourth

orders, they are grouped at the oral end of each mesenterial filament. They are scattered along almost the full length of the mesenteries of the first and second orders, beginning with a compact bunch on each mesentery just below the aboral ends of the coiled mesenterial filaments of the shorter mesenteries.

There is nothing essentially different from this in the distribution of these structures in *C. membranaccus*. On the mesenteries of the third and fourth cycles, however, are associated with them other structures of a type hitherto undescribed for any adult form, namely, the *cnidorages* described by van Beneden for

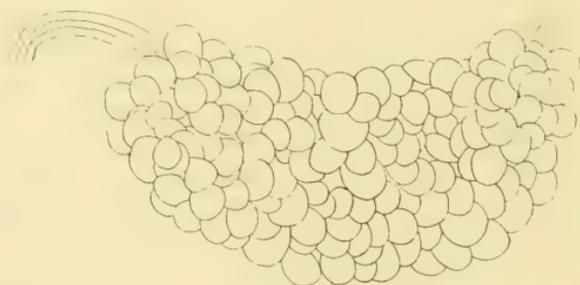


Fig. 3.—*C. benedeni*. Process of mesenterial filament loaded with cnidorages.

three pelagic larval forms. A cnidorage is a follicle packed with nettle cells, or cnidoblasts, that may be of several sorts, the largest and by far the most important equalling in length the diameter of the follicle and far surpassing all the others in bulk. In *C. benedeni*, the cnidorages are very numerous on the bunched filaments, as shown, for a single filament, by fig. 3; they are much less numerous on the scattered filaments. In the larval forms examined by van Beneden, the filament does not appear to have been prominent as such, as in the present species. The cnidorages were grouped together, however, like grapes in a bunch with little or no stalk. Such aggregates van Beneden called *botrucnides*, pointing out that they occupied the position of acontia and probably possessed the same morphological value.¹⁵

¹⁵“J'ai donné le nom de Botrucnides à des formations très curieuses qui dans les genres *Cerianthula*, *Hensenanthula* and *Calpanthula*, occupent la place des aconties et possèdent probablement la même valeur morphologique.” (p. 32).

Accepting the name, the rest of van Beneden's statement will hardly hold in view of the facts supplied by *C. benedeni*. The filaments bearing enidorages are identical in structure with the filaments not so furnished, such as those on the mesenteries of the third and fourth orders. Further, while enidorages appear most commonly and abundantly on the filaments bunched on the mesenteries of the first and second orders, they are also found commonly, in a less luxuriant development, on many of the scattered filaments of the same mesenteries. They are found only on filaments. Also, these filaments correspond perfectly to the filaments figured by von Heider for *C. membranaceus*. Since van Beneden insists (p. 33) that acontia differ totally—in position, morphological value, structure and function—from these filaments in *C. membranaceus*, the probability that acontia and botruenides are morphologically comparable vanishes. The single enidorage, not the aggregate of enidorages into a botruenide, would appear to be the essential unit of difference between all other species and those which possess it.¹⁶

***C. johnsoni*, n. sp.**

The two individuals from which the following facts were obtained, came from San Pedro Harbor, where they occupied approximately the same habitat as *C. benedeni* in San Diego Bay. They are much contracted, but were in life obviously much larger than *C. aestuari*, and considerably larger than our specimens of *C. benedeni*. One specimen is 12 cm. long and almost 2 cm. in diameter. The column wall is very thick, leathery and muscular. In the two specimens, the tentacles number: marginals, 108, 105; labials, 100, 100. Color notes are wanting.

The internal structure is represented in fig. 4. The siphonoglyph is narrow, with a seamlike groove opposite, as in *C. benedeni*. The mesenteries agree in number approximately with the labial tentacles. They are arranged in four orders, as in *C. benedeni*, though but one pair reaches the vicinity of the terminal pore; and the directives do not extend beyond the lower limit of the siphonoglyph.

¹⁶See van Beneden's distribution of larval Cerianthidae between two groups: Acontiferae and Botruenidae.



Fig. 4.—*C. johnsoni*. Similar to Fig. 2.

The mesenterial filaments are tightly coiled on the shorter mesenteries—of the third and fourth orders. The gonads, hermaphroditic, as in *C. benedeni*, are borne on mesenteries of the first, second, and frequently third, orders.

The acontia-like processes of the mesenterial filaments are similar in structure to those of *C. benedeni*, with the one exception that they lack the endorages characteristic of that species. They are bunched at the oral ends of the mesenterial filaments on the shorter mesenteries, and they are separated along the edges of the mesenteries of the first and second orders, being concentrated somewhat just below the lower limit of the mesenterial filaments of the second order of mesenteries.

The species most closely allied to the San Pedro form is the European *C. membranaceus*. The two agree in all characters except, possibly, the length of the directives, the arrangement of the other mesenteries associated with the siphonoglyph, and the coloration. On this basis, they are provisionally distinguished. From the Atlantic American *C. borealis* and *C. americanus*, *C. johnsoni* is distinguished at once by the fact that but a single pair of mesenteries approximates the terminal pore.

Zoological Laboratory,
University of California,
May 18, 1909.

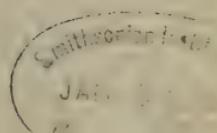
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THE LIFE HISTORY OF *TRYPANOSOMA*
DIMORPHON, DUTTON & TODD

BY
EDWARD HINDLE

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THE LIFE HISTORY OF *TRYPANOSOMA*
DIMORPHON, DUTTON & TODD.

BY

EDWARD HINDLE.

GENERAL ACCOUNT.

This species was discovered by Dutton and Todd (1903) in 1902, during their exploration of Senegambia for trypanosomiasis. They found the parasite occurring in the blood of horses, in which it is the cause of a very fatal malady. The strain was brought back to the Liverpool School of Tropical Medicine on the return of the expedition, and has since been kept going in the usual experimental animals, most of which are very susceptible to this trypanosome. Dutton and Todd (1903) described the existence of three different forms of this parasite, *viz.*, "tadpole forms," found chiefly at the commencement of infection; "stumpy forms," common during intermediate stages; and "long forms," preponderating in the later stages of infection. They considered the first two types to differ merely in size, thereby reducing the three categories to two, and accordingly gave the specific name *dimorphon*.

Laveran and Mesnil (1904), although on the whole agreeing with Dutton and Todd's description, came to a different opinion regarding the distinctness of the forms. They recognized the existence of "stumpy forms" and "long forms," denying the existence of any free flagellum, however, in the latter, but regarded them as representing only one type because of the existence of intermediate stages between the two extremes. The

.

“tadpole forms” were considered to represent another type, the fact that they divide being regarded as an evidence of maturity.

Since the discovery of this parasite in the horses of Senegambia, numerous other investigators have found various species of animals infected with it, and extended the range of its occurrence across Africa. Two other species of trypanosomes, *T. nanum* and *T. peccaudi*, closely resemble *dimorphon* in appearance, and it is possible that the three have been confused. But even making allowance for this possibility, its geographical range is not any the less extensive, and it may be found in most species of domestic animals. Horses are the most susceptible, but cattle, sheep, and even dogs, are all liable to natural infection.

The investigations of Roubaud (1908) have shown that *dimorphon* is transmitted from one animal to another by *Glossina palpalis*, but whether the transmission is merely by mechanical inoculation, or only after a sexual cycle has taken place in the intermediate host, is not as yet determined. Roubaud's theory that the trypanosomes merely undergo a culture in the proboscis of the fly is not in accordance with the observations on other species, by Prowazek (1905), Minchin (1908), and other investigators. Moreover, the morphological characters and life history of the trypanosome, when in the vertebrate host, are strongly in favor of the existence of a sexual cycle within an intermediate host.

In the following descriptions the flagellate extremity is regarded as anterior, for it seems probable from a consideration of the developmental stages of trypanosomes that they are derived from *Herpetomonas*-like ancestors in which the flagellum is anterior. The two nuclei are referred to respectively as trophonucleus and kintonucleus; the mode of division of the latter seems to be sufficient evidence for regarding it as a nucleus and not an extranuclear centrosome.

TECHNIQUE.

For the examination of the living parasite a drop of infected blood is placed on a slide and immediately covered with a coverslip, the edges of which are then tightly waxed down in order

to prevent evaporation. In such a preparation the trypanosomes will live but a few hours, and even when kept on a warm stage seem to be under unfavorable conditions. We have never even observed a trypanosome complete the whole process of division, and therefore fresh examination, which is usually of such great importance, has in this case been very unproductive of results.

Until recently the only method of staining blood parasites entailed the process of drying, and results obtained after employing such an unsatisfactory method are evidently untrustworthy. In consequence of the various objections to it to which attention was first called by Slavin-Moore and Breinl (1907), the use of dried films has been abandoned and their method employed.

A very thin layer of albumen is smeared over a clean slide. On this a drop of blood, or piece of an organ, is smeared out in the usual way and the slide immediately dropped face downwards into a jar of Flemming's strong solution. After fixation for about five minutes the slide is taken out, washed in water, and then passed through successive alcohols up to absolute. It is then taken back into 80 per cent. alcohol containing iodine and potassium iodide in such quantity as to produce a dark brown solution. After about ten minutes the slide is taken out, passed down to 30 per cent. alcohol, and then stained by either of the following methods:

(a) The film is stained in a solution of aniline safranin (Babes) for about one hour; then washed in water and stained in a 1 per cent. aqueous solution of polychrome methylene blue for another hour. The blue is then washed off and the film differentiated with Unna's orange tannin as long as dark clouds are seen to come out. After washing in water the slide is passed up through the alcohols into absolute, and thence into aniline oil. (The passage through the alcohols must be as rapid as possible owing to the extraction of the stain that takes place.) Then the film is cleared in xylol and mounted in Canada balsam.

(b) The film is mordanted for one hour in a 3.5 per cent. aqueous solution of iron alum and then stained for an equal length of time in a 0.5 per cent. aqueous solution of haematoxylin, artificially ripened by the addition of a few drops of

lithium carbonate solution. The slide is then differentiated in iron alum and mounted in the usual way.

With this method it is easy to get good results but the stain is liable to precipitate in the cell and dissolve out unequally in the iron alum, thereby producing artifacts. Method A is more reliable for nuclear details and therefore has been used to confirm the results obtained by the other method.

THE MORPHOLOGY AND LIFE HISTORY.

The experimental animals employed were rats and guinea pigs, especially the former, which are very convenient on account of the large number of parasites occurring in the circulation. The trypanosomes first appear in the blood about eight to ten days after inoculation and gradually increase in number until numerous (100 or more to a microscopical field), after which the death of the rat ensues in about three days. The duration of the disease may vary considerably, but is usually from three weeks to a month.

The first trypanosomes that appear are generally of the form shown in fig. 22 (Pl. 15). These small forms are sluggish in motion and often rotate about one extremity, so that they do not progress much in any particular direction. The posterior extremity is frequently rounded off, and the thickness of the animal diminishes towards the anterior end. In the living animal a continuation of the protoplasm can be seen extending beneath the flagellum to the anterior extremity.

In stained specimens the trophonucleus can be seen as an oval lightly-staining vesicle containing a distinct intranuclear centrosome. In trypanosomes stained by method A this latter structure appears less dense than the kintonucleus, and, moreover, the two differ in color in well-stained specimens, a further evidence of their different nature. The kintonucleus is a densely-staining rod-shaped body situated close to the posterior extremity and, compared with that of most pathogenic trypanosomes, is rather large. Situated a short distance away from the kintonucleus is a round, somewhat lightly staining body from which the flagellum arises. It is sometimes possible to trace fine connecting fibres between the kintonucleus and this end-bead.

These forms may divide (Pl. 16, figs. 27-28) but eventually they grow up into a form of trypanosome intermediate between two extreme types (figs. 23-26). In consideration of the facts of their development and subsequent life-history these small forms may be regarded as immature indifferent forms. The fact that they divide is no evidence of their maturity, for in *T. lewisi* the corresponding immature forms also multiply (Salvin-Moore Breinl and Hindle, 1908).

The type of trypanosome resulting from the growth of these small forms is most abundant during the earlier stages of infection. Its form is shown in Pl. 15, figs. 1-3, from which it may be seen that the posterior extremity is rounded off, and the body of the trypanosome tapers gradually towards the anterior extremity. No part of the flagellum is free, a very fine continuation of protoplasm extending to the very tip. The movements of these forms are rather sluggish, the parasites slowly wriggling amongst the red cells, and often describing circles. Their average dimensions are about 18μ in length and 2μ in thickness, but they vary considerably.

The protoplasm stains rather densely, especially with method A, and, as in the immature forms, consists of a fine reticulum generally free from granules. The flagellum originates from an end-bead which is distinct from the kinetonucleus, and usually lies a little to one side of it.

Both the nuclei resemble those described above with the exception that sometimes the trophonucleus may be slightly longer than in the immature forms. These trypanosomes multiply by longitudinal fission, the first sign of which is seen in the kinetonucleus. This seems to swell up, resulting in the formation of an oval vesicle (fig. 2) throughout which the chromatin is evenly distributed. The chromatin then aggregates together in the form of a band lying across the middle of the vesicle, which now becomes slightly drawn out in a longitudinal direction. This band then divides transversely and the two halves move apart (fig. 3), one of them usually approaching the trophonucleus, and apparently without any further changes, beyond the disappearance of the vesicle, constitute the two daughter kinetonuclei. During this process we have never been able to dis-

tinguish any chromosomes, but the arrangement of the chromatin in the form of an equatorial plate clearly supports the view that it is to be regarded as a form of mitosis. The end-bead together with the flagellum appears to take no part in this process of division, but after the separation of the two daughter nuclei the one closer to the trophonucleus seems to throw off a round body from which a new flagellum develops parallel to the old one. After the division of the kinetonucleus is complete the trophonucleus commences to divide. The intranuclear centrosome becomes drawn out into a dumb-bell shaped form and the two halves move apart until they lie one at each pole of the nucleus, still remaining connected, however, by a fine line (Pl. 15, fig. 4). The chromatin contained in the surrounding vesicle then precipitates out in the form of an equatorial plate, lying transversely with regard to the two centrosomes (fig. 4). This stage of division has been observed only on very few occasions and so must be passed through very rapidly. The equatorial plate then splits transversely and each half moves up towards its respective centrosome (fig. 5), finally collecting around it (fig. 6). The connecting line between the two centrosomes eventually disappears and each daughter nucleus gradually assumes the usual form (fig. 7). In what manner the chromatin reconstructs the clear oval vesicle around the intranuclear centrosome is not quite clear. Meanwhile the second flagellum has been elongating and by the time the trophonucleus has divided is almost as long as the original one (fig. 7).

The animal then splits longitudinally, the fission commencing at the anterior end and extending down until the two halves are connected merely by their posterior extremities, in which position they may remain for some little time before finally separating (Pl. 15, fig. 8).

At certain stages of development this type of trypanosome proceeds to the formation of cysts, or latent bodies. The posterior extremity of the parasite swells up (fig. 14) and the protoplasm, together with the trophonucleus, concentrates towards this end (figs. 15-16), finally resulting in the formation of a round or oval mass of protoplasm containing both nuclei and provided with a long flagellum (fig. 17). This is eventually

cast off and the cysts are carried by the blood into the spleen, and other organs of the body, in which they may remain dormant for some time.

In *Trypanosoma raiac* cysts are formed in exactly the same manner as in *dimorphon*, but the process seems to take place only in the crop of *Pontobdella muricata*, the intermediate host (Robertson, 1909).

If rats infected with *T. dimorphon* are injected with 0.2 gm.

of a solution of "Atoxyl" ($C_6H_4-AsO-\overset{OH}{\underset{NH_2}{ONa}}$), all the trypano-

somes are killed off with the exception of certain of these encysted forms which may still be found in the spleen. After an incubation period of about four weeks they start to develop, and the parasites reappear in the peripheral circulation. In infected rats which have been treated with Atoxyl it is possible, therefore, to obtain the developmental stages of the cysts without any other types of trypanosomes being present. Each cyst (Pl. 16, fig. 19) consists of an oval, or round mass of dense protoplasm surrounded by a very distinct membrane, and contains a typical oval-shaped trophonucleus beside which is the kintonucleus. At the commencement of development an end-bead is thrown off from the latter and from it a new flagellum grows forward. As it develops the kintonucleus travels backwards until it arrives at a position close to the rounded posterior extremity. The growing flagellum draws the protoplasm with it, and in this way the ordinary trypanosome form is produced. At immature stages of development, the parasites frequently multiply by longitudinal fission before proceeding to the fully developed forms described above.

This type is characterized, therefore, by its external form; absence of chromatoid granules; the rather dense protoplasm; the shape and size of the two nuclei; and especially by the formation of cysts (or latent bodies).

From this type of trypanosome are developed two distinct forms and chiefly for this reason it is regarded as representing the indifferent type. The fact that it possesses a complete asexual cycle (the cyst formation) which does not occur in the other two

types to be described below, is a further proof of its distinctness.

In certain of the indifferent trypanosomes a small quantity of the substance of the kinetonucleus is budded off and passes up the middle of the cell towards the trophonucleus (Pl. 15, figs. 9-12). It swells up and eventually appears as a lightly staining vesicle in close proximity with the trophonucleus. At times a succession of these bodies is budded off from the kinetonucleus, giving an appearance such as that shown in fig. 13. From the irregularity of this phenomenon it is probably of no significance, but it may be found in all types of this species.

Some of the indifferent trypanosomes early in the course of infection proceed to the formation of a distinct type of trypanosome known as the "stumpy forms" (Pl. 16, figs. 29-34). The latter are very obvious in preparations of the living parasite, as they have a peculiar habit of slowly rotating about one extremity and are extremely sluggish in all their movements. A free flagellum is absent in the fully developed forms and moreover the undulating membrane is not well developed. The posterior extremity is bluntly rounded, and the whole body of the animal is very short in proportion to the width. Even in the fresh state the remarkable dense and granular character of the protoplasm is noticeable. The average dimensions of these forms is about 18μ in length, and 4μ in thickness.

The protoplasm of such trypanosomes stains very densely and usually contains numerous chromatoid granules, that seem to arise from the trophonucleus. The kinetonucleus is very large and close to the posterior extremity of the body; in close proximity to it is situated a large end-bead from which arises the short flagellum. The trophonucleus is a large, round vesicle containing a centrosome relatively twice the size of that found in the indifferent form (Pl. 16, figs. 33-34).

The first evidence of the development of the stumpy form is seen in the trophonucleus. The intranuclear centrosome divides (fig. 29), and one half passes out of the nucleus taking with it a spout-like mass of chromatin (fig. 30). This becomes detached (fig. 31), and passes away from the nucleus (fig. 32); it finally degenerates, thereby giving rise to some of the chromatoid granules that are so common in the stumpy forms. The whole

body of the trypanosome then swells up and the posterior extremity is gradually drawn in until it appears bluntly rounded. As a result of this the kintonucleus and locomotor apparatus is situated closer to this extremity than in the indifferent forms.

The kintonucleus meanwhile enlarges, attaining a length of 1μ in extreme cases, and the end-bead in relation with it also increases in size. The trophonucleus swells up and becomes spherical, while the intranuclear centrosome also enlarges. Both nuclei stain more densely than those of the other types. On consideration of the characters of this type of trypanosome and comparison with other blood parasites, we have come to the conclusion that these stumpy forms may be regarded as female forms.

In the blood of the rat they may be observed in all stages of degeneration and probably therefore do not develop any further in this host. Examples of them may be found during all but the earliest stages of infection and some of the indifferent forms may always be found developing into this type.

Some of the indifferent forms give rise to another type which has been previously described under the name of "long forms." Their movements are more active than those of any of the others. They are long and narrow with a pointed posterior extremity, and a well-developed flagellum along which, however, a fine continuation of protoplasm extends to the anterior end. The broad undulating membrane is thrown into a series of folds by the flagellum. The average dimensions of these trypanosomes are about 27μ in length, by 1.5μ in thickness.

The protoplasm stains less densely than that of the other types and is generally free from chromatoid granules. The kintonucleus is situated some considerable distance (1 to 2μ) from the posterior extremity, and is comparatively small.

In close proximity to it the end-bead of the flagellum appears as a small round body; it may be situated either in front or behind the kintonucleus. The trophonucleus is typically of the form shown in Pl. 17, fig. 44, with a distinct intranuclear centrosome surrounded by an elongated vesicle. The distance between the two nuclei is greater in these long forms than in the stumpy ones.

The long forms multiply very rapidly by a form of mitotic

division similar to that described above for the indifferent forms, and as a result are more abundant than any other in the later stages of infection. We have been unable to decide whether the trophonucleus extrudes chromatin, as in the female forms, or not; but the intranuclear centrosome often exhibits budding (Pl. 17, figs. 38-40). The masses which thus arise simply disappear.

Mitosis is observed more distinctly in this elongated trophonucleus than in any other, the equatorial plate being very distinct, and the two centrosomes widely separated, with a series of very fine fibres extending between them.

The long, slender body of this extreme type of *dimorphon*, and absence of granules, together with its well-developed flagellum and elongated nucleus, and also comparison with other forms of trypanosomes, supports the view that it is to be regarded as the male form.

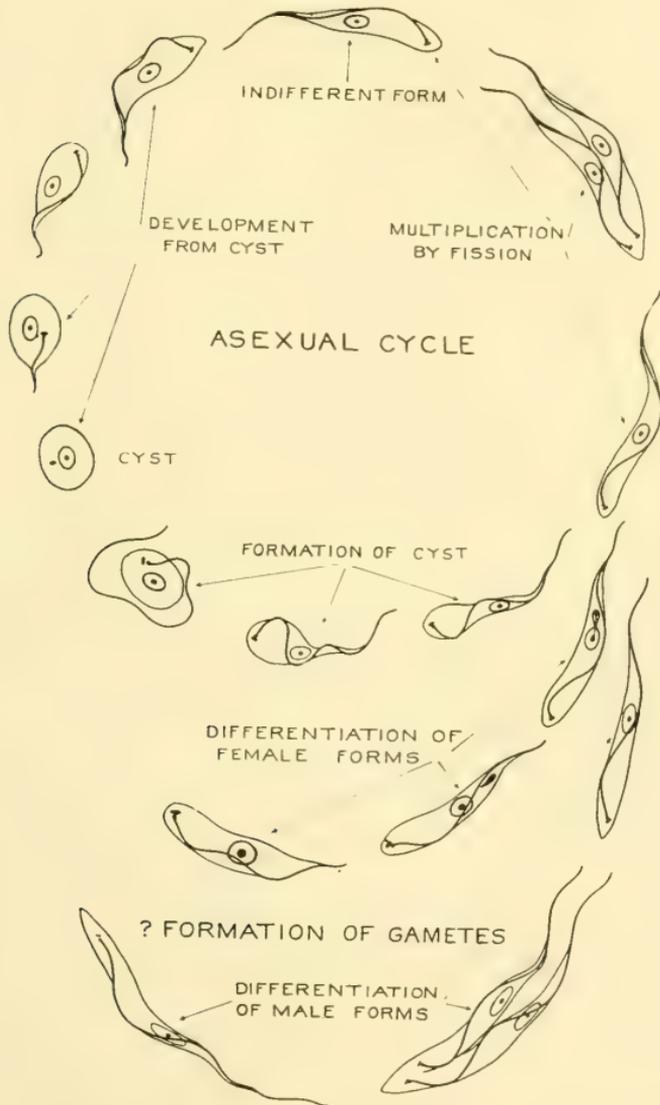
The life-cycle of *T. dimorphon* within the vertebrate host may therefore be briefly summarized in the accompanying diagram.

SUMMARY.

In *Trypanosoma dimorphon* there are three distinct types which may be regarded as indifferent, male, and female forms, respectively.

The indifferent trypanosomes, from which the other two types originate, are especially characterized in this species by possessing a complete asexual cycle (cyst formation) that goes on in the vertebrate host. This cycle is very similar to that of *Crithidia* described by Patton (1909) and other authors. In at least one other species of trypanosome the cyst formation occurs in the alimentary canal of the blood-sucking invertebrate that serves as the intermediate host (Robertson, 1909).

In addition to this cycle, some of the indifferent forms may develop further along two lines, culminating in the "stumpy" and "long" forms described above, which perhaps may be female and male respectively. The evidence for regarding them as such is inconclusive since we have never observed conjugation; probably it takes place in the intermediate host. The "stumpy" forms certainly seem to correspond with the short female gametes



Text-fig. 1.—The life-cycle of *T. dimorphon* within the vertebrate host (diagrammatic).

of *T. lewisi* described by Prowazek (1905), and also with the "stout forms" of *T. gambiense* which Minchin (1908) and others regard as female. Similarly the long forms correspond with male gametes of *lewisi* and the "slender trypanosomes" of *gambiense*.

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EXPLANATION OF PLATES.

All these figures are drawn to a magnification of 3000 diameters and are from specimens stained with iron haematoxylin. No camera lucida was employed, but the dimensions were obtained by measurement with an eyepiece micrometer. A Zeiss, 2 mm., apochromatic objective was employed, together with the 6 and 18 eyepieces.

PLATE 15.

Figs. 1 to 16 from the peripheral circulation.

Figs. 17 and 18 from the spleen.

Fig. 1.—Typical indifferent form showing oval trophonucleus and rather large kintonucleus, with a distinct end-bead on the flagellum.

Fig. 2.—First stage in division of kintonucleus.

Fig. 3.—A later stage in which the chromatin has separated in the form of two bands lying across a lighter-stained area.

Fig. 4.—Division of intranuclear centrosome and arrangement of chromatin in the form of an equatorial plate.

Fig. 5.—Cleavage of chromatic plate into two halves. A new flagellum has commenced to grow from the region of the new kintonucleus.

Fig. 6.—Late stage of division of trophonucleus showing the chromatin aggregated around each intranuclear centrosome, these latter still remaining connected by a fine line.

Fig. 7.—Commencement of division of protoplasm.

Fig. 8.—Late stage of division showing the two parasites still remaining connected by their posterior extremities.

Figs. 9-12.—Trypanosomes showing successive stages in the passage of chromatin from the kintonucleus to the region of the trophonucleus.

Fig. 13.—Trypanosome showing a number of chromatic bodies between the two nuclei.

Figs. 14-18.—Various stages in the formation of a cyst from the indifferent form of trypanosome.

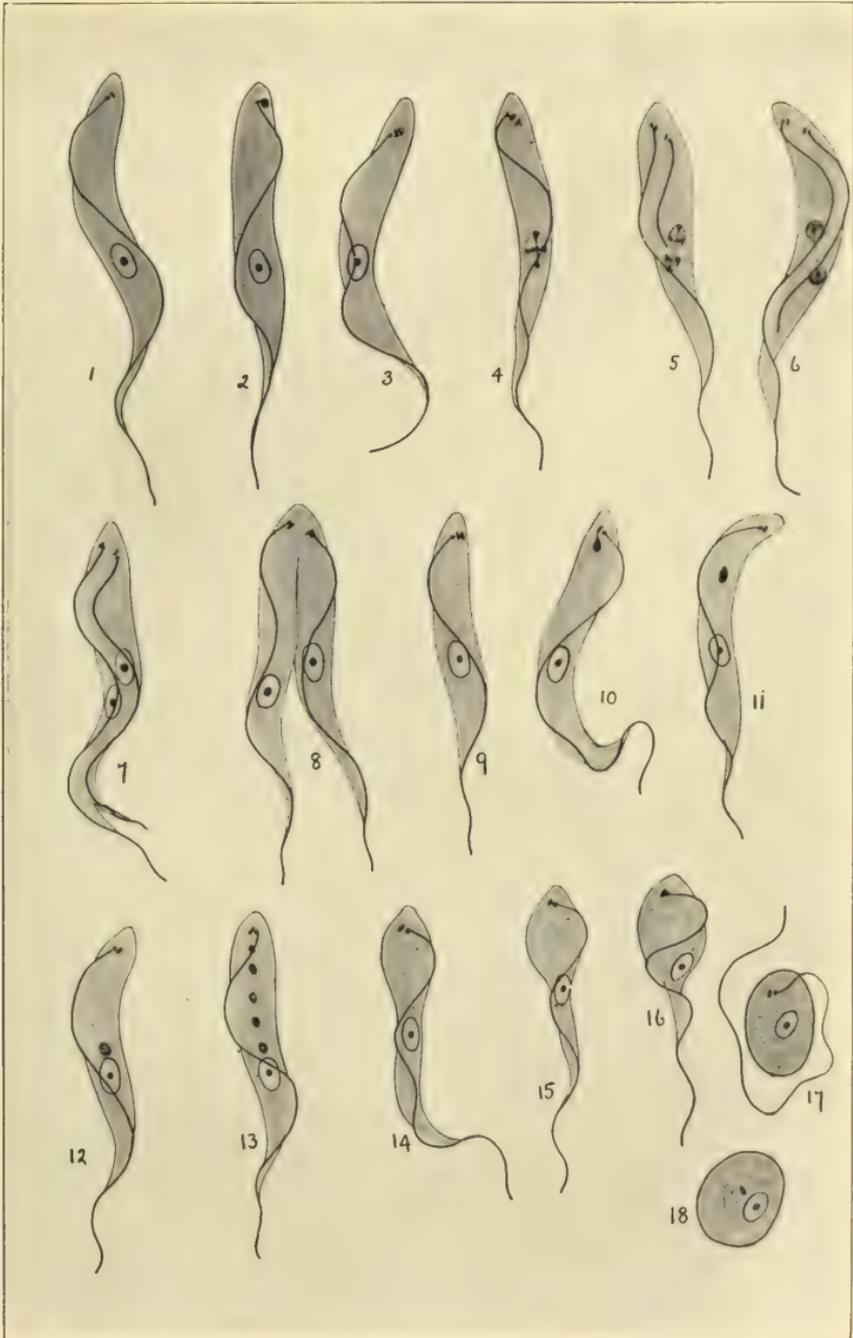


PLATE 16.

Figs. 19-20 from the spleen.

Figs. 21-36 from the peripheral circulation.

Fig. 19.—Cyst showing the kintonucleus lying in the neighborhood of the trophonucleus.

Fig. 20.—Commencement of the development of the cyst.

Fig. 21.—Further growth of the flagellum and the passage backward of the kintonucleus.

Figs. 22-24.—Various stages in the elongation of the trypanosome, resulting in the formation of a small indifferent form.

Figs. 25-28.—Division of small, immature, trypanosomes.

Figs. 29-34.—Successive stages in the differentiation of the female form from the indifferent type of trypanosome.

Fig. 29.—Division of the intranuclear centrosome together with slight precipitation of chromatin around the anterior daughter centrosome.

Figs. 30-31.—Budding-off of a portion of the trophonucleus, together with the anterior daughter centrosome.

Fig. 31.—Trypanosome showing the passage of this budded-off chromatin to the anterior extremity.

Figs. 33-34.—Fully developed female forms showing large nuclei, short flagella and dense protoplasm.

Figs. 35-36.—Stages in the degeneration of the female forms.

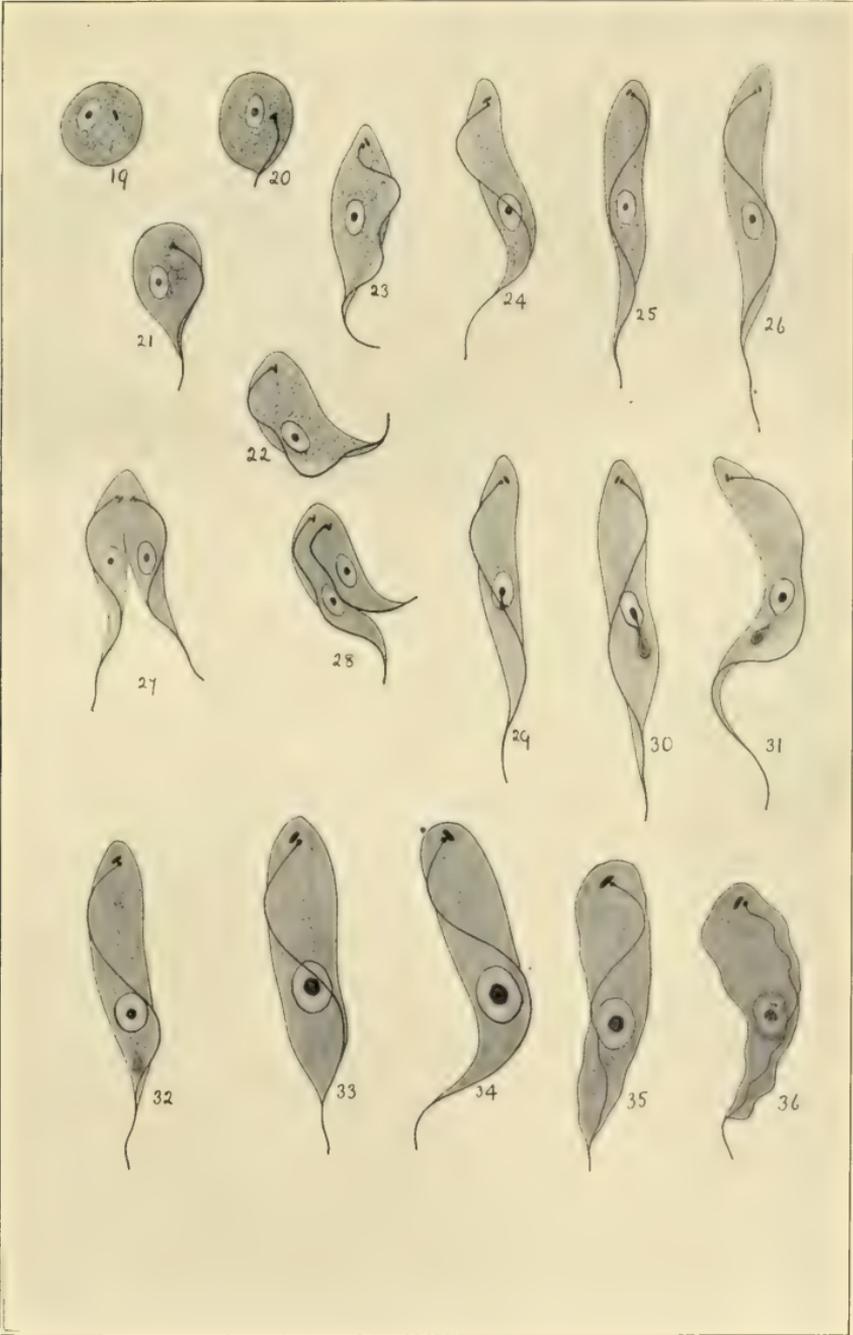


PLATE 17.

Fig. 37.—Elongation of indifferent form.

Fig. 38.—Male type of trypanosome showing a mass of chromatin, derived from the kinetonucleus, lying close to the trophonucleus. The intranuclear centrosome exhibits budding.

Fig. 39.—Budding of intranuclear centrosome in male type of trypanosome.

Figs. 40-44.—Various stages in the division of the male forms.

Fig. 45.—Abnormal form of trypanosome, showing multiple division of nuclei without separation of protoplasm.



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XXVIII

A QUANTITATIVE STUDY OF THE
DEVELOPMENT OF THE SALPA
CHAIN IN *SALPA FUSIFORMIS-
RUNCINATA*

BY
MYRTLE ELIZABETH JOHNSON

BERKELEY
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A QUANTITATIVE STUDY OF THE
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BY

MYRTLE ELIZABETH JOHNSON

Research Assistant in Zoology, San Diego Marine Biological Laboratory.

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* A thesis submitted in partial satisfaction of the requirements for the degree of Master of Science in the University of California.

1. INTRODUCTION.

This paper embodies the results of an attempt to discover the laws governing the growth and development of the zooids of the Salpa chain. The investigation was instigated largely by a reading of Dr. Raymond Pearl's memoir, "Variation and Differentiation in *Ceratophyllum*" (Pearl, '07), in which the author has outlined certain laws which he has found operative in the growth of this plant. A sentence from one of his opening paragraphs will give his point of view: "Since the condition of the adult organism is, with respect to every character, the result of a process of gradual development and growth, it is clear that in order to gain anything approaching a satisfactory analysis from the biological standpoint, we can not take the adult structure as something given, but must investigate the laws according to which the morphogenetic processes concerned in its production operate."

The general problem undertaken here is similar to Dr. Pearl's but the difference in the material used makes necessary a difference in the method of attack.

Dr. Pearl's problem was "to determine and formulate so far as possible, the laws according to which differentiation with growth occurs in *Ceratophyllum*" on the basis of the *number of leaves in the leaf whorls of the plant*. *Ceratophyllum* bears a large number of whorls, some with a larger and some a smaller number of leaves. The whorls with different numbers of leaves distribute themselves in a characteristic way. Quoting his further statement: "We have, then, by analysis of the gross frequency distribution for the plant as a whole, to investigate the biological laws which lead to the production in this particular organism of the characteristic distribution observed. In biometrical terminology, our problem is one of *intra-individual variability*."¹ Moreover, Pearl dealt with the adult organism. The plants were still growing, it is true, but *leaf-number* even in the tiny leaflets at the tip of the branch was already established, so that the results were, strictly speaking, for the adult organism rather than for differentiation with growth, as stated.

¹ The italics are mine.—M. E. J.

With the salpa chain, on the other hand, the problem is one of growth, for we are considering size relations in a repetitive series of *developing* parts.

The working out of the problem as well as the summing up of results has been done under the direction of Professor Wm. E. Ritter of the University of California. Dr. Pearl has assisted in the treatment of some of the data. Professor A. W. Whitney and Mr. Joseph Lipke of the mathematics department of the University of California have also given helpful advice in the mathematical work.

2. THE MATERIAL.

The material used was from collections made at the Marine Biological Station at La Jolla, California. *Salpa fusiformis-runcinata*, the species chiefly employed, occurs there in large



Fig. 1.—*S. fusiformis runcinata*—asexual or solitary generation: *br.*, branchial orifice; *at.*, atrial orifice; *ch.*, chain.

numbers during the summer months, especially during June and July. At this time individuals of all sizes are taken and well developed chains are found in almost all of the solitary generation.

A general description of the species, especially of its manner of asexual reproduction, is the first essential to a clear understanding of the problem.

The salpae are notable for their two generations. The one known as the "solitary" generation (Fig. 1) produces offspring asexually by budding. The buds are arranged in chains which are sometimes circular and sometimes linear. These buds, when

grown, become separate from each other and constitute the sexual generation (fig. 2), each individual producing one of the "solitary" type which, in turn, propagates by budding, and so on.

Individuals of the bud-producing generation of this species are nearly cylindrical and both orifices are terminal. The length

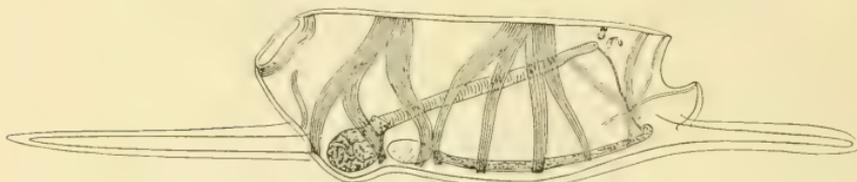


Fig. 2.—*S. fusiformis runcinata*—sexual or aggregate generation.

of the largest specimens is 70-90 mm. The test is thin and soft anteriorly but thick and firm posteriorly, especially on the ventral side of the posterior third, where it forms a thick, firm gelatinous mass. The heart is on the ventral side, immediately in front of the intestinal tract called the "nucleus." A chain of buds encircles this nucleus and all but its most proximal portion is embedded in the thick test. (Fig. 1, *ch.*)

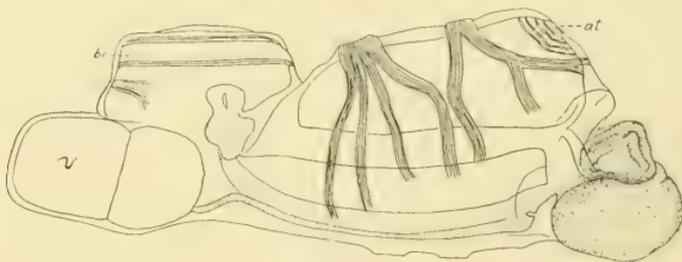


Fig. 3.—Young zooid of *S. fusiformis runcinata* taken from the chain: *at.*, atrial orifice; *br.*, branchial orifice; *v.*, vascular canal.

The individuals of the aggregate or sexual generation are somewhat elliptical in outline with processes at each end. The processes are always asymmetrical at the outset. The branchial orifice is inclined upward, while the atrial is directed nearly backward. There are seven body muscles, the anterior four and

posterior three being confluent on the dorsal side. Fig. 2 shows the free swimming or fully developed zooid, while the younger one shown in fig. 3 was detached from the chain. It is thus seen that the individuals of the two generations are very different in structure as well as in mode of origin.

3. MORPHOLOGICAL OBSERVATIONS.

The main problem in the investigation has been, as stated, the quantitative relation of the developing zooids, but it has also been found necessary to give some attention to certain questions of structure and function which affect the final results. These

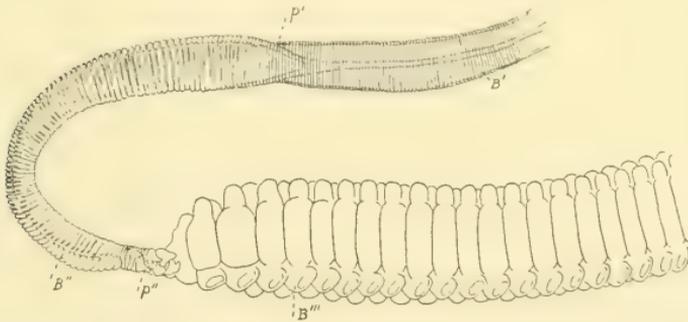


Fig. 4.—Portion of chain of *S. fusiformis runcinata*: *B'*, first block; *B''*, second block; *B'''*, third block; *p'*, deploying point; *p''*, intermediate piece.

are chiefly, the manner of segmentation of the chain, the arrangement of the zooids, and their mode of nutrition at various stages in development.

The chain originates in the median line, just anterior to the "nucleus." (Fig. 1.) It extends toward the oral extremity for a few mm. and then bends to the left, encircling the nucleus so that the distal end of a well-developed chain is found at the right of the nucleus, the chain reaching three-fourths of the way around.

The zooids of the chain, instead of being in an evenly graduated series, the least developed at the proximal and the more mature at the distal end, are arranged in groups, or blocks (fig. 4), those of each block being approximately the same size. The

chain may have one, two, or three of these blocks, the number varying with the age of the parent and the size of the zooids. We will refer to the proximal block (*B'*, fig. 4) as the first. The proximal end of this first block is directly continuous with the proliferating stolon, microscopical examination of which is necessary to determine the region of transition between the segmented and the unsegmented parts. The difference in size between the zooids of the first and second blocks is abrupt, especially if there are only two blocks in the chain. If there are three, the difference in size between the first and second is slight, but the difference between the second and third is very marked.



Fig. 5.—Intermediate piece in a chain of *S. fusiformis runcinata*: *B'*, second block; *B''*, third block; *p''*, intermediate piece.

The region of junction between blocks needs special attention. The one between the second and third blocks is shown best in figs. 4 and 5. The sharp distinction between the first zooids of the last block and those of this intermediate region is plainly seen. I call this region the intermediate piece, it not having been given a name by previous writers, so far as I can find. In the specimen figured, which is typical for a long chain, it is apparent that the zooids of this piece not only are much smaller than those of the block, but are distorted and imperfect. Those at the left in the figure, *i.e.*, toward the proximal end of the chain, merge somewhat gradually into those of the second block. It will also be noticed from the figure that the largest zooids of this second

block are those which are a short distance from the end, not those next to the intermediate piece. The region between the first and second blocks, I will call the "deploying point." (p' , fig. 4.) It is different in structure from the intermediate piece and will be understood better after the development of the chain is described.

When the terminal block of the chain is not the first one produced by the parent, others having been thrown off, there is present at the distal end a number of small, abortive zooids. It seems probable that these zooids are the remnant of what would be an intermediate piece if a fourth block were present. If one removes a large block from the chain, the separation occurs at the first zooid of the block, leaving the entire intermediate piece as the terminal remnant of the block that remains.

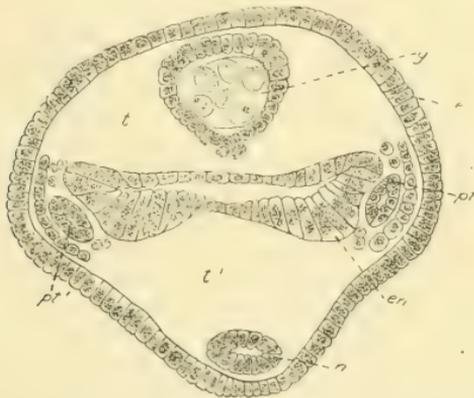


Fig. 6.—Cross-section through the first block of a chain of *S. fusiformis-runcinata*.

Examination of a cross-section close to the proliferating stolon (Fig. 6) shows it to consist of a tubular sheath of ectoderm c , a nerve tube n , an entodermal tube en , two perithoracic tubes pt and pt' , two blood tubes t and t' and a genital rod g . These run throughout the chain, their relative positions usually remaining the same as far as the deploying point.

As the development in *Salpa fusiformis-runcinata*, so far as I have examined it, agrees in most respects with what Brooks

found in *S. pinnata* and *S. cylindrica*, I quote from his description (Brooks, '93, p. 78) and then point out certain particulars in which *S. fusiformis-runcinata* differs.

"The first indication of the segmentation of the stolon is a series of ectodermal folds, which first appear at the sides, but soon extend up and down and completely encircle it, and pushing inwards, mark out the body cavities of the salpae and also cut up the tubular structures inside the stolon into segments.

"The active agent in this process of segmentation is the growth of the ectodermal folds, and the other structures are actually *cut by these folds*.^{1a} As the result of this process, the nerve tube becomes cut up into a series of ganglia, one for each salpa, the perithoracic tubes become cut up into a series of perithoracic vesicles, two for each salpa; the genital string becomes cut up into a series of eggs, one for each salpa, inclosed in a follicle; and the thickened endodermal epithelium at the sides of the endodermal tube, becomes cut up into a series of vertical pouches or pockets, two for each salpa, the rudiments of the right and left halves of the pharynx."

"At this stage each salpa is bilaterally symmetrical, and its plane of symmetry is the same as that of the stolon, while its long axis is at right angles to that of the stolon, which becomes converted into a single row of salpae, so placed that the dorsal surfaces of all of them are toward the base of the stolon, their ventral surfaces towards its tip, their right and left sides on its right and left respectively, their oral ends at its top, or neural side, and their aboral ends at its bottom, or genital side."

"The single row of salpae becomes converted into a double row, which consists of a series of right-handed salpae and a series of left-handed ones, placed with their dorsal surfaces out, their ventral surfaces towards the ventral surfaces of those in the opposite row, and the left sides of those on the right and the right sides of those on the left towards the base of the stolon."

"In order to illustrate these secondary changes of position let us represent the series of salpae by a file of soldiers, all facing the same way. Now imagine that each alternate soldier moves to the right, and the others to the left to form two files still

^{1a} The italics are mine. M. E. J.

facing the same way. Now let them face about so that the backs of those in one row are turned towards the backs of those in the other row. They will now illustrate two rows of salpae."

"To make the illustration more perfect, suppose that, instead of stepping into their new places, the soldiers grow until they are pushed out by mutual pressure, and suppose that their *heads, growing fastest*, form two rows while their feet still form one row, and suppose furthermore that as each soldier rotates, his feet turn first and that the twist runs slowly up his body to his head which turns last.² We must also imagine that these various changes all go on together, and that while they are taking place, each soldier not only grows larger, but also develops from a simple germ to his complete structure."

This is an admirable description of the essential facts of segmentation and shifting of position. The region which I have called the "deploying point," which is shown in fig. 4, *p'*, is the point where the zooids change from single to double file.

A study of the longitudinal sections of a chain shows that the segmentation is, as in *S. pinnata*, initiated by the ectoderm. Folds, or undulations, appear in the ectodermal layer at regular intervals along the length of the chain. (Figs. 7, 8, and 12.)

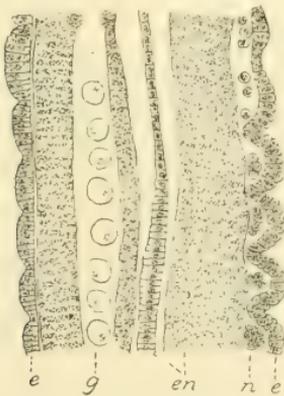


Fig. 7.—Longitudinal section through the first block of a chain of *S. fusiformis runcinata*.

The raised part of these folds becomes thicker while the constrictions marking the divisions between segments are but little, if any, thinner than the original ectoderm. The constrictions increase in depth, cutting into the other structures and dividing them up into segments. The inner strands follow the lead of the ectoderm in segmenting, the undulations in them appearing first where their surface is in contact with the ectoderm. No trace of the division appears along these inner strands until the ectoderm reaches them.

² The italics in the above citation are mine.—M. E. J.

I have not been able to determine certainly whether in this species segmentation begins at the sides and extends around as Brooks describes. The infolding is farther advanced on the neural side of the chain than on the side of the genital rod, so the infolding either begins at the sides and works more rapidly toward the neural tube or it begins at the neural tube and extends around, reaching the ectoderm next the genital rod last.

Near the base of the stolon, the genital cells are grouped together irregularly, but passing distally these cells come to lie

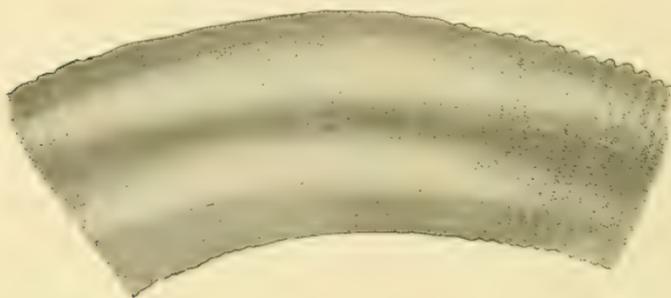


Fig. 8.—Surface view of stolon, showing point where segmentation begins in chain of *S. fusiformis-runcinata*.

more and more in a single row. Where the segmentation is as plainly marked as in fig. 7, there is approximately one cell for each segment. As it is usual in this species to find but a solitary embryo in the aggregate individual, the final distribution of ova in the chain probably gives one to each segment.

An examination of whole mounts of chains showing the most recently segmented portion next to the stolon, shows that a break in the regularity of the progress of segmentation sometimes occurs (Fig. 8). The constrictions marking off the segments of the stolon almost or quite disappear for a short distance and then reappear beyond, they being again gradually lost as one approaches the root of the stolon. Some chains do not seem to have this break in continuity of the segmentation, the constrictions being only lost as they disappear gradually at the root of the stolon.

We turn next to the orientation of the zooids relative to the parent. When we compare the cross-sections with the sketch showing the position of the whole chain, it would seem that the genital rod is toward the dorsal side of the parent, a condition the reverse of that described by Brooks. As this matter of position has no vital connection with the present problem, I have not taken time to make sure of this point so far as the first block is concerned. It is certainly true that in the second block the genital rod is toward the dorsal side of the parent, the zooids standing on their heads. Frequently, as the chain grows larger, this position is altered gradually until in the largest block the zooids come to lie on their sides with their oral extremities turned toward the nucleus of the parent.

The blood tubes pointed out in the segmenting stolon persist while the zooids change their shape in shifting from single to double file. Their position in the distal part of the chain is shown in fig. 3, *v*. As the zooids grow, the vascular canal becomes gradually smaller and the zooids by their own growth pull apart from one another and the vascular connection is lost entirely. The rotation of the zooid on its own axis after the two rows have been formed, as described in the quotation from Brooks, involves a structural change which is clearly shown in his sections and diagrams but not so well in my sketches.

In chains whose zooids are almost ready to fall apart, the connection between zooids is by papillae. Quoting from Brooks (Brooks, '93, p. 87): "The members of the community are united to each other by processes from the walls of their bodies, which are hollow and contain diverticula from their body cavities, although there is no communication between the body cavities of adjacent salpae." These papillae grow gradually as the vascular canal decreases in size and the zooids grow apart.

The axis of the zooids in most blocks is at right angles to the axis of the chain, but in blocks which are ready to leave the parent or are found floating in the water, they become more and more inclined.

This gradual loss of connection with the parent and the assumption of independent life by the zooids involves a change in the source of food supply which may affect the rate of growth,

as will be noted later. Before the vascular canal disappears, the nourishment reaches the zooids by way of the *blood tubes*.

The disappearance of the blood tubes begins at the distal end of the block. If zooids are removed from different portions of a large block the canal opening (fig. 3, *v*) will be seen to be much smaller at the distal end of the block than at the proximal end. If this gradual disappearance is brought about in such a way as to still allow a continuous circuit through the portion of the canal that remains at any given time the younger, proximal zooids will receive nourishment from the parent for a longer period than the more distal ones.

The possibility still remains that there may be a transfusion of nourishment between the zooids by way of the papillae or by protoplasmic connection at this point, but there is no sure evidence to this effect.

4. QUANTITATIVE OBSERVATIONS AND DATA.

In choosing the zooids for measurement, the terminal block only was taken from any chain, as the vascular connection in the younger blocks is too intimate to allow the zooids to be separated without mutilation. In the case of the first five blocks measured, only one measurement was taken of each dimension. The zooids were removed one at a time, first from one row and then from the other. These first zooids were not kept after being measured. The measurements were made with the ocular micrometer in the Zeiss binocular microscope (ocular 2, low power objective). A unit in the table is equal to 0.1 mm. and the scale could be read to 0.5 of a unit or 0.05 mm. In entering the results in the tables, each row of zooids in the block was treated as a separate series, so that from the five blocks first measured I have ten series of measurements. (Table 1.)

In obtaining the data for the three later blocks (table 2), a greater effort was made to avoid errors. In the first place, it seemed desirable to complete the measurement of a series all at one time to avoid changing conditions of light, etc., as far as possible. As it takes considerably more than four hours to separate the zooids of a block and measure them, they were first separated and each put into a bottle containing the number of

TABLE I.

Measurements of first five blocks of *Salpa fusiformis-runcinata*; including length, mean length, width, mean width, means of products of length and width, and means of the ratios length divided by width for each place in the chain.

Roman numerals indicate the number of the series. For example, series I-II are the two rows of the first block; III-IV, the second, etc. Unit = .1 mm.

Only one measurement of each dimension was taken.

Serial No. in Block	Length										Width										Mean Length	Mean Width	Means of Products of Length & Width	Means of Ratios of Length to Width
	I	II	III	IV	V	VI	VII	VIII	IX	X	I	II	III	IV	V	VI	VII	VIII	IX	X				
1	17.0	16.0	15.0	14.0	7.5	6.5	11.0	12.0	9.0	10.0	8.0	7.0	6.0	6.0	3.0	3.0	4.5	4.5	4.0	4.0	11.8	5.00	64.25	2.577
2	18.0	19.0	16.5	16.5	9.5	8.0	11.0	12.0	10.5	10.5	8.0	8.0	7.0	7.0	4.0	3.0	4.5	5.0	4.5	4.5	13.2	5.55	78.30	2.889
3	19.0	19.0	17.0	17.5	14.0	12.0	12.0	12.0	11.0	11.5	9.0	9.0	8.0	7.0	6.0	5.0	5.0	4.5	5.0	5.0	14.5	6.15	91.50	3.274
4	20.0	19.0	17.5	18.0	15.0	12.0	12.5	13.0	11.5	12.0	9.0	9.0	6.5	7.0	6.0	6.0	5.0	5.0	5.0	5.0	13.2	6.32	103.88	3.436
5	20.0	20.0	18.0	18.0	15.0	14.0	12.5	12.5	12.0	12.0	9.0	9.0	7.0	7.0	6.5	6.0	5.0	5.0	5.0	5.0	15.4	6.45	103.85	3.433
6	20.0	20.0	18.0	19.0	16.0	14.5	13.5	13.0	12.0	12.0	8.5	9.0	7.0	8.5	6.5	6.0	5.0	5.0	5.0	5.0	15.7	6.53	107.09	3.416
7	21.0	21.0	18.0	19.0	15.5	14.0	13.0	13.0	12.0	12.0	9.0	9.0	7.0	7.5	6.5	6.0	5.0	5.0	5.0	5.0	15.9	6.50	108.33	3.449
8	21.0	21.0	18.5	19.0	16.0	15.0	13.0	13.0	12.0	12.0	9.0	9.0	7.0	8.0	7.0	6.0	5.0	5.0	5.0	5.0	16.1	6.60	111.15	3.447
9	21.0	22.0	18.0	19.0	16.0	15.0	13.0	13.0	12.0	12.0	9.5	7.0	8.0	6.5	6.0	5.0	5.0	5.0	5.0	5.0	16.2	6.70	115.44	3.472
10	22.0	22.0	18.0	19.0	16.0	15.0	13.0	13.0	11.5	12.5	9.0	9.0	7.0	7.5	7.0	6.0	5.0	5.0	5.0	5.0	16.3	6.80	115.65	3.478
11	22.0	22.0	18.5	19.0	16.0	15.0	13.5	13.5	12.5	13.0	10.0	9.0	7.0	8.0	7.0	6.0	5.5	5.5	5.0	5.0	16.5	6.90	117.75	3.445
12	22.0	22.0	18.0	19.0	16.5	15.0	13.5	13.5	13.0	12.5	10.0	9.0	7.0	7.0	6.5	6.0	5.0	5.5	5.5	5.0	16.5	6.95	115.99	3.498
13	22.0	22.0	18.0	19.5	16.0	15.0	14.0	13.5	12.0	13.0	10.0	9.5	7.0	8.0	7.0	6.0	5.5	5.0	5.0	5.0	16.5	6.80	118.25	3.457
14	22.5	22.5	19.0	19.0	17.0	15.5	14.0	14.0	13.0	13.0	9.0	10.0	7.0	8.0	7.0	6.0	5.0	5.0	5.0	5.0	17.0	6.80	124.85	3.548
15	22.0	23.0	19.0	19.5	17.0	16.0	14.0	14.0	13.0	13.0	10.0	9.0	7.0	8.0	7.0	6.0	6.0	5.0	5.0	5.0	17.1	6.80	121.50	3.523
16	22.0	22.0	19.0	20.0	17.0	17.0	14.0	14.0	13.0	13.0	10.0	10.0	7.0	8.0	7.0	6.0	6.0	5.5	5.0	5.0	17.1	6.95	124.50	3.495
17	23.0	23.0	19.0	20.0	17.0	16.0	14.0	14.0	13.0	13.0	11.0	10.0	8.0	8.0	7.0	6.0	5.5	5.5	5.0	5.0	17.2	7.10	129.40	3.605
18	23.0	23.0	19.5	20.0	17.5	15.5	14.0	14.0	13.5	13.0	10.0	9.5	8.0	8.0	7.5	6.5	6.0	5.5	5.0	5.0	17.3	7.10	129.90	3.625
19	23.0	23.0	19.5	20.0	17.0	16.0	14.0	14.5	13.0	13.5	11.0	9.0	8.0	8.0	7.0	6.0	6.0	5.5	5.0	5.0	17.4	7.05	128.72	3.605
20	23.0	22.0	19.0	20.0	17.0	16.0	14.0	14.0	14.0	13.5	9.0	9.0	7.5	8.0	7.5	6.5	6.0	6.0	5.5	5.5	17.3	7.00	125.12	3.468
21	23.0	22.0	19.5	20.0	17.0	16.0	14.5	14.0	13.5	13.0	10.0	9.5	8.0	8.0	6.5	6.0	5.5	5.5	5.0	5.0	17.3	7.20	128.85	3.445
22	23.0	21.5	20.0	20.0	17.0	16.0	14.0	14.0	14.0	14.0	10.0	9.0	8.0	8.0	7.0	6.0	5.5	6.0	5.5	5.5	17.4	7.30	133.25	3.689
23	23.0	22.0	20.0	20.0	18.0	16.5	14.5	14.0	14.0	14.0	10.0	9.0	8.0	8.0	7.5	6.5	6.5	6.0	5.5	5.5	17.6	7.25	132.25	3.644
24	23.0	22.0	20.0	20.0	18.0	17.0	15.0	14.5	14.0	14.0	10.0	9.0	8.0	8.0	7.0	6.5	6.5	6.0	6.0	5.5	17.8	7.40	136.01	3.691
25	23.0	21.5	20.0	20.5	18.0	17.0	15.5	15.0	14.0	14.0	10.0	9.0	8.0	8.0	7.5	7.0	6.5	5.0	6.0	6.0	17.9	7.30	135.11	3.663
26	23.0	19.0	20.0	21.0	18.0	16.5	15.0	14.5	14.0	14.0	10.0	9.0	8.0	8.0	7.5	7.0	6.0	5.5	6.0	6.0	17.5	7.30	132.63	3.443
27	24.0	20.0	21.0	21.0	18.0	17.0	15.0	14.5	14.0	14.0	10.0	9.0	8.0	8.0	7.5	7.0	6.0	5.5	6.0	6.0	17.9	7.30	138.78	3.653
28	23.5	22.0	21.0	21.0	18.0	17.0	15.0	14.5	14.0	14.0	9.5	10.0	8.0	8.0	7.0	6.0	6.0	6.0	6.0	6.0	18.0	7.45	138.73	3.448
29	23.0	21.0	21.0	21.0	18.0	17.0	15.0	15.0	14.0	14.0	9.0	9.0	8.5	8.0	7.5	7.0	6.0	6.0	7.0	6.0	17.9	7.40	137.85	3.445
30	24.0	23.5	21.0	21.0	18.0	18.0	15.0	15.0	14.0	14.5	10.0	10.0	9.0	8.0	7.0	7.5	6.0	5.5	5.5	6.0	18.4	7.45	142.96	3.487
31	24.0	24.0	20.0	20.0	18.0	17.0	15.0	15.0	14.0	14.0	10.0	11.0	9.0	8.0	7.0	6.0	6.0	6.0	6.0	6.0	18.1	7.50	144.50	3.561
32	24.0	23.5	20.0	21.0	18.0	17.0	15.0	15.0	14.0	14.0	10.0	11.0	9.0	8.5	8.0	7.0	6.0	5.5	6.0	6.0	18.2	7.75	146.80	3.557
33	24.0	23.0	21.0	21.0	18.0	17.0	15.0	15.0	14.0	14.5	11.0	11.0	8.0	8.5	7.5	7.0	6.0	6.0	6.0	6.0	18.3	7.70	148.83	3.581
34	24.5	24.0	21.0	21.0	18.0	17.0	15.5	15.0	14.0	14.5	11.0	11.0	9.0	8.5	7.0	7.0	6.0	6.0	6.0	6.0	18.5	7.75	150.00	3.494
35	25.0	24.0	21.0	20.0	18.5	17.5	15.5	15.0	14.0	14.0	11.0	11.0	9.0	8.0	7.5	7.0	6.0	5.5	6.0	6.0	18.5	7.90	149.28	3.423
36	25.0	24.0	21.0	21.0	18.0	17.0	15.0	15.0	14.0	14.5	11.0	11.0	9.0	8.5	7.0	7.0	6.0	6.5	6.0	6.0	18.5	7.80	147.75	3.489
37	27.0	24.0	21.5	21.5	18.0	17.5	15.0	15.5	14.5	14.5	11.0	11.0	8.0	8.0	7.0	6.0	6.0	6.0	6.0	6.0	18.7	7.80	152.85	3.589
38	25.0	24.0	21.5	22.0	18.0	17.0	15.5	15.0	14.5	14.5	11.5	11.0	9.0	8.0	8.0	7.0	6.5	6.0	6.0	6.0	18.7	7.90	154.88	3.589
39	25.0	23.0	22.0	22.0	18.0	17.5	15.0	15.0	14.0	14.5	12.0	11.0	9.0	8.5	8.0	7.0	6.0	6.0	6.0	6.0	19.0	7.95	158.95	3.446
40	25.0	25.0	22.0	21.5	18.0	17.5	15.0	15.5	14.5	15.0	12.0	11.5	9.0	8.0	7.0	6.5	6.0	6.0	6.0	6.0	18.9	8.00	159.15	3.287
41	26.0	24.0	22.0	22.0	18.0	17.5	15.0	16.0	15.0	15.0	11.5	11.0	9.5	9.0	7.5	7.0	6.0	5.5	6.5	6.0	19.1	7.95	159.30	3.432
42	26.0	26.0	22.0	21.5	18.0	18.0	16.0	16.0	15.0	15.0	12.0	11.5	9.5	8.0	7.0	6.5	6.0	7.0	6.0	6.0	19.4	8.05	163.25	3.427
43	26.0	25.0	21.5	22.0	18.0	18.0	16.5	16.5	14.5	15.0	12.0	12.0	9.0	9.0	8.0	7.0	6.0	6.5	6.0	6.0	19.3	8.15	165.58	3.413
44	26.0	25.0	22.5	21.5	18.0	18.0	16.0	16.5	15.0	15.0	11.0	12.0	9.5	9.0	7.5	7.0	6.5	6.0	6.0	6.0	19.4	8.05	163.73	3.438
45	26.0	26.0	22.5	22.0	18.0	18.0	16.5	16.5	15.0	15.0	11.0	12.0	9.0	9.0	7.5	7.5	6.5	6.0	6.5	6.0	19.6	8.20	169.43	3.441
46	26.0	26.0	22.0	22.0	18.0	17.5	16.0	16.0	15.0	15.0	12.0	12.0	9.5	8.5	7.5	7.0	6.5	6.0	6.5	6.0	19.3	8.15	163.23	3.441
47	26.0	26.0	22.0	21.5	18.5	18.0	16.0	16.0	15.0	15.0	12.0	12.0	9.5	9.0	8.0	7.0	6.5	6.0	6.5	6.0	19.4	8.25	168.80	3.445
48	27.0	27.0	22.0	22.0	18.0	18.0	16.0	16.0	15.0	14.5	12.5	12.0	9.0	8.0	7.5	7.5	6.5	6.0	6.0	5.5	19.6	8.05	169.07	3.447
49	26.0	26.0	22.0	22.0	18.5	18.0	16.0	16.0	14.5	14.0	12.0	12.0	9.0	8.0	7.5	7.0	6.5	6.0	6.0	6.0	19.3	7.90	167.17	3.437
50	26.0	26.0	22.0	21.5	17.5	18.0	16.0	16.0	14.5	14.0	12.0	12.0	9.0	9.0	7.0	7.0	6.5	6.0	6.0	5.0	19.2	7.95	167.11	3.438
51	27.0	25.0	21.5	21.5	18.0	17.5	16.0	16.0	14.0	14.0	12.0	13.0	9.0	9.0	7.0	7.0	6.5	6.0	5.5	5.0	19.1	8.00	171.11	3.441
52	26.0	26.0	21.0	20.5	17.5	18.0	16.0	15.5	14.0	13.5	12.0	13.0	9.0	8.0	7.0	7.0	6.5	6.0	5.5	5.0	18.8	7.90	168.80	3.441
53	27.0	26.0	19.0	20.0	17.5	18.0	16.0	16.0	14.0	13.0	12.0	12.0	7.5	8.0	6.5	7.0	6.0	6.0	5.5	5.0	18.7	7.55	167.55	3.441
54	26.0	25.0	19.0	18.5	17.0	17.0	15.5	15.0	13.0	12.0	11.0	12.0												

the series and the serial number of the zooid. With this much done it was possible to measure all of a series at one sitting. Several little ways were found in which errors may have crept into the first measurements. For instance, with so small a scale, a change of focus, though very slight, often makes considerable difference in the reading. One ordinarily changes the focus constantly when looking through the microscope but it was found to be possible to do without this. By keeping the same dish, keeping the zooid in the same part of the dish and seeing that the amount of water remained constant, the image was clear through the entire series and the measurements are probably more free from error. In order to avoid unconscious forcing of results, the zooids were measured out of their regular order as much as possible. Two sets of measurements were made of each of the last three blocks and the mean of the two was taken for the final result.

In the blocks measured, the number of individuals varies from 53 to 80. The measurements taken were length and dorso-ventral diameter (spoken of as width). The real width being very small

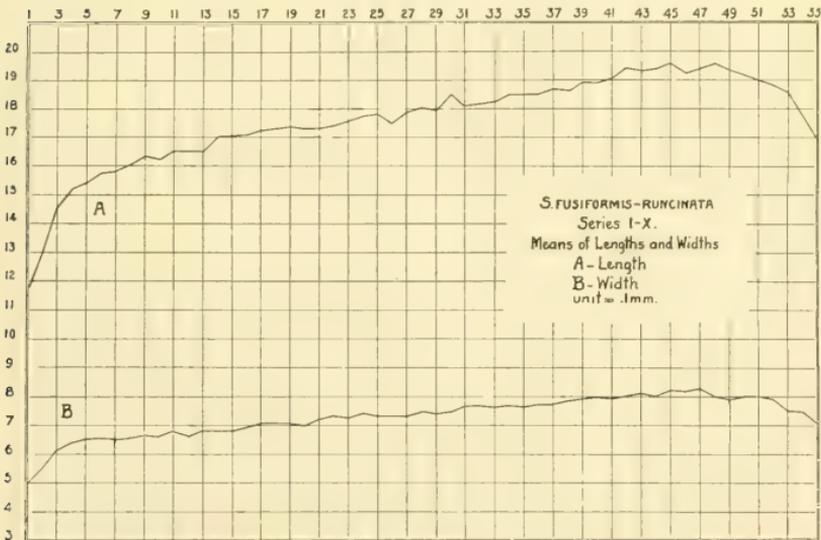


Figure 9.

could not be taken accurately. For length and width, the zooid can be measured fairly accurately and the results will be comparable, as the zooid lies flat in the dish for both measurements, but I have not been able to devise a reliable way for taking the third dimension. The zooids of these preserved chains too are so collapsed that the third measurement would probably not be of much value. Consequently we cannot obtain volume relations of zooids, which would be more valuable than mere length.

The measurements for the first five blocks were tabulated (table 1), the means computed, and this result was plotted as the length-graph. (Fig. 9 A.) The abscissae for this curve represent the place of the zooid in the series, while the ordinates represent the means of the ten series for each place in the series, so that number one is the mean length of the youngest zooids of all the series, number two is the mean of the next youngest, and so on. The same plan was followed with the graph for the widths. (Fig. 9 B.)

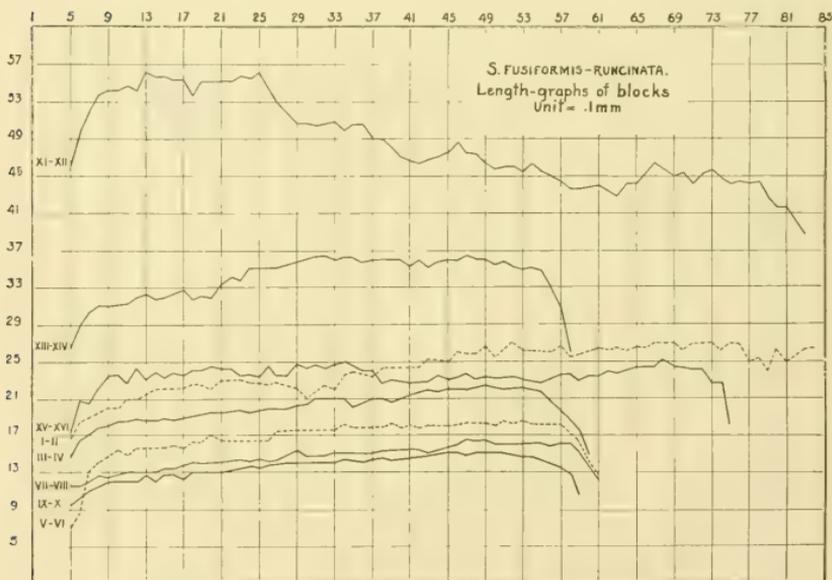


Figure 10.

TABLE II.

Measurements of 6th, 7th, and 8th blocks of *Salpa fusiformis-runcinata* including length and width measurements. Each measurement is a mean of two measurements.

Roman numerals indicate the number of the series; series XI-XII making up the sixth block, etc. Unit=.1 mm.

Serial No. of Zooid	Length						Width					
	XI	XII	XIII	XIV	XV	XVI	XI	XII	XIII	XIV	XV	XVI
1	45.0	46.5	25.5	27.0	16.0	18.3	22.5	20.5	11.0	13.0	6.0	8.0
2	43.5	51.0	28.3	29.8	21.5	20.3	25.5	26.0	13.0	13.8	9.35	9.3
3	51.5	52.5	30.0	30.8	20.3	20.8	28.0	27.0	13.8	13.8	10.0	9.3
4	54.0	53.5	30.3	31.5	21.3	23.2	27.5	28.0	13.5	14.0	9.35	10.3
5	53.0	55.0	30.5	31.5	23.5	23.0	27.5	28.0	14.0	13.5	11.0	10.3
6	53.0	55.0	30.5	31.8	23.8	23.2	28.0	27.5	14.3	14.5	11.0	10.3
7	53.5	56.0	31.0	31.5	21.8	22.8	27.5	29.5	14.3	14.3	10.35	10.0
8	52.5	55.5	31.5	32.5	23.3	25.5	27.5	31.0	15.0	14.0	10.5	11.3
9	56.0	56.0	32.0	32.8	22.5	23.5	29.5	29.5	14.3	14.8	10.3	10.3
10	56.0	55.0	30.8	32.3	24.0	24.0	29.5	29.5	14.0	14.3	11.0	10.8
11	55.5	56.0	31.8	31.8	23.0	23.3	29.0	28.5	15.3	15.0	10.5	10.3
12	55.5	55.3	30.8	34.0	24.5	23.8	28.5	30.0	15.0	15.3	10.8	10.8
13	55.5	55.3	32.8	33.0	23.3	24.0	23.5	29.0	14.3	14.5	10.3	11.0
14	55.0	52.0	29.5	33.3	24.0	24.3	30.0	25.0	13.8	15.0	10.8	10.8
15	55.0	55.0	33.0	31.0	24.3	24.8	29.5	29.0	14.5	15.5	11.3	11.0
16	55.5	54.5	31.5	32.0	24.8	24.8	30.5	27.5	14.0	15.3	11.3	11.0
17	55.0	55.0	33.0	33.3	24.0	25.3	29.5	29.5	16.3	15.7	10.8	11.0
18	55.0	55.0	32.5	35.5	23.8	25.0	30.0	30.0	15.5	16.0	10.0	10.8
19	55.5	56.0	33.5	33.3	22.3	24.0	29.5	30.5	14.5	15.0	9.5	10.8
20	55.0	56.0	34.3	35.7	22.8	23.8	28.0	30.0	14.5	16.0	10.0	10.3
21	56.0	56.0	34.8	35.0	22.3	23.8	27.5	30.5	15.0	15.5	10.0	10.3
22	55.5	54.0	35.3	35.0	23.2	26.3	27.5	28.5	14.0	14.8	10.0	11.0
23	53.5	52.5	35.0	35.3	22.5	24.3	28.0	26.0	15.0	15.5	9.8	10.3
24	53.0	50.5	35.0	35.5	22.8	23.3	24.0	26.5	15.0	15.5	10.3	10.0
25	50.5	50.0	35.5	35.5	24.5	25.0	24.5	27.0	14.8	16.0	10.5	10.5
26	50.5	50.5	35.8	36.3	24.0	24.5	25.0	26.3	15.8	15.0	10.8	10.5
27	50.0	50.5	36.3	36.3	25.0	24.5	25.0	26.5	16.0	14.5	11.3	10.8
28	50.0	51.0	36.3	36.3	24.0	24.3	25.5	26.5	14.5	15.5	11.5	10.5
29	50.7	51.0	36.3	35.5	24.8	24.8	25.5	26.0	15.0	15.5	11.3	10.8
30	49.5	50.0	36.0	36.5	25.3	24.8	25.5	25.0	15.5	14.5	10.8	10.8
31	50.5	50.0	37.0	36.0	23.8	25.5	26.5	26.5	15.0	15.5	11.0	11.0
32	50.0	50.5	36.7	34.5	24.5	22.8	24.5	26.0	15.0	14.5	11.0	9.8
33	49.5	48.5	36.3	36.0	24.5	22.8	24.5	25.0	14.5	15.0	11.0	10.0
34	49.0	49.0	36.5	36.0	22.5	22.5	25.0	23.0	15.0	15.0	10.3	9.8
35	47.0	48.5	36.5	35.5	22.5	23.3	24.0	23.5	15.0	15.0	10.0	9.5
36	47.0	47.0	36.3	36.0	23.0	22.8	25.0	24.0	15.0	14.5	10.0	9.2
37	47.0	46.5	36.0	34.5	22.3	22.8	25.0	24.5	15.8	14.0	10.3	9.2
38	46.0	46.5	36.5	35.7	23.0	22.8	25.0	25.0	16.3	14.7	10.0	9.2
39	46.0	47.5	36.5	36.0	23.3	22.3	25.0	25.0	16.3	14.7	11.0	9.0
40	46.5	47.5	35.8	36.0	23.5	23.0	25.5	25.5	15.8	15.5	10.8	10.0
41	43.0	47.5	36.8	35.5	23.0	23.0	23.5	23.5	15.5	15.0	11.0	10.0
42	49.0	48.0	36.3	35.7	23.5	23.0	24.0	24.5	15.5	15.0	10.8	10.3
43	47.0	48.0	36.8	35.7	23.8	24.0	25.0	24.0	15.5	14.7	11.0	10.5
44	46.5	48.0	36.0	35.5	22.8	23.0	24.5	23.5	15.5	15.5	11.0	10.0
45	46.0	47.0	36.0	35.0	23.0	23.3	22.5	24.0	16.0	15.7	11.0	9.8
46	45.0	46.5	36.0	34.3	23.0	23.0	24.0	24.0	15.5	15.5	10.8	9.8
47	45.5	46.0	37.0	34.0	23.3	23.0	24.0	23.0	16.0	15.0	10.8	9.8
48	45.0	46.5	35.7	34.0	23.3	23.3	22.5	22.5	15.0	14.5	11.0	9.8
49	44.0	46.5	35.0	34.3	23.0	22.8	24.0	23.0	14.5	14.3	10.8	9.8
50	45.5	47.5	35.3	33.8	23.0	22.8	25.0	24.0	14.5	14.5	10.8	10.0
51	45.0	46.0	35.3	33.3	24.0	23.0	24.5	23.0	14.5	14.5	10.8	10.0
52	42.5	42.0	33.5	32.0	23.0	23.0	25.5	21.5	15.3	12.3	10.5	10.0
53	44.5	45.0	31.3	29.0	23.5	23.5	25.5	24.5	13.5	12.5	10.0	10.0
54	43.4	44.0	25.3		23.3	23.8	24.0	23.5	11.8		10.0	10.3
55	43.5	44.0			22.0	23.8	24.0	24.0			10.0	10.5
56	43.5	44.0			23.3	24.0	23.5	24.5			10.0	10.0
57	44.0	44.0			23.0	23.8	24.0	23.5			10.0	10.0
58	43.0	43.5			24.0	24.0	24.0	24.0			10.3	10.0
59	42.5	43.0			23.5	†	23.5	23.5			10.5	†
60	44.0	44.5			23.8	24.0	24.5	24.5			10.5	10.3
61	44.0	44.5			24.0	24.3	24.5	23.0			10.0	10.0
62	45.5	45.5			23.5	25.0	25.0	24.5			10.0	10.5
63	46.5	46.5			23.8	25.0	24.5	24.0			10.0	11.3
64	46.0	45.5			25.3	25.5	24.5	22.0			10.5	11.0
65	45.0	45.0			24.5	24.0	25.0	25.0			10.5	10.8
66	45.5	45.5			25.3	23.8	25.0	25.5			10.8	10.5
67	44.0	44.5			25.0	23.5	24.5	25.0			10.3	10.3
68	45.5	45.0			26.0	22.5	25.0	25.0			10.8	10.0
69	45.5	45.5			23.3	21.8	25.5	23.0			10.0	10.0
70	45.0	44.5			21.8	23.0	26.0	22.5			9.0	11.0
71	44.5	44.0			18.5	16.5	25.0	21.5			8.3	7.5
72	44.3	44.3					25.5	22.0				
73	44.5	44.0					24.5	22.5				
74	44.5	44.5					24.5	24.0				
75	42.5	42.5					22.0	23.0				
76	41.5	41.5					21.5	22.0				
77	42.0	41.0					21.0	21.5				
78	41.0	38.5					21.0	18.5				
79	39.5						18.0					

The fact that the blocks are of different lengths renders the taking of the means at each point in the series of less value than if all were the same or nearly the same length, so a comparison was made between the graphs of the different individual blocks. The mean of the two series of each block was taken for the graph of the block, giving eight graphs. (Figs. 10 and 11.) These series varied in number of zooids from 55 to 80 and the average size of the zooids differed greatly, as will be seen from the table, since vertical distances represent units of length.

The graph shown in fig. 9 presents a rapid increase in the zooids at first, the increment gradually decreasing as one goes out until the maximum is reached with the forty-fifth zooid, after which there is first a gradual and then a more rapid decrease.

A plot was made of the products of the corresponding lengths and widths. This gives a graph of the approximate areas of the zooids, and is necessarily a curve of the same character as the length and width curves with its maximum value near the end of the plot.

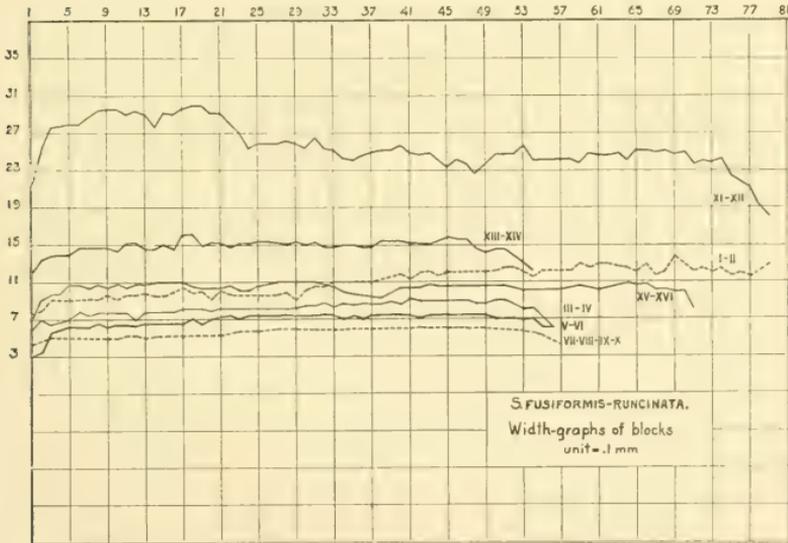


Figure 11.

An effort was made to get an expression for the shape-ratio of the zooids by plotting the $\frac{\text{length}}{\text{width}}$. The plot turned out to be a ragged line showing no semblance of order.

Taking the individual blocks as shown in figs. 10 and 11, the same general form is seen to hold in all the series measured. The end zooids of Series I-II and XI-XII were missing, but the other blocks are complete, all zooids being measured up to, but not including the imperfect ones of the terminal remnant.

In order to compare the different graphs more easily, they were reduced in such a way as to keep the relative curve of each the same as before, but to give them all a common origin and equal horizontal extent.

This plot is not given, as it brought the eight graphs almost on top of each other throughout their entire length. It is interesting to note that the plots differing the most widely from the others were XI-XII and V-VI. It will be seen from figs. 10 and 11 that XI-XII is the oldest and largest of the blocks. Its maximum value comes early in the series, the more distal zooids steadily decreasing in size, the last one being smaller than the first one of the block. On the other hand, V-VI starts with the smallest zooid found in any of the blocks and its terminal zooid is much larger than its first one.

In other words, *giving all the graphs the same point of origin and the same length*, the one having the smallest value at the distal end is the oldest block, the one having the largest is the youngest block.

Or, biologically speaking, in the youngest block the two or three most distal zooids are larger than the first two or three proximal ones; while in the oldest block, the first two or three zooids are larger than the end ones. The small amount of data under observation is not sufficient to warrant a definite statement, but these facts suggest that the distal zooids reach their maximum size first and the more proximal ones gradually catch up. The graphs of the blocks intermediate between the youngest and the oldest tend to confirm this hypothesis, the maximum values appearing nearer the distal end in younger blocks and nearer the proximal end in the older ones.

In series XI-XII, the vascular connection was evidently lost throughout the greater part of the block and about two inches of the chain protrude from the body of the parent. It is important to know when the zooids begin to take nourishment from external sources on their own account. The oral openings seem to be complete in all the chains that have been measured, but it is doubtful if nourishment is taken until the zooids have been set free. Examination of the digestive tract of some of the larger zooids indicates that nothing has been taken in this way. In the parent salpae, the intestines are always well filled, so that if the zooids have taken food we should reasonably expect to find some trace of it in the digestive tract. It is possible that the cleft in the test through which the block is discharged does not entirely close after a block is set free and that the water may have access to the cavity in which the developing block lies, thus bringing nourishment to the zooids before they leave the parent.

A question naturally arises concerning the comparative sizes of the newly formed segments of the first block. Is there a difference corresponding to the difference in the progressive segmentation, or is the block the same size throughout? So far as I can tell, there is no measurable difference in the diameter of different parts of this block. However, there is a slight constriction at the point where it passes into the second block and sometimes just in front of the stolon. Even in the stage of the second block in fig. 4, there is no measurable difference in the diameter at different points except in the few zooids at the ends. Therefore, the differences in size arise mostly with the later growth of individual zooids. At the same time, it must be remembered that these younger blocks are but little more than flimsy hollow tubes which are curved and sometimes twisted and very difficult to measure.

5. SALPA ZONARIA-CORDIFORMIS.

A brief examination of specimens of *Salpa zonaria-cordiformis* was made for comparison with those of *fusiformis-runcinata*. The chain in this case arises in the ventral median line about 0.5 cm. anterior to the nucleus, and extends posteriorly and to the right almost as far as the nucleus. Here it bends

abruptly to the left, reaching around the median line of the creature, forming thus a semicircle immediately in front of the nucleus.

The chain consists of two or three blocks which contain fewer zooids than those of *fusiformis-runcinata*, and there appears to be no intermediate piece. The end zooids of the blocks are slightly smaller than the middle ones, but none of them are rudimentary as in the other species. The deploying point is similar to that of *fusiformis-runcinata*.

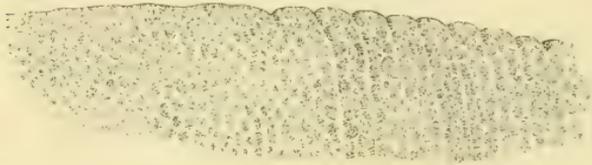


Fig. 12.—Surface view of stolon, showing point where segmentation begins in chain of *S. zonaria-cordiformis*.

Microscopical examination of the segmenting stolon shows that the segmentation stops abruptly (fig. 12) instead of being lost gradually. One block was measured and the average of the two rows taken as for the other species. (A higher power objective was used on account of the small size of the zooids so that one unit here is equal to 0.025 mm.) The same general scheme for the graph is seen as in the other blocks of *fusiformis-runcinata* as the following figures show (Table III). These figures are plotted in fig. 13.

TABLE III.

Serial measurements of a block of *S. zonaria-cordiformis*.

No. of zooid in series	Length	Width	No. in series	Length	Width	No. in series	Length	Width
1	34.0	18.5	9	45.0	23.5	17	50.1	26.0
2	39.5	21.5	10	45.5	23.5	18	51.5	28.0
3	40.5	22.5	11	45.5	24.0	19	52.0	28.5
4	40.5	22.0	12	49.0	24.0	20	51.5	28.5
5	43.5	22.0	13	49.5	25.5	21	50.0	28.5
6	46.0	24.0	14	47.5	23.5	22	49.0	26.5
7	44.5	22.5	15	51.5	26.5	23	47.0	22.0
8	44.0	23.0	16	50.0	25.5			

6. SALPA CYLINDRICA.

The chain here has no curves as in *S. fusiformis-runcinata* and several other species, but extends straight forward along the median line of the parent. This shows conclusively that the

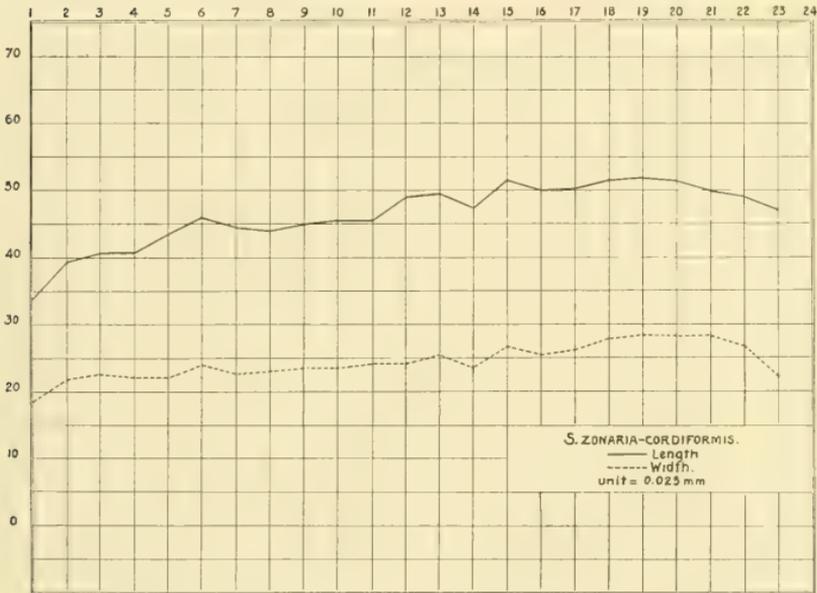


Figure 13.

bendings of the chain have nothing to do with either the double rowing of the zooids or the formation of blocks.

The chain consists of two or three blocks, and the number of zooids in a block is variable. The intermediate piece and deploying point occur as in *S. fusiformis-runcinata* but the zooids of the intermediate piece are less imperfect than the corresponding ones of *S. fusiformis-runcinata*. The terminal remnant, so far as has been observed, contains not more than one rudimentary zooid.

Microscopical examination of one segmenting stolon indicates that the segmentation is probably like that of *S. fusiformis-runcinata*.

Two blocks were measured and the average of the two rows taken for the graphs. (Fig. 14.) The short block was measured twice, the long one but once. For the short chain the graph shows twenty-three zooids. A twenty-fourth was present

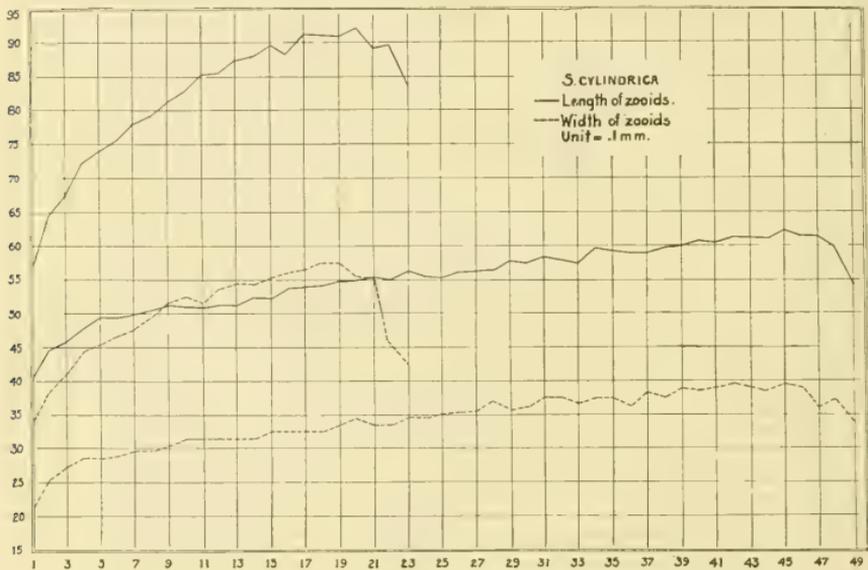


Figure 14.

but was so torn that it could not be measured accurately. Its length was certainly not more than seventy-five, probably less, and would make the form of the graph resemble the others more closely. The general scheme shown in the graphs of the other species holds here also as the figures show (Table IV).

TABLE IV.

Serial measurements of two blocks of zooids of *S. cylindrica*.

Serial No. of the Zooid	CHAIN I		CHAIN II	
	Length	Width	Length	Width
1	40.8	21.3	57.2	34.0
2	44.5	25.5	61.8	38.2
3	45.8	27.3	67.2	40.8
4	47.8	28.0	72.0	44.4
5	49.0	28.0	74.0	45.6
6	49.0	28.3	75.2	46.4
7	49.8	29.5	78.0	47.6
8	50.5	29.5	79.2	49.2
9	51.3	30.5	81.2	51.6
10	51.0	31.5	82.8	52.4
11	51.0	31.5	85.2	51.6
12	51.5	31.5	85.6	53.6
13	51.5	31.5	87.2	54.4
14	52.5	31.5	88.0	54.4
15	52.3	32.3	89.6	55.2
16	53.3	32.5	88.1	56.0
17	53.8	32.5	91.2	56.4
18	54.0	32.5	90.8	57.2
19	54.8	33.5	92.0	57.2
20	55.0	34.5	91.6	55.6
21	55.3	33.5	89.2	55.2
22	55.0	33.5	89.6	46.0
23	56.3	34.5	83.6	42.4
24	55.5	34.5	?	?
25	55.3	35.0		
26	56.3	35.5		
27	56.5	35.8		
28	56.5	36.8		
29	57.8	35.8		
30	57.5	36.3		
31	58.0	37.5		
32	57.8	37.5		
33	57.5	36.5		
34	59.5	37.5		
35	59.0	37.5		
36	58.8	36.3		
37	58.5	38.0		
38	59.5	37.3		
39	60.0	39.0		
40	60.8	38.8		
41	60.5	39.0		
42	61.5	39.5		
43	61.3	39.0		
44	61.3	38.5		
45	62.3	39.5		
46	61.3	39.0		
47	61.3	36.0		
48	59.7	37.0		
49	54.0	34.0		

7. DISCUSSION OF RESULTS.

In considering these developing salpa chains, the question immediately suggests itself, what does the division into blocks signify?

Classifying the stages of development of the whole chain, their outward manifestations fall into certain phases; first, the growth of the unsegmented stolon; second, segmentation of this stolon; third, growth of the individual zooids resulting in the formation of blocks; fourth, the final separation of the block of zooids from the rest of the chain.

What is the relation between these four phases, which are so balanced that there are always present in the chain at least two blocks? Does the growth of the zooids and shifting of position at the deploying point go on at the same rate as the segmentation and outgrowth of the stolon? If the latter processes are continuous would not the former be so also, and why should the abrupt break at the intermediate piece occur? In other words, if growth of the stolon, segmentation, and development of the zooids are continuous, how does the discontinuity represented by the intermediate piece and blocks arise and what is the cause of it?

If we could keep the parent salpae alive and watch the development of the chain, we could easily see how development proceeds, but the animals are so sensitive to the artificial conditions of the aquarium that this has not yet been found possible. We must for the present depend upon our observations on the preserved material for such answers as we may get to our questions.

The differences in the condition of the early segmentation are suggestive. It will be remembered that in *S. fusiformis-runcinata* a break in the continuity of segments sometimes occurs. The division planes almost or quite disappear for a short distance and reappear beyond, being again gradually lost nearer the root of the stolon. (Fig. 8.) Again, some blocks do not appear to have this break, the division planes being only lost gradually at the root of the stolon. The latter condition is also found in *S. cylindrica*. It will be remembered that the chain of both these species has an intermediate piece consisting of rudimentary zooids between the two largest blocks.

S. zonaria-cordiformis, on the other hand, has no intermediate piece. Also in this species there is no intervening unsegmented portion among the young segments of the stolon, and the first block ends abruptly.

As segmentation proceeds in the same way for all, *e.g.*, by an infolding of the ectoderm, thus cutting the stolon into segments, the differences must arise from differences in rate or continuity of the growth process. Two growth processes occur: *viz.*, outward growth of the stolon, and advance of segmentation. Suppose these two processes to be periodic, exhibiting alternate periods of activity and inactivity. Suppose further that these periods of growth of stolon and progress of segmentation coincide. Would not the result be the condition we have described above? The blocks would represent periods of activity in growth and segmentation. The intermediate pieces would be the result of the period of slower growth, while the absence of such a piece would indicate a complete cessation of growth between the periods of activity.

This hypothesis would account for the marked difference in the size of the blocks. One period of growth would mark out a block of zooids; a second would arrange the zooids of the block in double file; while a third would bring the zooids to the size of those whose measurements are given.

The salpa chain then presents an obvious periodicity, at least in its advanced stages of development. Do we not find a parallel to this in plants in what the botanists term the grand period of growth?³ This phenomenon is defined thus in Pfeffer's *Physiology of Plants* (Pfeffer, '03; vol. II, p. 6): "Every cell and part of a cell, every organ and the entire plant as well, pass more or less rapidly through a specific progress of development whose character is primarily determined by internal causes. This grand period of growth has definite limits and attains a maximum at a particular phase of development, besides frequently exhibiting secondary maxima. This law applies to animals as well as to plants, and it is not surprising that the grand periods for different organs, and even for special functions also, do not necessarily coincide either in amount or in time."

³ This question is raised by Professor Ritter and discussed by him at length in a general book now ready for publication entitled, "Living Things, A Study of the Nature of the Organism."

Examining farther, we find in the plant world what seems to be a parallel to segmentation in the chain. Quoting again (Pfeffer, '03; vol. II, p. 6) we find: "In flowering plants, the embryonic cells form the leaf-primordia and hence determine the number and position of the appendicular organs, which attain their adult shape by subsequent growth."

But there is a possibility that the phenomena we are studying should be compared rather with another phenomenon of plants called by Moll⁴ the "Langenperiode der Internodien." This relates to the widely observed fact that the internodes of a grown branch vary in length and that the differences in length are found to follow a certain order.

Results of quantitative investigations on this subject are given in a paper, "Die Periodicität morphologischer Erscheinungen bei den Pflanzen." (Tine Tammes, '03.) We find in this paper the following statement, "Betrachtet man die Stellung der Laubblätter an einer Pflanze etwas näher, so wird man bei vielen Pflanzen die kleinsten Blätter an der Basis und an der Spitze, die grössten in der Mitte finden. Auch bei den Seitenzweigen tritt dieselbe Erscheinung auf, die zuerst gebildeten Seitenzweige sind kurz, dann folgen längere und auf diese wieder kürzere. Die ganze Pflanze zeigt ein Bestreben anfangs kleinere Organe zu bilden, später grössere und gegen das Ende ihres Lebens wiederum kleinere."

Observation of plants shows this scheme to hold true in large numbers of cases. We see it in the shape of the leaf, in the size of the leaves on a branch and in many cases in the sizes of the branches upon the main trunk. It is especially noticeable if one compares the size of the leaflets of a series in many compound leaves. The distances between the leaflets of a series, and between the leaves of a branch also bear certain definite relations. The leaves on a young tree will be found to be closer together at the base and tip than near the middle. This much we can see, but just what these relations are, whether they are the same for all the branches of a tree, young and old, and the same for all trees of a species, and whether another definite relation holds true for all leaves on a branch, those at the base, middle and tip, or

⁴I have not, unfortunately, had access to Moll's work, but know it chiefly through Tamme's paper.

whether these relations change as the parts grow, these and many other related questions can be answered only by accurate measurement of carefully selected material.

The two phenomena, the grand period of growth, and the length period of the internodes, are regarded by Moll and some other botanists as wholly different. Whether they are different or not, it is not within my province to discuss. However, if they are wholly different phenomena, since the blocks of zooids are developing structures, they would seem to be more comparable with the grand period of growth than with the length period of the internodes.

These considerations, while dealing with a different aspect of the problem, suggest the law of differentiation with growth which Dr. Pearl found in *Ceratophyllum*—*i.e.*, that “The mean number of leaves per whorl increases with each successive whorl and in such a way that not only does the absolute increment in leaf-number diminish but also the rate of increase diminishes as the ordinal number of the whorl, measured from a fixed point, increases. It means, broadly speaking, that the form of any particular whorl of a *Ceratophyllum* plant is a function (in a mathematical sense) of the number of whorls which have been produced before it on the same axis.”

“The same law of growth holds (with appropriate changes of the constants) for all axial divisions of the plant (main stem, primary, and secondary branches).”

The second law of growth given by Dr. Pearl is as follows, “As whorls are successively produced by a growing bud, they are formed with ever increasing constancy to their type, the ultimate limit toward which the process is tending being absolute constancy.”

In other words, Dr. Pearl found that the “leaf-number” in *Ceratophyllum* is a function of its place on the axis, and that the leaf number becomes more constant as one goes out on the stem. In our problem we are dealing with size rather than with number, but we have found the length and the width of the zooid to be a function of its position in the block.

But when we try to correlate our results with Dr. Pearl’s second law a discrepancy appears. The mean leaf-number in-

creases with each successive whorl, the increment decreasing so that the leaf-number in the later whorls is practically constant. Our curve of the size of the zooids takes the same course as the curve for variation in leaf-number until the mean length or width becomes fairly constant, when it suddenly drops. Observation shows that in leaf-size also there is a decrease at each end of the branch.

The question suggests itself—Did Dr. Pearl take all of the whorls into account, or would more whorls have been produced at the tip of the branches, and if so, would their leaf *number* remain constant for a time and then toward the end of the life-time of the plant, vary again and grow smaller?

If he had taken *size* of leaflets rather than *number*, the graph would probably have been like the graph for the length of zooids, the maximum occurring toward but not at the base where the oldest whorls were found.

The two results for leaf number and size of zooids might possibly be brought into harmony by further observation of the size curves. From a study of the graphs of the block (figs. 10 and 11), it seems likely that the maximum value shifts to the proximal portion of the chain as the zooids grow; in fact the graph for the oldest block is almost the reverse of that for the younger blocks. Would this graph, if the zooids were all full grown, show a gradual approach to a constant size as one approaches the proximal end of the block and would the most proximal zooid of all, once the smallest, catch up with those near it? The nature of the material makes it unlikely that we will be able to determine this definitely; since, aside from the fact that chains of this age break apart so easily, the distal zooids are increasing in width so rapidly that length alone is not an accurate method of indicating size.

With the leaves of a branch, we see that those at the tip seldom or never catch up in size with those at the base. In almost every instance of periodicity in growth in the plant world we find that this condition holds; that smaller members of a series are at the beginning and at the end of the period of growth while the maximum ones are in between. We conclude then, that the curves from the serial measurements of the blocks of zooids of

the salpa chain are in general accord with previous observations on repetitive series in plants and that the chain furnishes an excellent and hitherto unnoticed example of periodicity in growth.

8. GRAPHS AS SPECIES CHARACTERS.

A comparison of the graphs of the chains for the three species shows slight differences and suggests that there may be a characteristic graph for each species. It is possible that the course of the graph may be affected by many things such as the form of the chain—straight or curved,—the number of zooids in the block, the size of the parent, rate of growth of the chain, and possibly by other less evident conditions.

If several chains of each species were measured at different times of the year it might be found that the differences suggested by these preliminary graphs or other differences are constant for the species. Any such investigation would have to take into account the season of the year and the size of the parent; thus showing for a given species, the size relation of the zooids to each other at different stages of their growth and any possible seasonal variation as well as variation dependant upon the age or size of the plant. These sets of observations could then be compared to see if the graphs are in any way constant for the species.

9. EUISETUM ROBUSTUM.

Since this relation is found to exist in such widely differing structures as the zooids of a salpa chain and the leaves of a branch, it is advisable to extend the investigation farther to include repetitive series of as many kinds as possible in both the plant and animal world. While it is not within my province to go extensively into the matter so far as plants are concerned, I will include a figure showing graphically the measurements made upon a fertile shoot of *Equisetum robustum*. (Fig. 15.)

I first measured the length of each internode and then the diameter of each internode at each end and at certain intermediate points. The measurements showed that the longest internode is near, but not at the base of the stalk and that in each internode the maximum diameter occurs in the middle and

the smallest at the ends. The length of the internodes would be an example of Moll's "Langenperiode der Internodien" while each internode by itself is an illustration of the grand period.

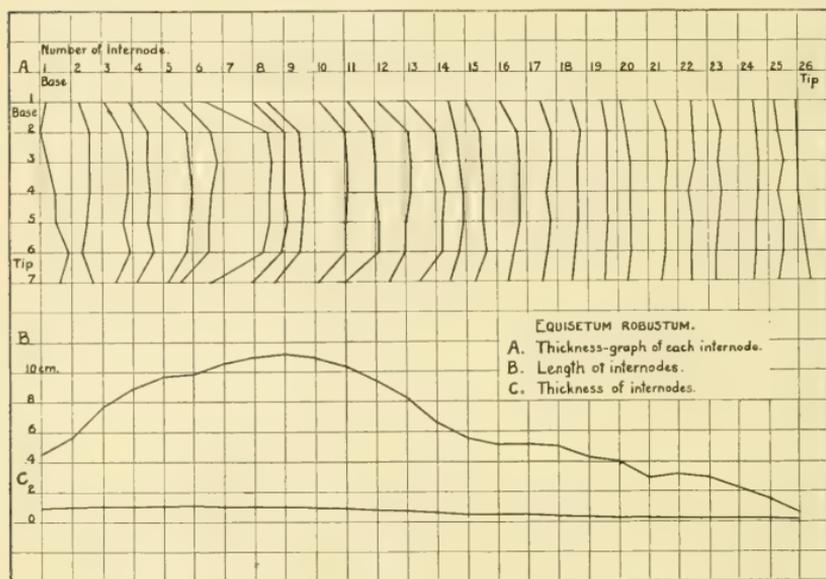


Figure 15.

10. IRREGULARITIES IN THE SERIES.

A point which may be noted incidentally in connection with the measurements of the series, is that in all the chains one finds now and then a very small zooid in a series of almost uniformly increasing ones. It is often the case that one of the zooids across from it in the other row is correspondingly larger than its neighbors.

The following are instances taken from series I-II and XIII-XIV:

TABLE V.

I.	II.	Ave.	XIII.	XIV.	Ave.
27.0	25.0	26.0	31.8	31.8	31.8
26.0	26.0	26.0	30.8	34.0	32.4
27.0	26.0	26.5	32.8	33.0	32.9
26.0	25.0	25.5	29.5	33.3	31.4
25.5	26.0	25.8	33.0	31.0	32.0
27.0	25.0	26.0	31.5	32.0	31.8
26.5	26.0	26.3	33.0	33.3	33.2
28.0	24.0	26.0			
27.0	26.0	26.5			
26.0	26.0	26.0			

Though the individual series show irregularities, when the mean is taken the results form an evenly graded series.

There seems to be a compensation here, the full significance of which is hard to see without a better knowledge of the nature of the connection between the zooids and the manner of appropriation of the food supply. As the zooids stand in the chain, the connection between a zooid and its neighbors in the same row is less intimate than with its neighbors of the opposite row. For this reason it is to be expected that the correlation should come between the zooids of opposite rows rather than in neighboring zooids of the same row. But apparently there is no reason for a zooid pairing off with one of the two opposite zooids rather than the other.

GENERAL SUMMARY.

This paper deals with the *manner* and *rate* of growth of the zooids of a salpa chain. The observations were made chiefly upon chains of *Salpa fusiformis-runcinata*. Brief examinations are made of chains of *Salpa zonaria-cordiformis* and of *Salpa cylindrica*.

The subjects dealt with are (*a*) the species and its manner of reproduction, (*b*) the form and structure of the chain, (*c*) the method followed in taking measurements, (*d*) a discussion of conclusions that can be drawn from the study.

Some of the chief observations may be summarized as follows:

1. The chain of *Salpa fusiformis-runcinata* is made up of a series of blocks, the zooids of each block being approximately the same size.

2. Between the last two blocks is found a short piece, the intermediate piece, containing imperfect or undeveloped zooids, while in the proximal portion of the chain is a deploying point where the zooids change from single to double file.

3. A terminal remnant of imperfect zooids is found at the distal end of the chain, unless the distal block is the first ever produced.

4. The unsegmented chain consists of a tubular sheath of ectoderm enclosing strands containing the various embryonic elements.

5. The chain elongates and becomes cut up into a series of segments, each containing its share of the embryonic elements.

6. This segmentation is initiated and carried on by the infolding of the ectoderm.

7. As the zooids grow, they push each other out of line so that they change from a single file to double file.

8. The regular segmentation of the proximal portion of the chain is sometimes interrupted by an unsegmented space.

9. The blood tubes which run through the chain grow smaller and disappear before the zooids are set free. This disappearance begins at the distal end.

10. As the vascular connection disappears, papillae develop, which unite adjacent zooids and may or may not furnish nutritional connection.

11. The zooids at the ends of the block are much smaller than the intermediate ones. The maximum size (length or width) is near the distal end in the younger blocks.

12. In one block of large zooids the maximum size is near, though not at the proximal end of the block.

13. In the oldest block, the most proximal zooids are larger than the most distal ones; in the youngest, the distal ones are larger than the proximal.

14. *S. zonaria-cordiformis* has no "intermediate piece" or "terminal remnant," and the segmentation at the base is not interrupted by an unsegmented portion. The zooids of the blocks are smallest at each end, the maximum occurring near, but not at the distal end.

15. *S. cylindrica* has an intermediate piece. The zooids are

smaller at each end of the block, and the maximum size occurs near, but not at the distal end.

16. These results suggest that farther investigation may show the graph of the block to be a reliable species character.

17. A stalk of *Equisetum robustum* has shorter internodes at the base and at the tip, the maximum ones occur near the base. The diameter of the internodes is least at each end and greatest in the middle.

18. An unusually small zooid is often found opposite an unusually large one in the salpa chain.

The conclusions reached of a more general, or theoretical character, are:

1. The periodicity occurring in the salpa chain may be a phenomenon comparable with the grand period of growth and also with the length period of the internodes, as defined by botanists.

2. Dr. Pearl's first law of growth finds a parallel for the salpa chain, since the size of a zooid is a function of its position in the block.

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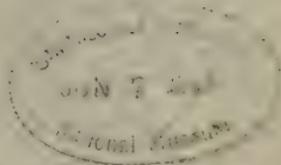
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A REVISION OF THE GENUS *CERATO-*
CORYS, BASED ON SKELETAL
MORPHOLOGY

BY
CHARLES ATWOOD KOFOID

BERKELEY
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A REVISION OF THE GENUS *CERATOCORYS*, BASED ON SKELETAL MORPHOLOGY.

BY

CHARLES ATWOOD KOFOLD.

INTRODUCTION.

The skeletal plates of the thecal wall of the Dinoflagellates are hard structures of definite shapes, numbers and relationships in the various genera of this subclass of Protozoa. They are subject to modifications in form and size due to a slight extent to growth and to age, and, in certain genera, as in *Gonyaulax*, to some interspecific differences in number, while in *Pyrophacus* considerable variation occurs within the species in the number of the plates. In the main, however, the morphology of the plates in this group is remarkably constant and affords a most satisfactory basis for classification and determination of relationships, with a definiteness and certainty rarely attainable among unicellular organisms.

Superficial resemblance to other genera in form and in organs of flotation on the part of the majority of the species of the genus *Ceratocorys* has hitherto hidden their true affinities which rest upon their skeletal morphology.

The Dinoflagellate genus of semi-tropical and tropical seas has been a source of great confusion to those who have found its representatives, with the result that it is now well-nigh impossible to determine from the literature its content of species or to

use the literature in connection with the material. Species belonging to it have been placed in genera so widely divergent in skeletal morphology as *Dinophysis*, *Phalacroma*, and *Goniodoma*, and on the other hand a species has been attributed to it which is a *Gonyaulax*, belonging to a different subfamily.

This confusion has resulted in part from the convergence in external form and superficial facies largely due to the outgrowth, or to the reduction, of spines and fins in the different species in certain fashions probably related to common needs of orientation and flotation. This convergence is exemplified in the superficial resemblances which *Ceratocorys jourdani* bears to *Dinophysis* and *Phalacroma*. In both the well-developed girdle-lists are placed anteriorly, and compensating outgrowths at the posterior end in the form of spines are of assistance in orientation and are found near the sagittal plane on the posterior end of *P. jourdani* somewhat as in *Phalacroma*, though their relation to each other and to the general skeletal morphology is quite different. This superficial resemblance doubtless led Gourret (1883) to place *C. jourdani* in the genus *Dinophysis* and Schütt (1895) to retain it in the family Dinophysidae though transferring it to the genus *Phalacroma*. It is, however, utterly different in its skeletal morphology and location of the fission plane from any of the Dinophysidae. This same convergence later led Entz (1902) into the error of maintaining that *Phalacroma jourdani* is a connecting link between the two families Dinophysidae and Peridinidae, and to the proposal of a new nomenclatural anomaly of "*Phalacroma-Ceratocorys*" as the designation for these supposed "Uebergangsformen." In reality all of his intermediate forms, as figured, can not be distinguished from true *Ceratocorys jourdani*, and his discussion contains no critical evidence from careful analysis of skeletal morphology to justify his conclusion of continuity of the two genera.

The superficial resemblance which *Ceratocorys armatum* and *C. bipes* bear to *Goniodoma* is due largely to the general form of the body as seen in the location of the girdle, the somewhat angular contour, especially of the epitheca, the coarse pitting of the shell, and the heavy rugosities on its surface near sutures. These superficial features, combined with the absence of spines

such as characterize the first described, most abundant and most widely distributed species of the genus, *C. horrida*, have led Schütt (1895) to describe a *Ceratocorys* as *Goniiodoma acuminatum* var. *armatum* and Cleve (1903) to assign provisionally another species, *C. bipes*, also to *Goniiodoma*. Both are absolutely typical members of the genus *Ceratocorys* in their skeletal organization, agreeing with *C. horrida*, the type species.

A second reason for the confusion that has arisen in this genus is the fact that the skeletal structure is profoundly obscured, in *C. jourdani* by absence of well-defined suture markings, by small size of certain plates in other species, and by the excessive thickenings and surface pits, rugosities, spines and lists which are found upon most species of this genus to an unusual degree among the genera of the Peridinidae. The structures obscure the suture lines and even when the plates are parted render the analysis of their interrelationships difficult and often puzzling.

GENERIC CHARACTERS.

Ceratocorys Stein.

Body angular or rounded, both epitheca and hypotheca often flattened distally, girdle in the anterior third, girdle fins well developed, surface smooth or rugose, coarsely pitted, usually with fins and sheathed spines along sutures. Epitheca consists of three apicals about a minute apical closing plate, one intercalary upon the right shoulder and five precingulars; there are eight girdle plates, including one each at the proximal and distal ends which invade the ventral area. The hypotheca consists of six postcingulars, two of which at the left of the ventral area are small, one ventral intercalary just posterior to the two small postcingulars and one antapical. Skeleton retained at fission. Fission plane oblique. Chromatophores yellow or brown.

KEY TO SPECIES.

- | | |
|--|----------------------|
| 1. With five or more long, sheathed spines with included terminal brushes in hypotheca | 2 |
| 1. Without long spines and terminal brushes | 3 |
| 2. Spines spreading, outline of body subangular | <i>horrida</i> Stein |

- 2. Spines nearly in median sagittal plane, outline of body rounded
 *jourdani* (Gourret)
- 3. With rounded prominences at base of two short posterior spines
 *bipes* (Cleve)
- 3. Without rounded prominences 4
- 4. Resembling *C. horrida* in form but without long spines, very large,
 exceedingly rugose *magna* n. sp.
- 4. Resembling *Goniodoma* in form and size, smaller, rugose.....
 *armatum* (Schütt)

Ceratocorys horrida Stein

C. horrida, Stein (1883), p. 20, pl. 6, figs. 4-11.

Ceratocorys tridentata, Daday (1888), p. 103, pl. 3, fig. 3.

Ceratocorys spinifera, Murray and Whitting (1899), in part, p. 329,
 pl. 30, fig. 6c. Their figures of *C. spinifera* 6a, 6b, 6c are
 hitherto undescribed species of *Gonyaulax* (*G. ceratocoroides*
 n. sp.) and figure 6d is another species of *Ceratocorys* (*C.*
magna n. sp.).

Ceratocorys horrida forma *tridentata*, Entz (1902), p. 139, fig. 33.

C. horrida var. *longicornis*, Lemmermann (1899), p. 360.

C. horrida var. *africana*, Karsten (1907), p. 419, pl. 52, figs. 1-3.

Characterized by 5-10 long, spreading, stout spines from hypotheca, four of which arise from angles of antapical plate, one in the left ventral fin and the others along the postcingular sutures. These spines have a dense axial core with short riblets radiating on all sides within a hyaline shaft, giving it a pinnate appearance. Both epitheca and antapex are flattened, the latter obliquely from right to left. Girdle-lists very wide. Fins developed toward base of spines. Varies greatly in degree of development of spines, fins, and ribs in fins, from the short-spined forma *tridentata* of the Adriatic and Naples to the long-spined forma *longicornis* of tropical waters. The short-horned form originally described by Daday (1888) is hardly recognizable as a *Ceratocorys*; but as Entz (1902) figures a short-horned form as "*C. horrida* (*C. tridentata* Daday)" which is plainly a *Ceratocorys*, and since Daday's text states quite clearly the distinction between the species figured by Stein (1883) and his *tridentata*, we may conclude that Daday's name is available. This short-horned form and also the long-horned one described by Lemmermann (1899) and later by Karsten (1907) are in my opinion

merely extremes of fluctuating variations arising in response to temperature conditions, being therefore of seasonal local character though the short horns also appear at fission in the younger parts of the skeleton of otherwise long-horned forms.

Occasional in semi-tropical plankton at San Diego. Abundant at Naples.

***Ceratocorys armatum* (Schütt) Kofoid.**

Goniodoma acuminatum var. *armatum*, Schütt (1895), p. 153, pl. 9, fig. 32.

Goniodoma fimbriatum, Murray and Whitting (1899), p. 325, pl. 27, fig. 1, a, b.

Goniodoma armatum (Schütt), Schmidt (1901), p. 135.

Gonyaulax fimbriatum, Schröder (1906), p. 329.

A large species with 3-4 short spines arising at margins or angles of antapical plate, and at posterior end of left ventral fin. The girdle is prae-equatorial at the anterior third of the angular body. Epitheca about 0.5 of the altitude of hypotheca. Apical region small. Both apical and antapical regions tilted obliquely toward ventral region. Girdle-lists and ventral fins much less developed than in *C. horrida*. Superficial resemblance to *Goniodoma polyedricum*. Broad pore-free intercalary bands often along sutures which are sometimes marked by low, toothed, or stoutly ribbed fins. Pores large, especially so in apical plates and ventral regions and along suture lines. Contents dense, chromatophores brownish. Plates of typical generic type.

Abundant at San Diego and Naples.

The skeletal morphology of this species is unquestionably that of *Ceratocorys*, and there is no justification for its inclusion in *Goniodoma*. Murray and Whitting's (1899) *Goniodoma fimbriatum* is merely a heavily ribbed individual. Schröder (1906) gives no grounds for his transfer of the species to the genus *Gonyaulax* (lapsus?). Schmidt (1901) has correctly surmised the identity of Murray and Whitting's *Goniodoma fimbriatum* and Schütt's *G. acuminatum* var. *armatum* as well as its specific distinctness.

***Ceratocorys magna* n. sp.**

Ceratocorys spinifera in part, Murray and Whitting (1899), p. 329, pl. 30, fig. 6*d*.

A very large species, characterized by relatively narrow girdle-lists which are coarsely and heavily ribbed, as are also the heavily thickened suture regions where several lines of irregular, coarse denticulations are found. The apical region is reduced and tilted forward, somewhat as in *C. armatum*. As figured by Murray and Whitting (1899, pl. 30, fig. 6*d*), this species is nearly sixty per cent. larger than *C. armatum* (their figure 6*c* of *Ceratocorys spinifera* = *C. armatum*, which they figure elsewhere on pl. 28 as *Goniodoma fimbriatum*), and differs strikingly from it in skeletal markings and surface structure. These authors have plainly confused three species in their *Ceratocorys spinifera*. One of these, fig. 6*c*, their "young form of *C. spinifera*," is an epitheca of *C. armatum*; another, fig. 6*d*, is this new species *C. magna*, while the third organism, figs. 6*a*, *b*, *e*, is not a *Ceratocorys* at all, but belongs rather to the genus *Gonyaulax*. This is evidenced by the presence in the ventral face of this organism of a small triangular precingular plate, 6'' in my nomenclature (see Kofoid, 1909) which is absent in *Ceratocorys* but is characteristic of *Gonyaulax*. The large ventral intercalary plate (see Murray and Whitting, 1899, pl. 30, figs. 6*a*, *e*) on the left side of the ventral area (=longitudinal furrow) is also found in *Gonyaulax*. The pointed apex and displacement of the girdle are also suggestive of *Gonyaulax*, as for example, of *G. triacantha* Jörg. On the other hand, the fins and terminal brushes on the spines are similar to those of *Ceratocorys*. But these are superficial characters which converge toward *Ceratocorys* and do not have the significance that the fundamental skeletal features such as the number and relations of the skeletal plates possess in determining relationships.

Since the specific name *spinifera* is preoccupied in the genus *Gonyaulax* by *G. spinifera* (Clap. et Lach.) Diesing, I propose the new name *Gonyaulax ceratocoroides* for the species represented in Murray and Whitting's figures 6*a*, *b* and *e*, a part of their *Ceratocorys spinifera*.

The new species, *C. magna*, is plainly more nearly related to *C. armatum* than to *C. horridum*, that is to the section of the genus with short spines rather than to the long-spined ones.

Reported thus far only from the tropical Atlantic, by Murray and Whitting (1899).

***Ceratocorys bipes* (Cleve) Kofoid.**

Goniodoma (?) *bipes*, Cleve (1903), p. 371, fig. 2.

Ceratocorys (?) *asymmetrica*, Karsten (1907), p. 419, pl. 47, fig. 9 a-d.

The general form of the body of this medium-sized species is very characteristic. It lacks the angular features of *C. armatum* and *horridum*. The nearly circular girdle is far anterior; the epitheca is low and dome-shaped, and the hypotheca is laterally compressed posteriorly somewhat as in *Phalacroma*, while the antapical region bears in the sagittal plane two large constricted, bulbous enlargements, one placed at the posterodorsal angle of the antapical plate, and directed posteriorly and the other at the postero-ventral angle but directed at an angle of 45° from the major axis. Each bears a short, conical, terminal sheathed spine without brush. The whole surface is regularly pitted, but there are no fins along the sutures and the girdle-lists are low.

Reported thus far only from five localities in the Red and Arabian seas by Cleve (1903) and once from the Indian Ocean by Karsten (1907), who correctly, though with hesitation, assigns it to the proper genus but evidently did not know of Cleve's earlier figure and description.

***Ceratocorys jourdani* (Gourret) Kofoid.**

Dinophysis jourdani Gourret (1883), p. 79, pl. 3, fig. 55.

Dinophysis armata, Daday (1888), p. 193, pl. 3, fig. 6.

Phalacroma jourdani, Schütt (1895), p. 64, pl. 4, fig. 20 17.

Ceratocorys horrida (encysted), Murray and Whitting (1899), p. 329, pl. 30, fig. 5b.

Phalacroma Jourdani, Entz (1902), p. 130, figs. 6-8; (1905), p. 113, figs. 1-4.

Phalacroma Ceratocorys, Entz (1902), pp. 135-144, figs. 26, 33; (1905), pp. 120-127, figs. 22-28.

The body of this small species bears in lateral view a striking resemblance to *Phalacroma*. The girdle is far anterior and has

nearly the same position, proportions, and relationships as in that genus. The five spines, one ventral, three antapical, and one dorsal, all lie nearly in the sagittal plane as does the posterior fin in the Dinophysidae. The two ventral fins upon each side of the ventral area are likewise arranged in a general way as are the fins of *Phalacroma*. But the skeletal morphology is in all cases analyzed strictly of the *Ceratocorys* type and never of the *Dinophysis* type. The sheathed spines bear typical distal brushes and are sometimes connected by membranes. The spine of the ventral fin is of the *Ceratocorys* type, bearing no resemblance in structural details to those of the ventral fins of the Dinophysidae. The surface is evenly pitted with small pores. The sutures, in or near the sagittal line, as I have found them, are not sinuous as in the Dinophysidae and as figured by Entz (1902). The sutures are not marked by fins except in the sagittal region or by thickenings as in the *armatum* group, and are not readily distinguished. They can, however, be found with the oil immersion and the plates can be isolated by pressure and treatment with reagents. The whole superficial make-up of this *Ceratocorys* is most strikingly similar to that of the Dinophysidae, for example in the matter of spines to *Dinophysis uracantha*, and in form of body, ventral fins and girdle to *Phalacroma porodictyum*. Resemblance so striking as this occurring among the Hymenoptera or Lepidoptera might easily be regarded as a case of "mimicry." There is, however, among these organisms no satisfactory evidence to justify such an interpretation, for we have as yet no evidence of selective feeding on the part of larvae and other organisms of the plankton which prey upon the Dinoflagellates. The smaller plankton organisms are either taken *en masse*, as in Salpa, or apparently without discrimination, as by the Copepoda. The species in question are also, in so far at least as observation has gone, altogether too rare to justify reasonably an interpretation of this resemblance as mimicry resulting from natural selection. *Gonyaulax ceratocoroides* resembles in a very striking way *Ceratocorys horrida* whose numbers are sufficient to supply the basis for its use as a model. But in this case, as well as in that of *C. jourdani*, it seems more probable that the resemblances rest upon convergence in structure to meet common

needs of flotation and orientation rather than upon mimicry of an objectionable model and consequent survival by natural selection.

Taken at San Diego and Naples. Widely distributed in warm-temperate and tropical seas.

Described by Gourret (1883) as a *Dinophysis jourdani* and again by Daday (1888) as *D. armata* and shifted to the related genus *Phalacroma* by Schütt (1895). In 1883 Pouchet describes and figures as *Dinophysis galea* a complex of four species belonging in three cases to the genera *Phalacroma* and *Ornithocercus*, while the fourth (the third in the unnumbered row) is possibly *Ceratocorys jourdani*. Klebs shortly afterward (1884) finds *Dinophysis jourdani* at Naples and states that it appears to him to be the same as Stein's *Ceratocorys horrida* but that Gourret has more correctly established its systematic position in *Dinophysis*.

Entz (1902) endeavored to show that this was a connecting link between the two genera *Phalacroma* and *Ceratocorys* belonging to two different families, and even that *C. horrida* was a "Wachsthumform," of *Phalacroma Ceratocorys* as he designated this new connecting link. His evidence, as far as it goes, shows rather that *Phalacroma jourdani* is a *Ceratocorys* and had he fully analyzed the plates the transition to that genus would doubtless have been completed. I find no evidence whatever to support his hypothesis that *C. horrida* is in any way a part of the life-cycle of *C. jourdani*, or to substantiate Murray and Whitting's very tentative suggestion that the form they figure (pl. 30, fig. 5a) is an "encysted" stage of *C. horrida*. It is a typical *C. jourdani*, a species not elsewhere recognized by them.

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MARINE BIOLOGICAL ASSOCIATION OF SAN DIEGO

XXIX

PRELIMINARY REPORT ON THE HYDRO-
GRAPHIC WORK CARRIED ON BY THE
MARINE BIOLOGICAL STATION OF
SAN DIEGO

BY
GEORGE F. MCEWEN

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CONTRIBUTIONS FROM THE LABORATORY
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XXIX.

PRELIMINARY REPORT ON THE HYDRO-
GRAPHIC WORK CARRIED ON BY THE
MARINE BIOLOGICAL STATION OF
SAN DIEGO.

BY

GEORGE F. McEWEN,
Physicist of the Station.

The idea of a "Biological Survey of the Waters of the Pacific adjacent to the Coast of Southern California," set forth in the articles of incorporation of the Marine Biological Association of San Diego as the main reason for the existence of that organization, has from the outset included, as an integral part of its program, hydrographic as well as biological investigations.

Although a considerable number of observations on temperature and density have been made, beginning with the summer of 1901,¹ the resources of the Station did not permit the work

¹ During June and July, 1901, Professor W. J. Raymond of the Department of Physics, University of California, made a considerable number of both temperature and density determinations on the water about San Pedro. Since then Professor Skilling of the State Normal School of San Diego has done some work for the vicinity of San Diego Bay. Furthermore many temperatures have been taken from time to time by different persons connected with the laboratory. These data are all on record and may be put in shape for publication some time should this seem desirable.

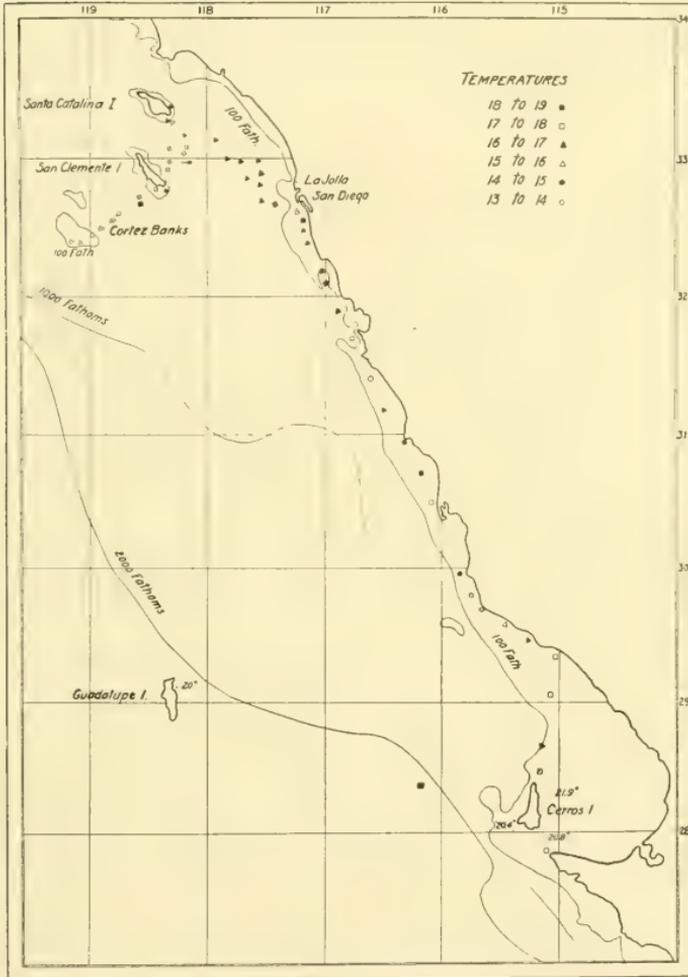
to be taken up in earnest until the summer of 1908, when the writer was asked to become a regular non-resident member of the staff of the Station, to be on duty at La Jolla for some portion of each year, in charge of the water investigations. The present report is the first of the hydrographic results to be published, and will be understood to contain but a small portion of all the data that have been collected, even during the last two years.

The plan adopted contemplates the employment, as soon as possible, of the methods and instruments used by the International Council for the Exploration of the Sea.

The work done during the summer of 1908 consisted of temperature and density determinations of the ocean and bay waters, and a series of soundings of the ocean; the area covered lying between parallels $33^{\circ} 20'$ and $32^{\circ} 30'$ of north latitude, extending from the coast to longitude $118^{\circ} 30'$. This area does not include two trips to the Cortez Banks, which are situated about fifty miles southwest of the eastern end of San Clemente Island, and a trip south, below Cerros Island, to latitude $27^{\circ} 40'$.

The temperature and density work was carried on as follows: A pail full of surface water was dipped up, usually every twenty minutes while the boat was moving along its course, and also whenever catches were made; the temperature of the water was immediately measured to the nearest tenth of a degree in terms of the Centigrade scale. A pint of the water was then sealed tightly in a glass fruit jar, so that a reference to the corresponding number in the log book and on the map, showing the ship's course, would give the temperature and position of the sample, and the time when it was obtained. The average rate of the boat being seven knots per hour, surface samples were obtained at intervals of $2\frac{1}{3}$ knots along the course.

At a few stations water was taken from various depths by means of the "Kofoid closing water-bucket." The temperatures were taken and the samples preserved as before. The bucket, which is open at the ends, is let down by means of a cable, wound on a drum operated by the hoisting engine. When the desired depth is reached the bucket is closed by means of a cast-iron messenger, sent down the cable, and is immediately drawn up.



The volume of the bucket is about twenty liters, and since a test showed that the temperature of the contents rose from 15.5° to 15.75° when standing in the open air at 19.5° , in 20 minutes, it was thought that deep-water temperatures could be determined with but little error. However, when drawn up from a depth of two hundred fathoms or more, the temperature at the top of the bucket was repeatedly found to be as much as 2° or 3° warmer than at the bottom. The bottle being of bronze and being uninsulated, this temperature change is probably due partly to conduction when in the warmer water, and partly to the friction of the surrounding water when the bucket is drawn up. The temperature recorded was usually, though probably not always, that of the coldest portion. This temperature, however, may be too large, and there may be some irregularities due to the fact that the coldest portion was not always tested. This difficulty, however, does not affect the accuracy of the density determinations. At the end of each cruise all the samples were taken ashore, and the density of each was tested either by means of a specific gravity bottle, capacity fifty or one hundred cubic centimeters, and a chemical balance or a hydrometer. The specific gravity bottle was of the Gay-Lussac pattern, provided with a ground glass stopper, having a fine perforation, so that in closing the bottle an excess of water might be forced through the perforation and wiped off with a piece of filter paper. In this way the bottle could be filled to a definite volume, the exact volume depending upon the temperature of observation. The weight and volume being determined, the absolute density was calculated, in C. G. S. units, the probable error being $\pm .00002$.

A set of five hydrometers (by Dr. R. K uchler, Hmenau in Th uringen) was provided, having a range from 1.000 to 1.031, the range of each being .007. The stem was graduated to .0001, and its diameter was about 3.5 mm., the volume of the body being 115 c.c. A series of water samples was tested both by the hydrometers and by the specific gravity bottle, the temperature of observation varying from 14° to 25° , and a reduction formula deduced for each hydrometer used. By means of a hydrometer the density could be determined with a probable error of $\pm .00005$.

The water samples are designated by numbers 1, 2, 3, etc., in the order taken, and the results tabulated as follows:

Water sample number; Date; Haul number; Position; Depth in fathoms from which sample was taken, D; Temperature (Centigrade) of water—At the depth D; T, During observation, t; Hydrometer—Number of instrument, Reading, R; Specific gravity—Observed at t° c, S, Reduced to its value at 15.56° C, S, T° C, Sr; Chlorine in grammes per kilogram of water.

The readings and instrument numbers refer either to the specific gravity bottle used and its apparent weight in grams when full of water or to the number of the hydrometer and its reading. The reduction of the densities to the last two temperatures was made in accordance with the method described by Dittmar, Reports of *Challenger* Expedition, Physics and Chemistry, Vol. 1, page 70. The chlorine, in grammes per kilogram, was computed from the density according to Dittmar's method, described in the same volume, page 80.

From this collected data, the physical conditions for that region, at the time they were determined can be obtained, but these conditions are not constant; therefore they must be repeatedly determined at different times, and these results must be studied for the purpose of obtaining a knowledge of the manner in which the changes proceed, so that from a comparatively few discontinuous observations taken at various times and places, the conditions at intervening times and places can be deduced.

The density of the water depends upon three independent conditions: its temperature, the pressure which it supports, and the amount of material dissolved in it. If the density is reduced to a standard temperature and pressure, the only variable affecting it is the amount of dissolved matter, and the density defined as above is a measure of the salinity, or quantity of matter dissolved in unit mass of the water. If the density of a given sample is represented by S , at any pressure, and by S_p at a pressure p in excess of the first value, the temperature remaining constant, then the following equation holds approximately: $S_p = S (1 + 3 \times 10^{-6} p)$ where p is expressed in pounds per square inch. If, then, we know the density of a water sample under atmospheric pressure and at any given temperature, and want to know what its density would be at the same

temperature under the pressure existing d fathoms below the surface of the sea, we have, on substituting for p in the above formula, its value in terms of the depth (d):

$$S_d = S (1 + 7.9 \times 10^{-6} d) \text{ approximately.}$$

If the temperature is the only variable, the following approximate formula holds between 10° and 30° Centigrade:

$$S_t = S_T [1 + (T - t) (.00025)]$$

where S_T is the density at the temperature T and S_t is the density at the temperature t , using the Centigrade scale. So, in order to find the actual density of the water under the conditions existing in the sea, the value under standard conditions must be corrected for both temperature and depth. More exact methods for making these corrections are given in volumes I and II of the *Challenger* report on Physics and Chemistry, and in Knudsen's hydrographic tables, *Publications De Circonstance*, No. II, May, 1904. All densities given below are expressed in absolute C. G. S. units and reduced to the standard temperature 15.56° ; the value used in the *Challenger* report.

PROPERTIES OF THE SURFACE WATER EXAMINED.

In order to give a summary of this work, the day was divided into eight periods of three hours each, the day beginning and ending at midnight; the season was divided into periods of one week each or one day, as seemed advisable, and the average temperature was computed for each period. The number in brackets represents the number of observations used to determine the average. In case there were no observations for any given period, the value was found by interpolation and inserted, so that the weekly or hourly average would all depend on the same number of temperatures, distributed in the same way.

It was found that certain in-shore and shallow water regions had a temperature two or more degrees less than the rest of the ocean, though there was no appreciable difference in the density. The average weekly, hourly, and seasonal temperatures are computed only from the warm water observations, which are much more numerous and are representative of the normal surface temperatures of the region.

THE SAN DIEGO REGION OUTSIDE THE BAY.

During the summer of 1908, from June 12 to July 28, three hundred and eighty-eight temperature and three hundred and forty-two density measurements were taken. Forty-three temperatures were less than 16.5° . The minimum temperature was 15° , the maximum was 22.5° , the average for the season was 18.99° . The minimum density was 1.02467, the maximum was 1.02520, the average for the season being 1.02591. The average temperature increased at the rate of about $.7^{\circ}$ per week from June 12 to July 28. The following table shows the hourly and weekly averages of temperatures:

Date	3-6	6-9	9-12	12-15	15-18	18-21	Weekly Average
6/12-6/19	17.85 (0)	17.78 (15)	17.82 (9)	17.70 (7)	17.58 (5)	17.65 (0)	17.59 (36)
6/20-6/27	18.55 (2)	17.95 (5)	18.44 (10)	18.8 (9)	18.70 (8)	18.35 (2)	18.46 (36)
6/28-7/5	19.18 (5)	17.68 (17)	17.70 (13)	18.27 (13)	18.70 (13)	18.8 (0)	18.39 (61)
7/6-7/13	17.60 (9)	17.78 (15)	18.63 (25)	18.83 (22)	19.7 (0)	19.25 (0)	18.63 (71)
7/14-7/21	18.83 (15)	18.87 (9)	19.68 (14)	20.63 (17)	20.72 (6)	19.69 (9)	19.74 (70)
7/22-7/29	20.2 (10)	20.83 (5)	21.35 (6)	22.38 (5)	21.42 (0)	20.4 (9)	21.10 (35)
6/12-7/29	18.7 (41)	18.48 (66)	18.94 (77)	19.44 (73)	19.49 (32)	19.03 (20)	18.99 (309)

During the summer of 1909, from June 8 to July 27, one hundred temperature and density measurements were taken; five temperatures were less than 16.7° , none were less than 15.6° . The minimum temperature was 16.3° , the maximum was 20.8° , the average for the season being 18.70° . The minimum density was 1.02479, the maximum was 1.02492. The average temperature increased at the rate of about 0.3° per week from June 8 to July 25. The following table shows the hourly and weekly averages:

HOURLY AVERAGES.

Date	3-6	6-9	9-12	12-15	15-18	18-21	Weekly Average
6/8-6/15	18.0 (0)	17.0 (2)	18.28 (10)	18.2 (1)	18.6 (2)	17.8 (0)	17.99 (15)
6/16-6/23	18.3 (1)	17.9 (1)	18.55 (0)	18.5 (0)	18.43 (3)	18.13 (4)	18.23 (9)
6/24-7/1	17.9 (3)	18.15 (2)	18.82 (0)	19.0 (0)	18.36 (4)	18.09 (10)	18.39 (19)
7/2-7/9	17.84 (5)	17.15 (8)	19.07 (14)	19.56 (13)	19.3 (11)	18.7 (7)	18.61 (58)
7/10-7/17	18.96 (8)	19.17 (3)	19.2 (1)	19.6 (1)	19.1 (1)	19.17 (6)	19.20 (20)
7/18-7/25	19.26 (0)	19.47 (0)	20.35 (4)	20.6 (1)	19.4 (0)	19.47 (0)	19.78 (5)
6/8-7/25	18.37 (17)	18.15 (16)	19.05 (29)	19.24 (16)	18.88 (21)	18.49 (27)	18.70 (126)

THE REGION SOUTH OF SAN DIEGO BAY.

From August 26 to September 5, 1908, a trip was made due south of San Diego to latitude 28° , then east to Cerros Island, then north along a line from two to ten miles from the coast. Four hundred and fourteen temperature and four hundred and two density measurements were taken; sixty-one temperatures were less than 16.5° and fourteen were less than 15.0° . The minimum temperature was 13.0° , the maximum 21.85° , the average being 19.22 .

The minimum density was 1.02447, the maximum was 1.02491. The following table shows the hourly and daily averages. Numbers *in italics* are not used in the final averages:

HOURLY AVERAGES.

Date	0-3	3-6	6-9	9-12	12-15	15-18	18-21	21-24	Daily Average
8/26/08	17.6	17.9	19.86	20.92	20.04	19.32	18.88	19.27
8/27		(0)	(1)	(8)	(9)	(10)	(9)	(8)	
8/27	18.35	18.65	18.77	18.92	18.37	19.2	18.9	18.81
8/28	(9)	(10)	(8)	(9)	(9)	(9)	(0)		
8/29	19.07	19.37	20.1	20.32	20.25	19.95	19.84
8/30		(0)	(7)	(10)	(8)	(10)	(0)		
8/30	20.0	20.3	19.28	18.91	18.84	18.54	<i>19.57</i>	19.31
8/31		(0)	(2)	(4)	(6)	(9)	(10)	(8)	
8/31	18.95	19.05	17.54	17.82	20.0	20.38	19.0	18.97
9/1	(10)	(9)	(9)	(9)	(9)	(9)	(1)		
9/1	19.5	19.54	20.8	20.9	20.6	20.3	20.28
9/2		(2)	(8)	(9)	(7)	(0)	(0)		

HOURLY AVERAGES—(Continued).

Date	0-3	3-6	6-9	9-12	12-15	15-18	18-21	21-24	Daily Average
9/2	19.6
9/3	(2)
9/3	18.33	18.42	18.5	17.92	17.6	17.30	18.01
9/4	(3)	(0)	(5)	(10)	(0)	(0)
Average	18.65	18.90	18.84	19.34	19.62	19.56	19.05	19.22	19.22
8/26-9/4	(19)	(24)	(34)	(54)	(58)	(47)	(20)	(16)	(237)
9/3	17.0	15.87
9/4	(8)	(7)
9/4	14.0	14.92	16.07	17.28	18.07	16.48	16.55
9/5	(6)	(9)	(9)	(8)	(9)	(10)	(8)
9/5	16.28	15.13	17.36	17.99	17.22	18.21
9/6	(10)	(8)	(10)	(8)	(9)	(5)

FROM SAN DIEGO TO SAN CLEMENTE ISLAND.

From February 19, 1909, to February 20, a trip was made to San Clemente Island from San Diego Bay, ninety temperature and seventy-six density measurements being taken. The minimum temperature was 12.0°, the maximum 14.6°, the average being 13.57°. The minimum density was 1.02410, the maximum, 1.02488, the average being 1.02460.

HOURLY AVERAGES.

0-3	3-6	6-9	9-12	12-15	15-18	18-21	21-24	Average for the Trip
13.2	13.28	13.48	13.82	13.79	13.72	13.68	13.07	13.57
(10)	(12)	(13)	(17)	(17)	(15)	(5)	(3)	(92)

PROPERTIES OF THE INTERMEDIATE AND BOTTOM WATERS.

From June 12 to July 28, 1908, there were twenty-four temperature and density measurements taken in the San Diego region. The maximum density was 1.02557.

From June 8 to July 7, 1909, there were twenty-nine density and twenty-seven temperature measurements taken in the San Diego region. The minimum temperature was 6.5° and the maximum density was 1.02556.

During the trip to Cerros Island, from August 26 to September 5, 1908, there were nineteen temperature and density measurements taken. The minimum temperature was 8.0° and the maximum density was 1.02572.

On February 19, 1909, there were five temperature and four

density measurements taken. The minimum temperature was 9.9° and the maximum density was 1.02525.

Usually the temperature is found to decrease continually with increase of depth and the rate of change decreases rapidly as the depth increases, and the density increases as the depth increases. The following table of temperatures and densities which applies to a station ten miles west of La Jolla is a good illustration of the above rule:

Depth in Fathoms	Temperature	Density
0	21.5	1.02486
75	11.0	1.02512
150	10.5	1.02525
250	9.7	1.02523
350	9.2	1.02531

There were, however, several striking variations from the normal relation of temperature and density to depth. For example, a rise of 1.1° , from 9.4° at two hundred and fifty fathoms to 10.5° at three hundred and eighty-five fathoms, was observed on June 15, 1908. The densities were 1.02543 and 1.02541 respectively. A rise of 3° , from 7.5° at five hundred and sixty fathoms to 10.5° at five hundred and eighty-five fathoms, was noted on June 18, 1908, twenty-five miles west of La Jolla. Similar phenomena were observed during the summer of 1905 between La Jolla and San Clemente Island. In nearly every case where the temperature rose with increase of depth, the density diminished.

The error in the above temperatures due to heating of the bucket was eliminated by taking the temperature of the coldest portion of the water, so the temperature variations found above could not be due to the method of measurement.

THE OCCURRENCE AND PROBABLE SIGNIFICANCE OF COLDER IN-SHORE SURFACE WATER.²

As will be seen from the map, page 191, from latitude $28^{\circ} 36'$, longitude $115^{\circ} 9'$, northward to the coast and thence along a line from two to ten miles from the coast, swinging off towards

² All temperatures referred to under this title were observed during the summers of 1908 and 1909.

Avalon, Catalina, from La Jolla and south of Avalon to latitude 33° , the temperature is from 13.5° to 16.5° . The temperature is about 18.5° from that point to latitude $32^{\circ} 37'$, longitude $118^{\circ} 41'$. Thence southwest across the Cortez Banks the average temperature is 15.5° . The average temperature of the rest of the ocean is 19.0° .

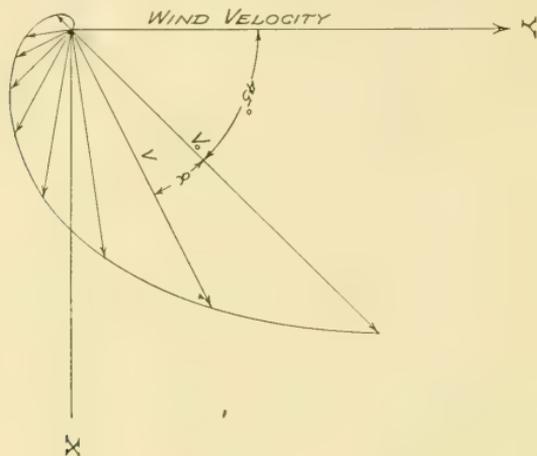
The breadth of this cold-water belt has not been determined accurately, though observations show that it is confined to water of one hundred fathoms or less in depth, and a drop of 2° or 3° in two miles has several times been observed in a line normal to the cold-water belt.

All of these low temperatures occur where the depth is from about twenty to one hundred fathoms, and are especially prevalent along the shallow belt of water parallel to the coast. During the summers, when these observations were taken, the winds were north or northwest and there was therefore a relatively large component of the wind velocity parallel to the coast. In October the winds shift to the west and the direction is then mainly perpendicular to the coast.

The temperature phenomena can be accounted for, qualitatively at least, by means of a modern theory of oceanic circulation due to V. W. Ekman. The most essential points of this extensive theory, which apply to this case, are here briefly set forth.

From the dynamical theory of the motion of the ocean water, when the effect of fluid friction and the earth's rotation is considered (it is understood that the wind is the only cause of the current), the direction of the surface water current is about 45° to the right of the direction of the wind, instead of being parallel to the wind, provided the depth of the water exceeds a certain amount (the amount will be determined later), and the region considered is north of the equator. The magnitude of the velocity continually diminishes as the distance below the surface increases, while the direction of the velocity continually turns to the right. To be more specific, if V_0 is the surface velocity and V the velocity at such a depth that the angle is α with V_0 , $V = V_0 e^{-\alpha}$ where $e = 2.718$ (natural base for logarithms), $\alpha =$ angle in radians; therefore when $\alpha = \pi = 3.1416$ radians or 180° , $e^{-\pi} = .043$ and $V = .043 V_0 =$ approximately

$\frac{1}{20}$ V_0 or $\frac{1}{20}$ of the surface velocity. Following is a diagram of the wind-velocity and of the water velocity at several depths:



The depth at which the velocity is V , and the angle with V_0 is α , depends on the wind-velocity, the friction, and the latitude.

By combining certain formulae developed in the theory, the following relation can also be obtained:

$$D = \frac{K}{V \sin \theta} h,$$
 where D is the depth in meters and h is the wind-velocity in $\frac{\text{meters}}{\text{seconds}}$ and K is a constant or approximately so as shown by the theory. By actually finding D , the depth at which the current is reversed in direction, and by measuring h , the value of K can be found from the formula. It is also possible to find the constants in the more fundamental formulae from which the above was derived, and then K can be computed from them. However, in all cases certain of the variables in the formulae must be actually observed before the constants can be found.

At the depth D at which the direction of the velocity has changed so that it is exactly opposite to that of the wind, its magnitude is only one-twentieth of the surface velocity. D , the

depth below which the effect of the wind is practically negligible, is called the "Reibungstiefe," D meters = $\frac{7.6}{V \sin \theta} h \frac{\text{meters}}{\text{seconds}}$, where D is the "Reibungstiefe," θ the geographical latitude, and h is the wind-velocity. It is to be understood that the depth of the water exceeds D , and that the value of θ is not less than about 2° . If the depth is less than D , the deflection of the current from the direction of the wind is less and as the depth diminishes the effect of the earth's rotation diminishes, though it is only when the depth is less than $\frac{1}{2} D$ that the above statements are not approximately true. If, where the latitude is 30° , the wind-velocity is $15 \frac{\text{miles}}{\text{hour}}$, D equals forty fathoms.

The average velocity in such a surface stream is such that the total quantity of water transported is zero in a direction parallel to the wind and is a maximum in a direction 90° to the right of the wind.

From this theory the component of the wind-velocity perpendicular to the coast would produce currents parallel to the coast, the direction of the currents being, for the California and Mexican coasts, towards the south when the wind blows from the west, towards the north when the wind blows from the east. Also the component of the wind-velocity parallel to the coast would produce currents running towards or away from the coast according as the direction of the wind is from south to north or north to south. In the latter case, which is true during the summer, the water for a depth of about forty fathoms would be flowing away from the coast because of the effect of the wind and earth's rotation, and the removal of this layer would cause an upwelling of the deeper and colder water to take its place.

In the winter, when the prevailing winds are nearly perpendicular to the coast, the currents would be parallel to the coast and no upwelling of the colder water would take place.

THE PROPERTIES OF THE WATER OF SAN DIEGO BAY.

From June 13 to July 18, 1908, fourteen observations of temperature and density were taken. The following table gives a series of values from the entrance to the bay to National City:

Location	Temperature	Density
Whistling buoy, just outside of the entrance to the bay	17.6	1.02500
La Playa, five miles from the buoy		1.02514
Spreckel's wharf, three miles from La Playa	19.4	1.02538
Ferry landing on Coronado side	20.0	1.02547
East end of Glorietta Bight	23.0	1.02592
West end of Glorietta Bight	24.3	1.02598
National City, one-quarter mile from shore	26.5	1.02670

The fluctuation of the above values due to the tides is illustrated by the following observations. At low tide on July 18, at 8 a.m., the temperature and density were 20.8° and 1.02564 respectively, near Spreckel's wharf; four hours later at the same place, during high tide, the values were 18.0° and 1.02513.

On a line from Spreckel's wharf to the west end of Glorietta Bight, Coronado, July 18, 1908, there were five observations of temperature and density. The minimum temperature was 20.0° in the channel, the maximum was 24.3°, the average being 21.22°. The minimum density was 1.02513, the maximum was 1.02598, the average being 1.02562. Along the same line on July 17, 1909, there were seven observations taken. The minimum temperature was 20.8°, the maximum was 24.3°, the average being 22.1°. The minimum density was 1.02644, the average being 1.02581.

On July 14, 1908, there were five observations taken at National City, about a fourth of a mile from the coast. The minimum temperature was 24.8°, the maximum was 27.5°, the average being 26.37°. The minimum density was 1.02670, the maximum was 1.02704, the average being 1.02690. For the summer of 1908 the average temperature and density of San Diego Bay were 23.79° and 1.02620.

It may be profitable to state briefly, in concluding this preliminary report, what the general hydrographic problems before the Station are: (1) In its exclusively hydrographic aspect the problem cannot be better worded than we find it in the *Second Report of the North Sea Investigations*, 1904 to 1905: "We want to know the physical conditions under which marine life exists, and we should like to know the conditions at all parts and all depths of the sea at all seasons of the year, and from one year to another. We want to learn the general, or average, hydro-

graphical conditions of temperature, density, and current at each place and at each depth, and then to learn the changes or fluctuations that these conditions undergo during the year or during longer periods." (2) Seen from the standpoint of specific biological investigations, the hydrographic problem may be stated thus: Assuming a large body of knowledge answering the demands and desires indicated under (1) to have been secured, the problem then becomes: What particular conditions, agreements with, or deviations from, the average conditions, already found, prevail at the particular time and place at which any particular biological observations are made?

Methodologically considered it will be noted that investigations designed to answer the needs indicated under (1) might be strictly, *i.e.*, exclusively, hydrographic, while those designed to answer the needs indicated under (2) would be always primarily biological, *i.e.*, the hydrographic observations would always be made concomitantly with and subordinate to, the biological observations.

Stanford University, March, 1910.

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OF THE
MARINE BIOLOGICAL ASSOCIATION OF SAN DIEGO

XXX.

BIOLOGICAL STUDIES ON CORYMORPHA
III.—REGENERATION OF HYDRANTH AND
HOLDFAST

BY
HARRY BEAL TORREY

XXXI.

NOTE ON GEOTROPISM IN CORYMORPHA

BY
HARRY BEAL TORREY



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XXX.

BIOLOGICAL STUDIES ON CORYMORPHA.

III.—REGENERATION OF HYDRANTH AND
HOLDFAST

BY
HARRY BEAL TORREY.

In the second study of this series¹ the normal development of *C. palma* was considered and its extraordinary plasticity pointed out. I shall now give an account of the differentiation of hydranth and holdfast after section of the column, both in the larva and the adult, and make comparisons with corresponding processes in the egg development.

I. REGENERATION IN THE ADULT.

1. DEVELOPMENT OF THE HYDRANTH.

The regeneration of a hydranth on a stem of *Corymorpha* from which the original hydranth has been removed by a simple transverse cut, is ordinarily accomplished by a transformation of the stem, as in *Tubularia*, but by a process which differs in some details from the process of the latter. The wound closes within a period varying widely between a few hours and several days. Immediately after section, the vacuolated cells composing the supporting axial tissue of the column swell out in the shape of a low dome, and the body wall soon begins to advance over them.

¹ II. The Development of *C. palma* from the Egg. Univ. Calif. Publ. Zool., 3, p. 253, 1907.

After transverse cuts this advance may be so rapid and vigorous as to constrict off a central nub of the axial dome. Such a movement is due undoubtedly to the activity of the circular muscles. Other factors, however, are involved. After oblique cuts, as in the case shown in fig. 1, the contraction of either longitudinal or circular muscles would cause the wound to gap rather than close.

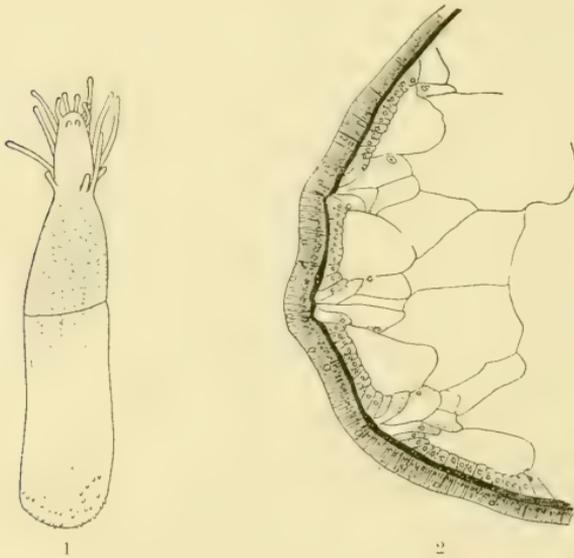


Fig. 1.—Regeneration of a segment of a column three days after an oblique cut. Two days later the tentacles were equivalent and equidistant.

Fig. 2.—Portion of transverse section of adult of moderate size, somewhat contracted, showing relation of axial parenchyma to the epithelium of the canals. $\times 88$.

In such cases, the edges of the wound are approximated by a local shrinkage in the axial endoderm in the manner described in my paper on the behavior of *Corymorpha*.² As the axial tissue withdraws, the body wall follows passively. Even after transverse section, this factor probably enters to some extent. As seen

² Univ. Calif. Publ. Zool., 2, p. 333, 1905.

in longitudinal sections, there is a terminal area of the body wall that is much attenuated just after the wound has closed. It appears to be a proliferating area, definitely bounded by the cut edge of the old mesogloea, its own mesogloea negligibly thin. Its attenuation suggests the formation of the fenestrated membrane in the larva, of wound closure in *Tubularia*, and is probably governed partly by similar factors. The new hydranth cavity is formed by the degeneration and disappearance of the axial endoderm cells at the end of the stem, the tip of the stem becoming the tip of the new proboscis. The withdrawal of the central core of axial endoderm puts the peripheral canals, indirectly, in communication, since they are normally bounded by axial endoderm on the inner side (fig. 2). Between them, however, the axial tissue remains for a time in the form of ridges (fig. 3) which are more or less prominent according to the size of the stem. By the disintegration of the largest, most highly differentiated cells³ and a decrease in size and an increase in granulation of others, it is converted finally into epithelium whose cells resemble the epithelial cells lining the peripheral canals (fig. 3). The epithelium of the hydranth cavity is thus derived from two sources. At first it is low, scarcely thicker than the ectoderm surrounding it. Gradually its cells become long and the low narrow folds between the canals give way to the much broader folds of what has now become the chief digestive epithelium of the hydroid.

Even before the wound has closed, in some cases (fig. 6), but usually afterward, the tentacles begin to appear. The proximal tentacles usually arise first, in two sets. The first set (fig. 4) appears as a circle of conical elevations just above the lower limit of the hydranth cavity, one to a canal. Though the canals, by the obliteration of the axial endoderm, may be parts of the hydranth cavity at this time, they are still separated by the ridges previously mentioned, which are continuous with intercanalicular tissues below.

The number of the tentacles in this set usually corresponds

³ Such loss, in connection with regeneration, of tissue so specialized as apparently to be incapable of a change of function, will be considered with the various phenomena of retrograde metamorphosis in another paper.

to the number of canals, but there are certain exceptions. The numbers always correspond in regenerating stems of small size, but in very large stems two tentacles may be found occasionally in one canal. The explanation of this appears to lie in the fact that the canals are larger on the large stems than on the small.



Fig. 3.—Transverse section of a portion of the wall of a hydranth developing from a stem of moderate diameter. $\times 60$.

Fig. 4.—Beginnings of proximal tentacles, one to a canal; zone of frustules below; somewhat contracted. $\times 9$.

There is a lower limit of size below which no canals are present. There is also a minimum limit to the size of the canals, reached when the stem possesses six to nine only. From this point the number of canals increases with the diameter of the stem; but there is also an increase in the diameter of each canal. In very large stems, the canals become exceptionally large, and apparently afford room for more than one tentacle on each. The number of canals may thus govern to a certain extent the number of tentacles appearing in the first proximal set by growing in

their greatest diameter more rapidly than the tentacle fundaments relatively to the diameter of the column, with which, in general, the size of both is correlated.

With the disappearance of the axial tissue in the ridges separating the canals, and the formation of a continuous epithelium, the second set of proximal tentacles arises, one by one, between and on the same level with those of the first set. The number in the latter usually ranges between twelve and eighteen, slightly more than half the total number (18-30);⁴ and the canals together ordinarily occupy a little more than half the surface of the stem. The correspondence between number of tentacles and diameter of stem is evident here.

The distal tentacles develop in successive groups. In the first group, they usually appear somewhat later than the first proximal set,⁵ in smaller number. The decrease in number is correlated with certain differences in the conditions. The stem at the level of the distal tentacles is less in diameter than at the level of the proximal tentacles, and partly because of this, the canals are disposed to fuse more readily in this region. When the canals are distinguishable, it may be seen that the first distal tentacles arise, one on each, as did the proximal, in a single whorl; succeeding tentacles appear after the canals have fused, more or less irregularly and below the first. When the end of the stem is much narrowed and the canals obliterated before any tentacles have appeared, the latter may develop in quartettes, as in the embryo, though the stem may be very much larger than the embryonic stem. Several cases of this sort have been observed, one of which is figured (fig. 5). The members of the second quartette arise at a slightly lower level than, and in alternation with, the first four tentacles; as in the embryo, they may appear singly or simultaneously. Apparently the quartette method is the direct result of the size of the stem; only a limited number of tentacles of a certain size arise on a limited surface. The regenerating tentacles are much larger than the developing

⁴ In one instance, thirty-four tentacles were borne on a small regenerating stem, more than I have ever seen in any other individual.

⁵ Their appearance may be delayed in exceptional cases, until the proximal tentacles have reached their full number.

tentacles of the embryo, the size of the fundament varying in general with the diameter of the stem.

In the embryo, at the time tentacles begin to appear, there is a single cavity, lined by endoderm cells which are larger and longer than the cells of the ectoderm, and closely resemble in size and vacuolation the axial cells of the tentacles. The axis

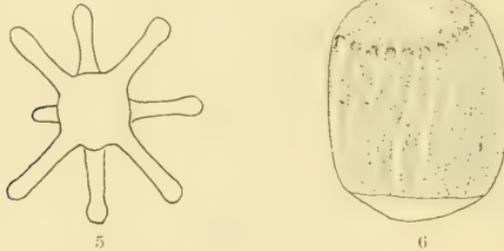


Fig. 5.—Distal tentacles regenerating in quartettes.

Fig. 6.—Regenerating segment of column much contracted. Wound not yet completely closed. Proximal tentacles indicated.

of both proximal and distal tentacles arises as a single row of cells which are pushed one after another out of the lining of the hydranth cavity. This axial endoderm in course of development, becomes several cells thick at the bases of the tentacles, though no cavities are formed.

In the regenerating adult column, the single cavity of the embryo is replaced by the peripheral canals, which are bounded on three sides by the vacuolated cells of the core of the column, and on the fourth (outer) by an epithelium (fig. 2). The cells of this epithelium measure about the same in height as those of the epithelial endoderm of the larva. They are more granular, however, and lack conspicuous vacuoles. The ectoderm is higher than the endoderm, especially in the naked portion of the column, and the mesogloea, almost invisible in sections of the embryo, has become a prominent layer.

The first indication of the regenerating tentacles in a surface view, is an increased opacity, depending on an increased granulation of the endoderm, at the points where the tentacles are to appear (fig. 6). At the same time, as sections show, the ectoderm

thickens slightly at these points, its cells increasing in number and length. The mesogloea thins somewhat, dissolved probably by the secretion of the endoderm cells.⁶

Differences between the normal and regenerative development of the tentacles now begin to appear, that are referable to the relative complexity of the column in the adult. Instead of the extrusion of a single row of cells from the simple endoderm, to form the axis of the larval tentacle, a mass of cells is pushed out, so that the tentacle, much broader from the beginning, reaches the stage of histological differentiation characteristic of the adult with exceptional directness. Viewed as changes involving mere masses of tissue, the processes differ only in magnitude. Viewed as changes in the structure of the tissues, and with respect to the behavior of the cells composing them, certain qualitative differences are manifest at once. These are smaller for the distal tentacles, whose development may be described in a few words. A local proliferation of epithelial endoderm produces a small group of cells that is pushed as it forms into a position below the endoderm, carrying the mesogloea and ectoderm out with it, the latter thinning slightly at the apex of the advancing endodermic core (fig. 7). This core is shortly separated by a sheet of mesogloea from the epithelium from which it has arisen, and thereafter is the sole source of the cells in the axis of the tentacle.

A certain complication is introduced into this simple process in the development of the proximal tentacles, correlated with the simultaneous development of the annular cushion of vacuolated endoderm that strengthens the hydranth wall in the region of their insertion.⁷ There is an enlargement and an increased vacuolation of the cells lining the canal (or hydranth cavity, as the case may be) at the point where the ectoderm has already thickened preparatory to the budding of the tentacle; and at the same time a layer of small cells makes its appearance below them, immediately against the mesogloea (figs. 8, 9). This layer is destined to produce the cells of the core. Its cells multiply rapidly and push out the ectoderm, assuming the form of stratified epithelial cells, compressed in the direction of the axis

⁶ Cf. development of frustules, *loc. cit.*

⁷ See fig. 27 in the paper already cited.

of the tentacle (fig. 9). A layer of mesogloea forms as in the case of the distal tentacles, though somewhat later in the development.

Gonosome. After the formation of the hydranth cavity, and while the proximal tentacles are little more than conical elevations the gonosome begins to develop as a circle of rounded

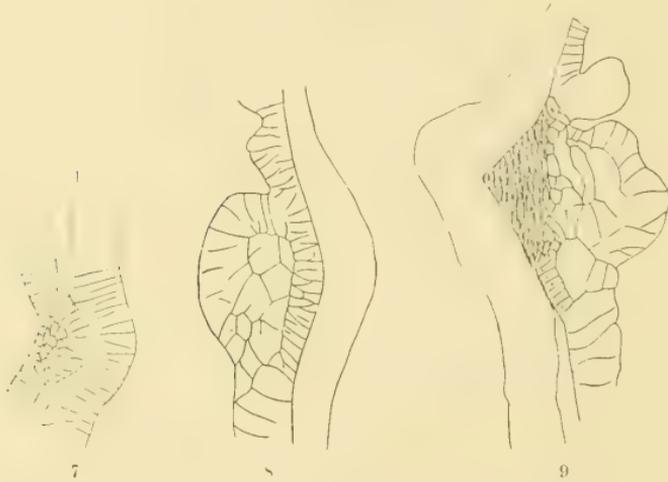


Fig. 7.—Section through early stage in development of distal tentacle.

Fig. 8.—Longitudinal section through outer edge of base of proximal tentacle; see fig. 4.

Fig. 9.—Longitudinal section through early proximal tentacle, somewhat oblique; see fig. 4.

protuberances immediately distal to the latter and, like them, one to a canal, developing only between the ridges of the intercanalicular tissue (fig. 10). These are the beginnings of the peduncles which bear the medusae. Their number from the beginning equals the number characteristic of adults with stems of a similar size, and is not increased as development proceeds. In this respect they differ from the tentacles, the difference being correlated with a more rapid growth in their diameter. For the number of peduncles to appear is conditioned by the diameter of the stem, as in the case of the proximal tentacles. This is well

shown in the development from the egg, where the plan according to which the peduncles arise, one or two at a time, is so like that followed by the tentacles, that they are only distinguished from the latter by their larger size, later origin, and cavity.

The development of the peduncles in the regenerating adult and in the embryo is the same in all essential features, involving

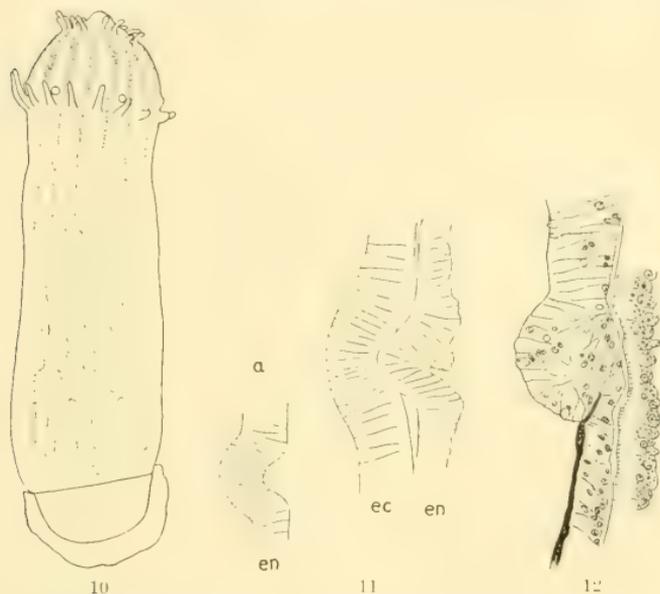


Fig. 10.—Regeneration of segment of column, showing gonosomal peduncles budding just distal to proximal tentacles. $\times 12$.

Fig. 11.—Two sections of young peduncle developing on regenerating column. *a* is median, showing endoderm only, with clear evagination.

Fig. 12.—Longitudinal section of body wall through edge of perisarc.

a distinct evagination of the endodermic epithelium (fig. 11). The only noteworthy difference, which applies equally well to the tentacles, is the greater rapidity of development in the regenerating stem.

For the sake of simplicity, the discussion has been concerned, up to this point, with the development of the hydranth (and the associated gonosome) on stems cut in the distal naked region;

with or without holdfasts, for the presence or absence of the latter has no influence on the result. At the edge of the perisarc the ectoderm changes abruptly by a shortening of epithelial cells and a marked decrease in number of netting capsules (fig. 12). When the cut is made in this covered portion of the stem, new perisarc is formed within the old, its distal edge proximal to the old edge, a certain proportional distance from the proximal tentacles of the new hydranth. The ectoderm of the region left naked by this shift rapidly acquires the characters that distinguish naked ectoderm on the intact column.

The position now occupied by the edge of the perisarc is about the same proportional distance from the proximal tentacles as it is in the young hydroid with a single canal, and very different from the usual position occupied in the normal adult. In the course of some days, the normal adult proportions are approximated, by an increase in the length of the stem, involving chiefly the naked portion, and a decrease in the diameter. There is in every regeneration of a hydranth some remodelling of the stem, to form a tapering proboscis and a slender "neck." As the proportions of the regenerating piece depart from the normal proportions of the species, this remodelling is more and more profound. The result in all cases is a more or less successful return to the normal form. This subject will be discussed more fully hereafter.

A hydranth may develop below a cut made just distal to the edge of the perisarc, so that the distal tentacles and the greater part of the proboscis arise from the naked stem, the proximal tentacles and base of the proboscis from covered stem. The development proceeds as usual. The edge of the perisarc moves back, uncovering ectoderm which soon becomes indistinguishable from the original naked ectoderm. One such case is represented in figs. 13, 14. The hydroid has lengthened so as to project from the original perisarc. New perisarc has been secreted, with its anterior limit the usual proportional distance below the proximal tentacles.

A similar transformation occurs when the regenerating piece has been cut from the naked part of the stem only. A new perisarc is secreted in the proximal region, the ectoderm taking

on the characteristics of the covered ectoderm, and the edge of the perisarc is established at the usual proportional distance from the hydranth. If the piece is small, and tends to return to an embryonic condition, this is the proportional distance characteristic of the embryo. If it is long, so that very slight changes in

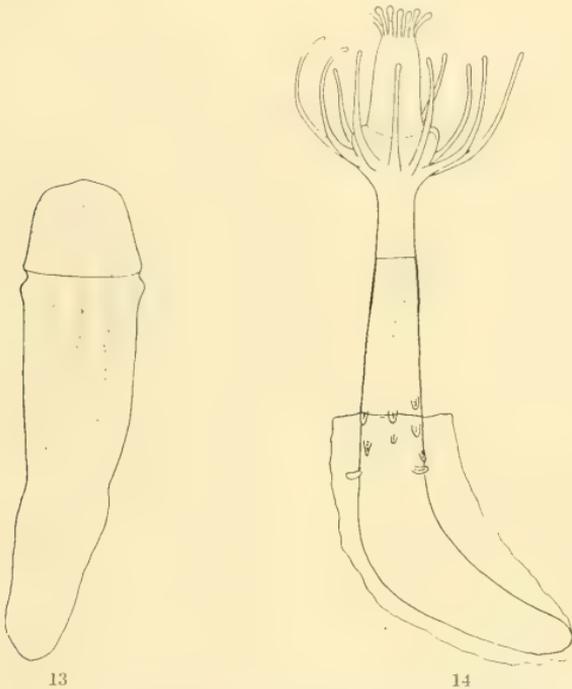


Fig. 13.—Hydranth developing in region of cut made just distal to oral edge of perisarc. Proximal tentacles appearing just below latter, gonosome buds just above.

Fig. 14.—Same hydranth as in fig. 13, twenty-one hours later.

form would produce the adult proportions, the adult ratio of naked to covered stem is approximated.

When the stem is cut obliquely, the process of regeneration differs with the obliquity of the wound. A number of stems were cut, so that the planes of the wounds made angles with the axes of the stems varying from thirty to ninety degrees. It was found

that when the angle was greater than forty to forty-five degrees, the tentacles almost invariably appeared parallel to the wound, the center of the latter marking the tip of the proboscis. The hydranth remained tilted on the stem to the end of the experiment, at which time it was well formed and symmetrical, though the tilt was always less evident in the extended than in the contracted polyp.

When the angle was less than about forty degrees, the tentacles appeared in circlelets in planes approximately perpendicular to the axis of the stem (as though the cut had been at an angle of ninety degrees), or somewhat tilted from the perpendicular, but away from instead of toward the wound. In fig. 1, both the distal and proximal tentacles appear above the lower limit of the wound, around an axis passing through the point of the stem, and therefore in a plane not quite perpendicular to the old stem axis. For a time the axis of the new hydranth in this case was not parallel with the stem axis. In two days, however, new tentacles had grown on the scar, all inequalities had vanished, and the remodelling of the stem as a whole had made the two axes coincident. This was the final result in all cases observed.

The position of the tentacles with reference to the obliqueness of the wound will be discussed further in connection with the subject of multiple monsters.

2. DEVELOPMENT OF THE HOLDFAST.

The root filaments, or frustules, that form the holdfast, develop throughout the life of the polyp. The details of their development, their position, histology, and the factors determining their form, have been treated in the preceding papers of this series, to which the reader is referred. The account there given will answer with but slight amendments for regenerating stems.

In the normal adult, the frustules occupy a zone girdling the column near its proximal end, and arise progressively toward the distal extremity. Proximally they are oldest and most completely functioning, becoming gradually less mature toward the distal boundary of the zone, where they may be said to be in a resting stage. Normally, their development is accelerated by the development and disintegration of the frustules proximal to

them. It can be shown experimentally that in a regenerating distal segment of the column, after a cut through the frustular zone, the removal of the older frustules accelerates the development of those near the wound; they may lengthen out within a day or two after the operation, when, without the operation their development would have been arrested for many days or weeks. It may be said, then, that the development of a given frustule is conditioned in part by the presence or absence of immature frustules proximal to it. On heteromorphic pieces, as will soon appear in the fourth paper of this series, frustules may arise in the region between the hydranths, usually in connection with a budding process, always after the piece has become attached to the substratum except in certain cases where an injury has been done the column in this region. The appearance of frustules in all such cases is an indication that physiological continuity between the heteromorphic individuals has been, in some degree, interrupted.

The position in which frustules arise on a segment regenerating as a single polyp, varies with the size, shape, and differentiation of the latter. On the segments of large diameter, they usually appear rather thickly over the rounded aboral end when the cut is transverse; at the lower end of the wound, that is, terminally, when the latter is oblique. They may arise singly, or in groups. On the segments of smaller diameter, in which regressive changes toward earlier stages of differentiation are more complete, the frustules may arise terminally or scattered. They reproduce the larval picture much more closely, however, and mass more rapidly in the zone characteristic of the species.

II. REGENERATION IN THE LARVA.

A number of experiments were made with larvae possessing 5-7 proximal, 4-5 distal tentacles at a period when the tentacles were being rapidly produced under the simplest histological conditions. It was expected, accordingly, that regenerative processes would closely approximate the normal development; and this expectation has been realized. A few typical instances may be given.

A larva with four distal and seven proximal tentacles (fig. 15)

was sectioned transversely at x , just below the oral edge of the perisarc. In forty-eight hours, the stem of the distal portion had increased in length and was anchored by a terminal frustule (fig. 15, d). The proximal portion was club-shaped, with hydranth cavity in the thickened oral region (fig. 15, p). Hydranth and

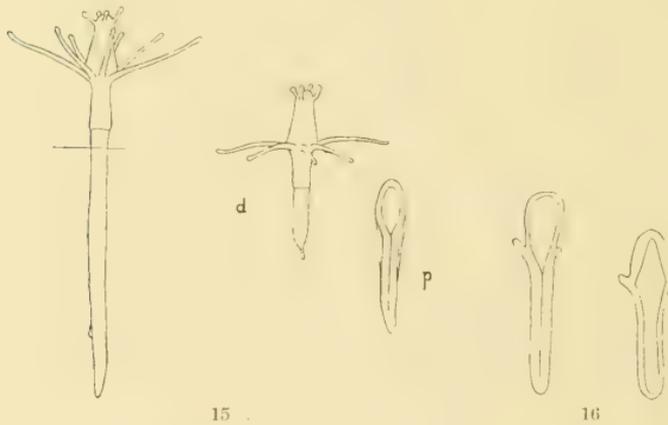


Fig. 15.—Larva, sectioned at x , with the condition of distal (d) and proximal (p) segments forty-eight hours later.

Fig. 16.—Regenerating larva, in two states of contraction, from proximal segment of stem after section just distal to edge of perisarc.

stem regions were proportioned as in the normal larva of about thirty hours, and the details of the development were the same for two days, when it died, after three distal tentacles had appeared. The stem had transformed directly into a larva, with the minimum of histological change. Similar transformations of pieces of adult stems will be considered in a later paper.

Fig. 16 represents in two stages of contraction, the proximal individual regenerating from the stem of a larva with six proximal and four distal tentacles, after section just distal to the oral edge of the perisarc. Here the direct transformation of the distal end into the hydranth has involved both naked and covered portions of the original stem, differing slightly in the character of their cells, especially in the ectoderm at the line of transition.

The hydranth is in every way normal, and the entire individual is essentially identical with a larva developed from the egg. Three proximal and three distal tentacles appeared on this individual.

Regeneration in the proximal portion of a larva with seven proximal and four distal tentacles, sectioned just below the edge of the perisarc led, in one week, to a normally proportioned larva with the original number of tentacles.

These cases will suffice to call attention to the ease with which larval stems regress to an earlier, non-tentacled stage, from which differentiation proceeds as in the original development. Just as the hydranth and stem regions are first defined in the larva by the slight differentiation of functional epithelial cells *in situ*, so the transformation of the distal end of a sectioned stem involves similar slight changes. The differences between the tissues of stem and hydranth are so small at this time as to facilitate the process.

III. CONCLUSION.

The plasticity which is so conspicuous a characteristic of the normal development of *Corymorpha* is also a striking feature of the regenerative development. The latter approximates the former, in fact, at every possible point, varying from it in detail only with the advancing differentiation of the regenerating piece. Tissues in larval stages of differentiation will produce larval structures in the larval way, whether in regeneration or normal development. Adult structures, arising on an adult stem, vary from this early normal type in the details of their development. The rootlets of the holdfast show the least difference in this respect, developing essentially as in the embryo throughout the life of the polyp. Yet they arise from larger fundaments involving larger numbers of cells. This is true of the tentacles also. Their development involves, further, a process more complicated in its details, evidently connected with the structure of the fully developed organ. Where the frustular axis is never composed of more than a single row of endodermic cells, whether in larva or adult, the axis of the tentacle is made up of rows of endodermic cells, especially numerous at the base. While, then,

the migration of endodermic cells one by one into the frustule occurs on polyps of all sizes, that method of establishing the axis has been abandoned in adult regeneration of the tentacles, an intrusion of a considerable group of cells in several rows leading more rapidly to the establishment of the structural characteristics peculiar to the tentacles of polyps the size of the regenerate.

I purposely avoid using the term "future significance," in this connection, since it possesses distinctly unfortunate connotations. The interpretation of the method of development exhibited by a tentacle is to be sought, not in the result of the process, but in the physiological conditions present in the regenerating piece and governing the process of regeneration. It is unfortunate to speak of a development proceeding toward a given end. Rather is the development proceeding in accordance with conditions existing in the developing region, with no possible reference to any end. I formulate this point of view here not for a novelty which it does not possess, but because it is so well supported by the facts obtained from *Corymorpha*. As will be shown more fully in another paper,⁸ regenerating pieces of *Corymorpha* shape themselves to a greater or less degree according to their length and diameter. In short pieces there may be very striking decrease in the diameter of the column and in the complexity of its structure. With this obvious simplification of structure, this retrogression toward the degree of differentiation characteristic of the larva, there is a corresponding decrease in the size of the tentacular fundaments and the tentacles developing from them. Short pieces do not always undergo a large degree of simplification. In such cases, the size of the tentacles is proportional to the diameter of the regenerating piece (which represents a certain degree of differentiation), not to its mass or volume.

If it is possible to make the facts obtained from *Corymorpha* the basis of a generalization, it would appear that the phenomena of regeneration are controlled primarily neither by considerations of future significance nor geometrical relations, but by the

⁸ See also Aspects of Regeneration in *Corymorpha*, Proc. 7th Int. Zool. Congress, 1910.

differentiation of the physiological mechanism in the region of development. This statement may be broadened to include all the phenomena of development, for the facts furnished by *Corymorpha* indicate that regenerative and normal development are but manifestations of the same fundamental property of living organisms, controlled by the same mechanism.

Berkeley, Cal.

May 26, 1910.

CONTRIBUTIONS FROM THE LABORATORY
OF THE
MARINE BIOLOGICAL ASSOCIATION OF SAN DIEGO.

XXXI.

NOTE ON GEOTROPISM IN CORYMORPHA.

BY

HARRY BEAL TORREY.

It was pointed out in a former paper,¹ that although the larva of *Corymorpha* exhibits a marked negative geotropism in locomotion,² attempts to determine whether gravity in any degree controlled the first locomotor movements of the embryo—as indicated, for instance, by the point at which it left the eggcase—gave answers in the negative. Recently the same experiment has been repeated; and though it has led to the same conclusion with respect to the point of emergence of the embryo, observations were made upon the development of the frustules that show gravity to be a factor controlling the direction of their locomotion.

Glass plates carrying several hundred freshly laid eggs were fixed at angles of about eighty-five degrees with



¹ Univ. Calif. Publ. Zool., 3, p. 260, 1907.

² See also Jour. Exp. Zool., 1, p. 419, 1904.

the horizontal. As soon as the embryos began to emerge, record was made of the numbers emerging respectively above and below the horizontal. The angle of divergence from the horizontal was usually small; very few approximated ninety degrees in either direction, and the neutrals were numerous. On one plate 20 emerged above, 20 below the horizontal; in another 19 above, 16 below. These were typical.

Gravity appeared to play no definite part in these phenomena. Over the frustules, however, it exerted a definite control. The frustules arose on the embryo always opposite the point of emergence, a position obviously not determined by gravity. But with elongation the clavate extremity of each frustule showed a distinct tendency to migrate downward, in many cases directly, even though the frustule arose at a point above the horizontal, as in the accompanying figure. The frustules accordingly exhibited a positive geotropism of definite mechanical value in the establishment of a holdfast firmly anchored over a considerable area.

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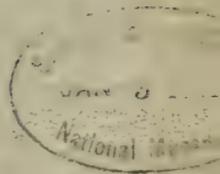
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SIGNIFICANCE OF WHITE MARKINGS

IN

BIRDS OF THE ORDER PASSERIFORMES.*

BY

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INTRODUCTION.

The present investigation was undertaken for the purpose of testing the validity of one of the earliest recognized categories of coloration, that of "Directive Markings," in a single order of birds. The term directive is used in the sense given it by Todd (1888) and not that of later writers (Marshall, 1902), who have used the word as expressing a different function of white markings in butterflies' wings—protective through drawing the enemy's attack away from vital parts. As here used it resembles the term recognition markings, and might be regarded as a

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synonym were there not good reasons for believing that the white markings exposed in flight serve rather as a clue to the *direction* taken by disappearing forms of birds, than as an aid to recognition of the species.

The investigation of the theory of directive markings in birds is hampered by the impracticability of carrying on field experiments such as those of Professor Reighard (1908) in pursuance of a similar inquiry in regarding warning coloration in fishes. Obviously it is out of the question to capture and liberate large numbers of birds with a view of detecting natural reactions under such artificial conditions. Field observations can, however, be offered, but these, in the nature of the case, do not afford evidence which is experimentally precise. Much depends upon the individual in the field—the personal equation. This source of error cannot be set aside by recourse to photographs, for the reason that the crux of the problem of directive markings, in so far as it concerns actual perception, is the effect of the *moving* white of the wings or other parts of the flying birds. Photographic plates show but the fixed effect of motionless patterns, and tell us nothing as to their efficacy in attracting visual attention to those patterns in motion.

I have, therefore, narrowed the field to a discussion of the *revealing* properties of flight-exposed white markings, and a study of the occurrence of such markings throughout the order Passeriformes, deducing from such occurrence a very suggestive correspondence of coloration with habit and feeding range. I have no direct evidence to offer as to the origin and mode of evolution of the white markings in birds. It may not be amiss, however, before proceeding further, to call attention to the limitations of explanations based on intrinsic factors alone.

INTRINSIC FACTORS IN THE EVOLUTION OF COLOR.

Riddle (1908) has proved that the melanin deposited in barbules varies with nutrition. He has also shown that fundamental bars in feathers may have their origin in rhythms of blood pressure. He thus establishes a presumption in favor of a continuously acting cause, apart from heredity, governing the degree of pigment deposited in birds' feathers. He is perhaps

right in asserting that further evolutionary studies of bird coloration should take their departure from this point. Nevertheless, if this be true, the gap between fundamental bars in feathers and the varied patterns in which white appears in every conceivable combination, often accompanied by intensification of pigment deposits in adjacent plumage, is one which can only be filled by difficult, expensive, and long continued research. In the meantime the discoveries of Thayer (1909) have greatly simplified the explanation from the selective standpoint, while those of Reighard point to an intrinsic tendency toward variety of pattern, needing only immunity such as that afforded by a coral reef, to develop colors and contrast that are neither adaptive nor due to sexual selection, and for which the physiological elements of nutrition, temperature, etc., do not account. Thus it is probable that the production of bars and stripes in feathers, and the rate of pigment deposit, are but secondary processes in a larger scheme. They may themselves be dependent on selective agencies which, if they exist at all, operate upon the whole organism.

If we were concerned here with the problem of bird coloration in general, we might linger upon examples of an apparent physiological basis for dark coloration, such as that of most species of *Corvidae*; these are largely omnivorous feeders, active and of exuberant vigor. But we should certainly be wrong if we failed to take account of the great degree of immunity which these birds enjoy from the attacks of raptorial birds, because of their size and aggressiveness. It is doubtful whether a seed-eating bird of delicate flesh and harmless disposition could have been permitted to develop such a black plumage as that of the raven, even had the physiological excuse for pigment excretion been as great in its case. Some other way would have been found, we may reasonably say, for the excretion of melanin, or else that type of bird would have become extinct for lack of protective coloration.

Similar difficulties involve such special varieties of the physiological explanation of color patterns as are connected with color distribution on the breast, crown, rump, etc., of birds, regarded as centers of high or of deficient circulation. A study

of any series of birds ranging through half a dozen families will give quite contradictory results. The crown will be found white on some, black on others; the breast usually light colored, but sometimes with a spot or chain of spots, or the throat spotted and the breast plain; and the rump white in some, heavily pigmented in others. Only patient ingenuity could long persist in seeking evidence for the correlation of pigmented areas with regions of fuller circulation; and the seeker for such evidence must shut his eyes to the patent fact that to produce a monochrome plumage such as that of the Leconte thrasher the dermal circulation must be uniform over the entire surface of the body; the existence of the theory would seem to demand the denial of such a condition.

Cunningham's suggestion (1900, p. 109) of a local stimulus incident to the elevation of plumes, etc., in courtship, is useful in accounting for the special development of certain epidermal features, but it sheds no light on the cause of intensification of color in the breeding male, in the plumage as a whole. The *vigor* theory attempts to do this, but leaves untouched a large number of instances in which there exists no sexual dimorphism in coloration, and still others in which the female takes over not only the color character, but also the courting antics of the male, leaving him the responsibility for incubation, as is the case in the knot (*Tringa canutus*).

The other class of intrinsic factors in color evolution grouped under the general term heredity, is one which this paper will merely recognize as existing, a potent but little understood influence. If it can be shown that white markings do not occur indiscriminately on birds of all habits and environments, but are associated with similar habits and ranges among birds not otherwise closely allied, it will be clear that they cannot be regarded solely as evidences of the manifestation of hereditary tendencies, but may fairly be attributed, at least in part, to selective influences.

Whatever the original cause of pigmentation or absence of pigment and its replacement by structural colors, and whatever the mode of evolution of such colors and combinations, the assumption of a principle of natural selection everywhere efficient

though sometimes *passive*, is justified by the facts as to the distribution of white patterns in passeriform birds of the United States.

WHITE MARKINGS AS VISUAL CLUES.

Coloration in birds, whatever its cause or the mechanism of its production, is conceded to be adaptive; it responds to their needs, forms a part of their life adjustments.

Concealment from its enemies is not the only need in a bird's life, not the only adjustment that affects color-patterns. The bird also needs to be made known to other individuals of its kind, and to other species associated with it; and this need has certainly been met. Just how it has been met depends upon the bird's manner of life, and upon its chosen habitat; this much we know. Without entering upon any disputed phase of the subject, we may state at the outset that the need exists and has been met, if not by special provision in coloration, at least by peculiarities of form and manner, or by qualities of voice.

The vital importance to a bird of seeing and being seen by its companions, hardly finds a parallel among the lower vertebrates; certainly not among most fishes, though a school of fishes bears a superficial resemblance to a flock of birds. Neither in organization nor in instinct does the one approach the high development of the other. A comparison of the brain of a perch with that of a pigeon shows the remarkable superiority of the latter in respect to cerebral development. The phenomena of the associations of a bird's life, the well-known facts of mutual independence in feeding, nesting and migration among nearly all of the class Aves, indicate the degree to which individualism has been subordinated, and coöperation of a certain kind developed.

There are, however, great differences within the class. If we are to make any comparison between these and the lower vertebrates, let it be between gregarious sea-birds and fishes, not between oscines and herring. Delicate life-adjustments are to be found among the higher genera of the perching birds that are missing from the more primitive divers or long-winged swimmers, as well as from fishes. The number and variety of perils

that daily surround our smaller land-birds, and the extent to which these may be diminished by the birds' keeping in touch with one another, point to the need of something more than concealing coloration, and admit of special adaptations that shall act in harmony with it and yet serve to reveal the bird to its kind.

Notwithstanding this distinction there will be some who fail to find in the life-relations of the Passeriformes anything to occasion the development of marks whose main function shall be that of revealing the birds to each other. Thayer (1900), exposing the weakness of the "banner-mark theory," indirectly implicates all theories of directive coloration, as well as that of warning colors, and has since made them the object of special attack (A. H. Thayer, 1909). The ground for his criticism—and it is a good one—is that birds, in order to profit by such aids as signs and signals, or at least to need them, must be less acute than human observers, who easily recognize species of birds by slight hints, such as are afforded by silhouette, by mode of flight, by mannerisms of one sort or another, rather than by special marks. This is so true that it must and does discredit the crude interpretations such as the title "banner-mark" suggests. We must distinguish between hypothetical functions, the creation of fancy, and a series of well-defined stripes, bars, or checks, which may be interpreted by any one of at least three categories, of which that of "concealing coloration" is only one.

Starting out with a presumption in favor of some form of revealing clues among the higher land-birds, and eliminating a terminology which has been misleading, it remains for us to determine, if possible, what these clues are, and whether color features form a part of them; if so, how this harmonizes with the function of the same or similar color features as concealing.

How do the birds of our woods and fields actually keep track of one another? Obviously to a great extent by vocal sounds which they utter frequently when moving about in the foliage, or in unison when leaving a feeding ground as a flock; by call-notes, when moving in pairs or companies; by location notes, when separated and seeking to come together. No one doubts the existence of such vocal clues or their vital necessity to birds belonging to the order under discussion.

There are birds that appear to depend almost entirely upon directive calls for keeping together; they have become habituated to feeding in close and uninterrupted cover where they see other birds only at close range, or very seldom at any great distance. Obviously they must keep within hearing, or be lost to their companions. Sound-clues are sufficient in their case. This is true of the bush-tit (*Psaltriparus minimus californicus*), some warblers, and nearly all the wrens. These are birds of plain colors, for the most part, and *without white patterns of any sort.*

Among arboreal birds of open feeding range that are constantly exposed to view, different conditions obtain. Call-notes are used, but glimpses of other birds in flight may be just as useful for purposes of direction, since such glimpses are frequently to be had. Sight plays a part of corresponding importance in the economy of bird-movement—to some extent replaces sound as a means of recognition.

As there is in the *general* coloration of open-ranging birds no response to the need of some rapid and easy means of recognition, and as the special color patterns that have heretofore been regarded as serving that purpose are now being claimed as a part of "concealing coloration" (A. H. Thayer, 1909), it might appear that the category of directive markings is soon to lose its status altogether. But general coloration is seen to be normally protective, for birds that need protection; and as for the special patterns, even a satisfactory demonstration of their "obliterative" effect does not warrant the conclusion that such is solely or mainly their effect in all cases.

For a discussion of the "disruptive effect of color patterns" the reader is referred to G. H. Thayer, 1909, pp. 77-79, and to A. H. Thayer, 1909, pp. 562 et seq. The evidence here offered of their value as *revealing characters*, must not be regarded as contradicting anything but the application of the "concealing" principle *to birds in flight.*

During the month of February the writer had under observation a flock of fifteen meadowlarks (*Sturnella neglecta*), which foraged in vacant lots and fields within the city limits of Berkeley. They were well spaced while feeding, and when disturbed some

would fly across a road into the neighboring field, where they would presently be followed by others. Their white tail-borders were often conspicuous during the entire flight of the birds, the tail remaining partly spread. As the meadowlarks on being flushed rose to the height of a man's head or higher, they must have seen the retreating forms from a similar view-point, *i.e.*, against a dark background. They would not commonly see them against the sky. For the birds themselves, white tail-borders would serve no purpose if not a directive one. Common observation does not seem to be at fault here, nor the term "white guides" ill-chosen.

It will be seen that the common assumption to the effect that white upon an object makes it conspicuous is well grounded in this case, for the reason that there is nothing corresponding to it in the usual background; further, because it does not in the least efface the outlines of the bird's contour, and finally because the bird is in motion at the time when the marking is displayed. We take note, therefore, of the distinction between a flight-exposed marking and one that appears at its full value when the bird is at rest. The former acquires added conspicuousness from the fact that a moving object fixes and holds the attention, indeed a white object moving across a dull background is the best mechanism that can well be devised for signalling at long distances.

Mr. A. H. Thayer, in the article to which we have just referred, indicates a supposed correlation between white rear-markings and the habit of nesting on the ground and flying from the nest when disturbed, stating that the markings are absent from birds that habitually run from it to escape a furred enemy. This would point to an obliterative function in the rear-mark, which shows white against the sky as seen from the level of a quadruped. This statement and conclusion seem to have been hastily made, for they apply only in the case of water birds such as rails, coots and gallinules which the author of the statement had in mind. The horned lark (*Otocoris alpestris*, all subspecies), the meadowlark (*Sturnella magna* and *S. neglecta*), and the vesper sparrow (*Pooecetes gramineus*), are among the

rear-marked birds that run from the nest, habitually, when disturbed.

In the foregoing paragraphs, the evidence for the revealing function of white rear-markings exposed in flight has been given as common observation, supplemented by psychological analysis of the facts; and the supposed instance of a concealing function in the case of certain birds has been shown to be quite inconclusive as regards perching birds. These considerations alone would point strongly to the other interpretation of the markings as advanced by Todd (1888), and rather generally accepted since. They are not, however, the only ones bearing on the question.

In giving recognition to the theory of directive markings of this type Wallace (1889, p. 222) alluded to their prevalent occurrence among flocking birds, as strengthening the theory, since it was just here that they would be of the greatest use. He did not, however, test the facts regarding such occurrence, or inquire into the question of a significant absence of white markings among non-flocking birds; nor has anyone else done so, heretofore. It is a test that is easily made by segregating all the birds bearing the white rear-marks, and making an inventory of those that remain. In order to judge of the significance of the resulting division it is necessary to know to what extent the birds thus arbitrarily separated differ in habits, especially as regards flocking; and this is not as easy as might be supposed, among the perching birds.

The accompanying list gives all the species of open-ground passeriform birds native to North America. Although the white tail-borders occur also on a few arboreal birds, these may be regarded as coming in the class of "top-patterns," which will be taken up in connection with birds of the forests and thickets.

PASSERIFORM BIRDS OF THE OPEN.

WITH CONCEALED WHITE.

ICTERIDAE	<i>Junco hyemalis</i> , all subsp.
<i>Sturnella magna</i>	<i>Junco aikeni</i>
<i>Sturnella neglecta</i>	<i>Junco phaeonotus</i> , 3 subsp.
ALAUDIDAE	<i>Junco bairdi</i>
<i>Otocoris alpestris</i> , all subsp.	<i>Junco insularis</i>
<i>Alda arvensis</i>	MOTACILLADAE
FRINGILLIDAE	<i>Anthus pratensis</i>
<i>Calcarius lapponicus</i>	<i>Anthus spraguei</i>
<i>Calcarius pictus</i>	<i>Anthus cervinus</i>
<i>Calcarius ornatus</i>	<i>Anthus rubescens</i>
<i>Rhyncophanes mccowni</i>	<i>Budytes flavus alascensis</i>
<i>Plectrophenax nivalis</i> , all subsp.	<i>Motacilla alba</i>
<i>Plectrophenax hyperboreus</i>	<i>Motacilla ocularis</i>
<i>Calamospiza melanocorys</i>	TROGLODYTIDAE
<i>Chondestes grammacus</i> subsp.	<i>Heleodytes brunneicapillus</i>
<i>Poocetes gramineus</i> , 2 subsp.	<i>Oroscoptes montanus</i>

WITHOUT CONCEALED WHITE.

FRINGILLIDAE	<i>Passerherbulus caudacutus</i>
<i>Leucosticte atrata</i>	<i>Passerherbulus nelsoni</i>
<i>Leucosticte australis</i>	<i>Passerherbulus maritimus</i> ,
<i>Leucosticte tephrocotis</i>	2 subsp.
<i>Leucosticte griseonucha</i>	<i>Peucaea aestivalis botterii</i>
<i>Passerculus bairdi</i>	<i>Peucaea mexicana</i>
<i>Passerculus princeps</i>	<i>Peucaea cassini</i>
<i>Passerculus sandwichensis</i> ,	<i>Aimophila ruficeps</i> , and subsp.
3 subsp.	<i>Aimophila carpalis</i>
<i>Passerculus beldingi</i>	<i>Spizella passerina</i>
<i>Passerculus rostratus</i>	<i>Spizella p. arizonae</i>
<i>Ammodramus savannarum austra-</i>	<i>Spizella breweri</i>
<i>lis</i>	<i>Spizella pallida</i>
<i>Ammodramus s. bimaculatus</i>	<i>Spizella atrogularis</i>
<i>Passerherbulus henslowi</i>	<i>Spizella pusilla</i> , and subsp.
<i>Passerherbulus lecontei</i>	

WITH WHITE IN NUPTIAL PLUMAGE.

ICTERIDAE
<i>Dolichonyx orizivorus</i>

FAINTLY MARKED WITH WHITE.

<i>Amphispiza bilineata</i>
<i>Amphispiza belli</i>
<i>Amphispiza nevadensis</i>

THE PROBLEM DISCUSSED FOR BIRDS OF THE OPEN.

The list shows five families that carry white markings, as against two families that do not. Of the twenty-six species or subspecies that carry them, all but three are to be classed as flocking birds; and even these are unquestionably gregarious to a marked extent. They may follow each other serially from place to place, as the cactus wren (*Helcodytes brunneicapillus*) and the sage thrasher (*Oroscoptes montanus*), or they may flock for a limited season, as the vesper sparrow (*Pooecetes gramineus*). The list contains the most perfect types of flocking birds in the whole order, such as the meadow pipits of the genus *Anthus*, and the horned larks (*Otocoris alpestris*), the lark sparrows (*Chondestes grammacus*), and all the juncos. Taken as a whole the white-marked group is unquestionably a flocking series. The bearing of this on the problem of white markings in birds is made clear by a comparison with the second list in which all but the species of two genera, *Leucosticte* and *Dolichonyx*, are seen to be of a non-flocking, skulking type, exemplified by the grasshopper and Savannah sparrows. Of these two exceptional genera the leucostictes are birds of the Boreal Zone exclusively, feeding on wind-blown insects at high altitudes; themselves conspicuous through their dark coloration and, by virtue of their Alpine-Arctic habitat, escaping most of the birds of prey. In short, they are of an environment altogether different from that commonly referred to as "open ground" in the sense of prairie and plains, and may be eliminated from the comparison. *Dolichonyx*, the bobolink, on the other hand, is a bird in its southern habitats palustrine, and only in its breeding range a bird of the meadows, where it displays the qualities of the second group, and is, in the case of the female, like them unmarked. The coloration of the male in breeding plumage evidently corresponds to that of the marsh blackbirds, to which it is closely allied. Our second list, then, if it be found to contain no flocking birds but the two just mentioned, is a striking proof of the absence of white markings in birds of the open ground that do not flock.

For an interesting exhibition of correspondence between habit and coloration, we turn to the grasshopper and Sandwich spar-

rows (*Ammodramus*, *Passerculus*). To quote a pertinent description: "Among the many inconspicuous, plain, little striped-backed sparrows of the Western United States, *alaudinus* is one of the commonest, plainest, and most inconspicuous. Anywhere in the meadows, prairie grass or weed patches, one may dart out from under your feet, zig-zag over the grass tops for a little way, and drop into the grass, hopelessly lost until he is again forced to take wing. At a distance you see and hear the birds giving their plain little song from the top of a tall weed or fence stake, but on nearer approach they drop into the grass and are lost." This characteristic is here emphasized because in all of the species mentioned as unmarked birds we shall find this or similar traits having a like bearing on our problem, while in all of them the typical flocking habit is lacking. The latter may be replaced by what might be termed a spurious form of flocking. As an instance: the rufous-crowned sparrow (*Aimophila ruficeps*), common on the Berkeley hills, may be surprised feeding in open patches when it at once takes to brushy cover far from which it does not stray; and when traveling moves in loose bunches of scattered individuals flitting from bush to bush unostentatiously.

Field ornithologists will observe, however, that others of the birds here mentioned are in some sense gregarious and gather at certain seasons for migratory or other movements. We have, however, evidence to the effect that such movements are sometimes, if not always, essentially different from typical flocking. Two western sparrows from the arid region are frequently seen in considerable numbers moving from their southerly winter range to a summer habitat to the northward. To the casual observer they might appear to be "flocking birds." A quotation from a memorandum made by Mr. Grinnell during the recent Museum Expedition to the region along the Colorado River, will show the error of such conclusions.

"Both *Spizella breweri* and *S. socialis* are now abundant on the desert in migrating flocks, not flocks, however, in the sense that pipits flock, but scattering companies. Each individual in a company moves wholly independently of any other; and they do not move en masse when alarmed, but helter-skelter in different

directions around and through bushes without call-notes. The helter-skelter disappearance of the flock certainly puzzles me and leaves me wondering where any one of the birds may be relocated. The eye gets no single permanent impression."

The behavior here cited is found when analyzed to be the exact opposite of what occurs in a typical foraging flock of birds having white rear-markings. In a flock of pipits the birds do not move independently, as a rule, in changing feeding grounds; they move in a body when alarmed, in one general direction, with great uniformity; not through bushes, always with call-notes, thus using every reasonable means of keeping the flock together. Under stress of alarm, growing darkness, or accidental scattering through considerable distance, the bright moving rear-marks must at least be of appreciable value to the bird in keeping others of the flock in sight. Whether or not that is the main reason for their existence is, of course, open to question.

THE PROBLEM DISCUSSED FOR ARBOREAL SPECIES.

We have been considering up to this point only the white markings characteristic of birds of the open. Among arboreal species the problem becomes more complicated both as to variety and distribution of the patterns and their possible significance. A form of "top-white" which can be shown to have the effect of making the wearer conspicuous is the basal patch of white upon flight feathers, usually the bird's primaries. It need not have this effect, however, when regarded as a fixed pattern against a foliage background. The latter gives it a disruptive value, as Thayer (1909) has shown for similar designs. In order to test the concealing values of this particular wing marking I mounted the green-backed goldfinch (*Astragalinus psaltria hesperophilus*) and the black-headed grosbeak (*Zamelodia melanocephala*) with spread wings and photographed them against sunlit foliage and backgrounds of leaves with spaces of sky showing through them. The birds were difficult to find in the resulting prints. Undoubtedly the photographs by their lack of relief exaggerated the concealing effect; yet that there is such an effect, in general, it is safe to admit.

When, however, the bird takes wing a wholly different principle comes into play. Suppose it be the goldfinch that has left its perch. What we actually see is a pair of wings opened and closed, alternately revealing and concealing a pattern which finds no background to blend with, because it consists of intermittent flashes of white, not haphazard like the ruffling of leaves, but rhythmical, emphasizing the essential features of the flying bird. This is not speculation but a description of facts—it is what one sees in the field. Those who are unfamiliar with the bird named may recall a similar flight-effect in the black-throated blue warbler (*Dendroica caerulescens*), and even more striking patterns in the common shrike (*Lanius ludovicianus*), the mocking-bird (*Mimus polyglottos*) and the “black mocker” (*Phainopepla nitens*). Concealed wing patterns are not the only ones that become conspicuous in flight. Obviously any white pattern located on primaries, secondaries, tertiaries, or wing coverts, will be expanded to the greatest extent during the motions of flight. It happens that even the comparatively obscure wing bars of the lazuli bunting (*Passerina amoena*) are easily distinguished as white bands on the flying bird. The white of scapular feathers, as in the magpie, is emphasized in the same way. Tail blotches on some warblers reveal their whereabouts as they flit from twig to twig, rather than conceal them. I have not, therefore, attempted to distinguish various classes of top markings among arboreal birds with a view to finding special functions for each. It is precisely such attempts that have discredited theories of the functions of these markings. Arbitrary distinctions do not occur in nature.

In order to give the reader an opportunity to review the entire series of white-patterned birds and to compare it with the complete series of those that lack top-white, I have prepared the accompanying lists. One family, the Mniotiltidae, has been reserved for more detailed study, and is given in a separate list. The ground-frequenting birds of the open have already been given. These lists, therefore, are fully representative of arboreal perching birds of the temperate zone, and include all species of the order Passeriformes regularly found in the United States.

PASSERIFORM BIRDS OF ARBOREAL HABIT.

A. BIRDS WITH WHITE WING OR TAIL MARKINGS.

FRINGILLIDAE

- Hesperiphona vespertina*
Pinicola enucleator leucura
Loxia leucoptera
Astragalinus tristis
Astragalinus psaltria
Astragalinus psaltria hesperophilus
Zamelodia melanocephala
Zamelodia ludoviciana
Passerina amoena
Sporophila morcelleti sharpei
Spizella monticola
Pipilo erythrophthalmus
Pipilo maculatus

LANIIDAE

- Lanius borealis*
Lanius ludovicianus

VIREONIDAE

- Lanius solitarius*
Vireo belli
Vireo huttoni

ICTERIDAE

- Icterus nelsoni*
Icterus melanocephalus auduboni
Icterus cucullatus sennetti
Icterus bullocki
Icterus parisorum
Xanthocephalus xanthocephalus

TROGLODYTIDAE

- Mimus polyglottos*

TURDIDAE

- Myadestes townsendi*
Planesticus migratorius
Planesticus confinis

SITTIDAE

- Sitta canadensis*
Sitta pygmaea

CORVIDAE

- Nucifraga columbiana*
Pica pica hudsonia
Pica nuttalli
Cyanocitta cristata

TYRANNIDAE

- Muscivora forficata*
Tyrannus tyrannus
Tyrannus verticalis
Myiarchus cinerascens
Myiarchus magister
Sayornis nigricans

SYLVIIDAE

- Polioptila caerulea*
Polioptila californica
Polioptila plumbea

HIRUNDINIDAE

- Hirundo erythrogaster*
Tachycineta thalassina

BOMBYCILLIDAE

- Bombycilla garrula*
Phainopepla nitens

PARIDAE

- Penthestes atricapillus*

B. BIRDS WITHOUT WHITE WING OR TAIL MARKINGS.

TURDIDAE

- Icterus naevius*
Hylocichla mustelina
Hylocichla fuscescens
Hylocichla guttata
Hylocichla ustulata
Hylocichla aliciae
Sialia sialis
Sialia mexicana

*Sialia currucoides**Cyanosylvia suecica robusta*

CINCLIDAE

Cinclus mexicanus unicolor

SYLVIIDAE

- Acanthopneuste borealis*
Regulus calendula
Regulus satrapa

CHAMAEIDAE

Chamaca fasciata

PARIDAE

Baeolophus bicolor
Baeolophus inornatus
Baeolophus atricristatus
Baeolophus wollweberi
Penthestes atricapillus
Penthestes carolinensis
Penthestes sclateri
Penthestes gambeli
Penthestes rufescens
Penthestes hudsonicus
Penthestes cinctus alascensis
Psaltriparus minimus
Psaltriparus melanotis lloydi
Auriparus flaviceps

SITTIDAE

Sitta carolinensis

CERTHIIDAE

Certhia familiaris

TROGLODYTIDAE

Dumetella carolinensis
Toxostoma bendirei
Toxostoma redivivum
Toxostoma lecontei
Toxostoma crissale
Toxostoma cinereum
Toxostoma longirostre
Toxostoma rufum
Toxostoma curvirostre
Salpinctes obsoletus
Salpinctes guadalupensis
Catherpes mexicanus
Thryothorus ludovicianus
Spiza americana
Arremonops rufivirgata
Guiraca caerulea
Passerina cyanea
Passerina versicolor
Passerina ciris
Pyrhuloxia sinuata
Pipilo fuscus
Pipilo crissalis senicula
Oreospiza chlorura

TANGARIDAE

*Piranga ludoviciana**Piranga erythromelas**Piranga hepatica**Piranga rubra*

ICTERIDAE

Molothrus ater
Tangarius aeneus involucratus
Agelaius phoeniceus
Agelaius gubernator californicus
Agelaius tricolor
Euphagus carolinus
Quiscalus quiscula
Quiscalus major macrourus

CORVIDAE

Cyanocitta stelleri
Aphelocoma woodhousei
Aphelocoma cyanotis
Aphelocoma californica
Aphelocoma texana
Aphelocoma sieberi
Aphelocoma insularis
Xanthoura luvuosa glaucescens
Perisoreus canadensis
Perisoreus obscurus
Corvus corax
Corvus cryptoleucus
Corvus brachyrhynchos

TYRANNIDAE

Tyrannus melancholicus couchi
Tyrannus vociferans
Pitangus sulphuratus derbianus
Myiodynastes luteiventris
Myiarchus crinitus
Myiarchus lawrencei olivascens
Sayornis phoebe
Sayornis saya
Nuttallornis borealis
Myiochanes pertinax pallidiventris
Myiochanes virens
Myiochanes richardsoni
Thryomanes bewicki
Thryomanes leucophrys
Thryomanes brevicauda
Troglodytes aedon
Troglodytes parkmani
Nannus hiemalis
Telmatodytes palustris
Cistothorus stellaris

FRINGILLIDAE

Pyrrhula cassini
Carpodacus purpureus
Carpodacus cassini
Carpodacus mexicanus frontalis,
 and other subsp.
Carpodacus amplus
Loxia curvirostra
Acanthis linaria
Acanthis hornemanni
Spinus pinus
Astragalinus lawrencei
Cardinalis cardinalis
Melospiza melodia
Melospiza georgiana
Melospiza lincolni
Zonotrichia albicollis
Zonotrichia leucophrys
Zonotrichia coronata
Zonotrichia querula
Passerella iliaca
Empidonax difficilis
Empidonax flaviventris
Empidonax traillii
Empidonax minimus

Empidonax hammondi
Empidonax igrigiti
Empidonax vireescens
Empidonax griseus
Empidonax fulvifrons
Pyrocephalus rubinus mexi-
canus
Camptostoma imberbe

HIRUNDINIDAE

Progne chalybea
Progne subis
Progne cryptoleuca
Iridoprocne bicolor
Riparia riparia

BOMBYCILLIDAE

Bombycilla cedrorum

VIREONIDAE

Vireosylva olivacea
Vireosylva philadelphica
Vireosylva gilva
Lanius flavifrons
Vireo atricapillus
Vireo griseus
Vireo vicinior

The facts as to the distribution of white markings among birds of the various local associations may be gathered from a study of the first list. It also affords a basis for finding any agreement of physical or temperamental characters among birds so marked, or the occurrence of habits that may have a bearing on their coloration. A similar purpose is served by the second list—with this drawback: it includes a number of color features that may be of a value similar to that of white patterns, and even more *revealing*. Accordingly we need not be surprised if we find among species bearing such features, for example, nearly all the crows and blackbirds, the habits and distribution that are characteristic of white-marked birds.

There is, moreover, a correspondence, especially among the unmarked groups, that appears to be due primarily to intrinsic influences producing family characters; like all color characters these are too inconstant for the systematist to utilize. Still, in some cases they suggest a persistence of some ancestral type dominating extrinsic influences. Such a correspondence is seen

in the family of wrens which an amateur can usually recognize by noting the superficial color pattern. A similar tendency appears in the vireos and also in the flycatchers. If, therefore, we find white patterns conspicuously lacking among Troglodytidae, Vireonidae and Tyrannidae, we are bound to consider whether or not this may be partly due to the stability of a type (intrinsic influence) or to selective influences alone. The occurrence of a perfect adaptation at variance with the type in the bleached, sand-colored monochrome of the Leconte thrasher (*Toxostoma lecontei*) indicates that the Troglodytidae may not be exempt from the strict enforcement of the principles of adaptive coloration, where the conditions of their life demand it.

There are some relative differences among birds that might conceivably enter into the explanation of correspondences in color, but apparently do not to an appreciable extent. Size is one of these. The only way in which it appears to affect coloration is by affording immunity from enemies. Size combined with vigor and aggressiveness opens the way for conspicuous coloration. But the need of concealment on the part of the aggressor neutralizes the effect of this immunity in most cases. The raven is one of the exceptions within the order of perchers, and the condor, Egyptian vulture, and turkey buzzard, outside it. These are birds that need no concealment for aggression, but profit by a conspicuousness that makes them recognizable to each other at great distances.

As for warning coloration, there seems no reason for believing that it occurs among perching birds. Were the principle thoroughly established we might be justified in regarding the magpie as an instance; but since other functions may readily be assigned to the contrasts in its plumage, and since these are not necessarily utilitarian, as the bird is largely "immune," the whole hypothesis is negligible for the birds under discussion.

Temperamental differences form another set of elements to be considered. A search for correspondences in this direction shows at least a few well attested instances of boldness of disposition accompanying the supposed conspicuousness of plumage. Such are the kingbird (*Tyrannus tyrannus*), the scissor-tailed flycatcher (*Muscivora forficata*), the mockingbird (*Mimus poly-*

glottos), the magpie (*Pica hudsonia*), and the shrike (*Lanius borealis*). These are interesting cases, but little can be inferred from them as to the significance of white markings in the group at large.

It is in the correlation of special color features with special feeding and breeding ranges that we get the first clear indication of a large underlying principle determining which birds shall possess the white pattern and which shall not. The top-marked finches are seen to be birds of open woods mainly, largely of roving disposition and wide feeding range. Unmarked species of the family are mainly birds of low zones and narrower feeding beat. Only two of the first list are characteristically low rangers and given to covert-seeking: these are our eastern and western white-marked towhees (*Pipilo erythrophthalmus* and *P. maculatus*). On the other hand nearly all of the second list are either confined to close foliage of medium height, or belong to such associations as the rank growth of humid regions, the dark borders of shady swamps, or thickets of the chaparral belt. They are the thrushes, painted in monochrome above; warblers, lacking top-patterns; wrens with their finely barred color scheme; flycatchers with dull olivaceous or other uniform shadings. These are correspondences that surely have significance, and require for their interpretation something more than the older theories of coloration could offer.

Finding such good illustrations of the disruptive effect of white or bright patterns among animals and birds, the authors of "Concealing Coloration in the Animal Kingdom" (Gerald and A. H. Thayer, 1909), have come to believe that no other explanation is needed to account for the presence of top-white in birds that show themselves against the sky, than natural selection working through this means. Their belief accords with the conditions just cited. It does not, however, take account of the fact already mentioned that markings often become conspicuous during the flight of the bird, nor does it take note of the correlation that has been shown to exist among open-ground birds, of flight-revealed markings with the flocking habit—a condition which we shall also find largely present among the arboreal birds. In the use of these lists of birds to determine the latter point,

the very arbitrariness of the grouping tends to be misleading. A list of all perching birds that have color features tending to conspicuousness in flight (whether white or some other color), would correspond much more nearly to a complete list of the flocking birds. It would include the gregarious species of the family Icteridae which mainly lack white patterns. It would include the pine siskin (*Spinus pinus*) which has yellow wing markings instead of white. Yet, even as it stands, the list is very suggestive. When we consider the value to all birds ranging in the open foliage of instant recognition at a distance, and sight-clues for the purpose of keeping together, we shall not easily believe that wing and tail white are solely features of concealing coloration. Their revealing function during flight is entirely in harmony with their concealing functions when at rest.

An apt illustration of this harmony of functions is found in the following description of the western evening grosbeak (Bailey, 1902, p. 308):

“On a Sierra grade we have passed a flock busily gathering wild cherries in a bush beside the road, and when camped under the firs of Mt. Shasta have had wandering bands stop for a drink from the camp brook, delighting us by their striking yellow and white plumage. Although they are so highly colored and in flight their white wing patches make such prominent directive marks, this very yellow and white coloration often becomes positively protective. While watching the birds on Mt. Shasta one day, I was struck by the conspicuousness of one that flew across an open space. As it lit on a dead stub whose silvery branches were touched with yellow lichen, to my amazement it simply vanished. Its peculiar greenish yellow toned in perfectly with the greenish yellow of the lichen.”

It is of interest to note that the above observation was made before the disruptive effect of white patterns had been demonstrated by Thayer (1909), or the theory of their directive function seriously questioned. There could be no better instance than the one cited, of a double office performed by a single color feature—revealing in flight, concealing when in repose. Precisely this relation, I believe, exists through the group as a whole

SPECIAL STUDY OF THE MNIOTILTIDAE

For a more minute study of the relation of white color marks to a bird's habitual range I have chosen the American wood warblers. Not only are the members of this family very well distributed among the more or less well defined strata of local vegetation, but, unlike the Sylviidae or old world warblers, they show the highest degree of specialization both in regard to variety of pigments and to white patterns. It seemed worth while, therefore, to investigate the actual distribution of the species in the three categories of high or open foliage, medium, and low or close coverts. The results of such a study are embodied in the following table in which the mean height of the bird's occurrence has been compared with that of its average nesting site as recorded by numerous observers, and its feeding beat gauged with some accuracy. While it has not always been possible to distinguish clear lines of demarkation, on the whole there is a surprising agreement among writers who allude to the feeding levels of the warblers.

WARBLERS WITH WHITE WING OR TAIL MARKINGS.

OF HIGHEST RANGE.			
	Level of Nest.		Level of Nest.
<i>Vermivora bachmani</i>	1'-3'	<i>Dendroica chrysoparia</i>	15' av.
<i>Compothlypis americana</i>	8' +	<i>Dendroica occidentalis</i>	2'-45'
<i>Compothlypis a. usnceae</i>	8' +	<i>Dendroica caerulesca</i>	40'-70'
<i>Compothlypis pitiayumi</i>		<i>Dendroica fusca</i>	20'-84'
<i>nigrilora</i>	8' +	(Syn. <i>blackburniae</i>)	
<i>Peucedramus olivaceus</i>	30'-50'	<i>Dendroica dominica</i>	20'-90'
<i>Dendroica magnolia</i>	3' +	<i>Dendroica graciae</i>	50'-60'
<i>Dendroica tigrina</i>	3' +	<i>Dendroica castanea</i>	15'-20'
<i>Dendroica auduboni</i>	4'-50'	<i>Dendroica striata</i>	1'-10'
<i>Dendroica nigrescens</i>	5'-52'	<i>Dendroica vigorsi</i>	8'-80'
<i>Dendroica virens</i>	3'-40'		
OF INTERMEDIATE RANGE.			
<i>Mniotilta varia</i>	ground	<i>Dendroica kirtlandi</i>	ground
<i>Protonotaria citrea</i>	5'-25'	<i>Dendroica discolor</i>	1'-12'
<i>Vermivora chrysoptera</i>	ground	<i>Wilsonia citrina</i>	1'-5'
<i>Vermivora pinus</i>	ground	<i>Cardellina rubrifrons</i>	ground
<i>Dendroica coronata</i>	4'-20'	<i>Setophaga picta</i>	ground
OF LOWEST RANGE.			
<i>Dendroica caerulescens</i>	1'-3'	<i>Dendroica palmarum</i>	ground
<i>Dendroica pensylvanica</i>	2' av		

WARBLERS WITHOUT WHITE MARKINGS.

OF INTERMEDIATE RANGE.

	Level of Nest.		Level of Nest.
<i>Fermivora peregrina</i>	ground	<i>Oporornis tolmiei</i>	6"-4'
<i>Fermivora celata cclata</i>	ground	<i>Wilsonia pusilla chryseola</i>	3'-5'
<i>Fermivora c. lutescens</i>	ground	<i>Wilsonia canadensis</i>	ground
<i>Fermivora c. sordida</i>	2'-8'	<i>Setophaga ruticilla</i>	2'-30'
<i>Fermivora rubricapilla</i>	ground	<i>Dendroica aestiva</i>	3'-25'
<i>Oporornis philadelphia</i>	6'-20'		

OF LOWEST RANGE.

<i>Helinaia swainsoni</i>	ground	<i>Oporornis formosa</i>	ground
<i>Helmitheros vermivorus</i>	ground	<i>Oporornis agilis</i>	ground
<i>Fermivora virginiae</i>	ground	<i>Geothlypis trichas</i>	ground
<i>Fermivora luciae</i>	2'-6'	<i>Geothlypis t. occidentalis</i>	6"-5'
<i>Seiurus aurocapillus</i>	ground	<i>Icteria virens</i>	1'-5'
<i>Seiurus motacilla</i>	ground	<i>Wilsonia pusilla</i>	ground
<i>Seiurus noveboracensis</i>	ground		

Of the fifty-seven warblers here treated, thirty-three have well-defined white top-patterns. Of these, twenty are high rangers, a number of them emphasizing their preference by choosing a nesting site at the extraordinary level of seventy, eighty, or even ninety feet from the ground.

It is a curious fact that a careful sifting of the recorded observations discovers no unmarked warbler belonging properly to the high feeding beats. A few, such as *Vermivora cclata*, occur at variable heights and may be seen in the tops of trees; but these usually nest low, upon or near the ground, and are usually assigned an intermediate feeding beat. It seems to be true on the whole that the plain "protectively colored" warblers are unrepresented in the upper strata of our deciduous forests, that they are common at the medium levels, and, as shown in the table, belong mainly in the lower stratum, that of thickets, brush areas, tangles about marshy places. Briefly put, the situation among warblers seems to be: no plain plumages seen at the highest levels. But the converse—no marked plumages at lowest levels—is not strictly true. No arbitrary line is drawn. About the same number of the marked and unmarked occupy the intermediate feeding beats and nesting sites. It seems reasonable to infer, however, from the results shown by this tabulation that

top-patterns have decided utilitarian value to high-ranging warblers. That the value of white patterns is at a minimum for ground nesters and low feeders, seems to be as clearly demonstrated.

For those who find the arguments for the concealing functions of top-white conclusive, the table will primarily serve as evidence of the correctness of Mr. Thayer's interpretation. And such they are in so far as they corroborate the view that birds often seen against open foliage with sky-illuminated spaces should have and do have bright patches imitating these spaces. There may be no opposing view that can rob this one of its convincing power once it has been perceived. There is, however, a further consideration deserving attention.

High and open foliages involve more than a broken sky and leaf background with the need for imitating them. They involve wider spaces to travel; the ability to see companions at a greater distance; the need of seeing and keeping track of them by other means than call-notes; the long continued habit of so doing.

The warblers are among the most mutually dependent of birds, the least solitary, migrating in flocks and social during the daytime-portions of their travel. Among the least social the shyest and most retiring of the family are the plain or somber-hued species, including the so-called water thrushes (*Sciuus noveboracensis* and *S. motacilla*) and the Connecticut and mourning warblers (*Oporornis agilis* and *O. philadelphia*). The bolder, the most familiar, are in the *Dendroica* group (*Dendroica coronata*, *maculosa*, *auduboni*, etc.). This need not be a mere coincidence. We have noticed the same tendency in the order at large. With a preference for close, leafy coverts and secluded forest ways go the somberer tones, the monochrome coloration, and shy, furtive habits. With a preference for open woods and roving ways, greater distances and separations to be adjusted, have come the greatest variety of top-patterns among birds, many of them showing excellent devices for a revealing flight from the opening wing.

SEXUAL SELECTION AS AFFECTING WHITE PATTERNS.

It remains for us to touch on the question, does sexual selection enter into the problem of white patterns? For open-ground birds we can promptly answer that it does not. There are, however, many instances among arboreal birds where the white marking is intensified in the male. This very fact militates against the physiological contention that greater vigor in the male sex accounts for all color differences. White blotches or bars are caused by the absence of pigment. Were it not for the more intense coloration of other parts we might conclude on this basis that the white-marked male is deficient in vigor. It also argues against the view that white patches afford the best possible concealing pattern, for in that case the female should not have them obscured. Adherents of the directive theory may find support for their views in the fact that white wing bars do actually persist in the female in many cases, as in the pine grosbeak (*Pinicola enucleator*) and the white-winged crossbill (*Loxia leucoptera*) and others, so that it cannot be regarded as due solely to sexual selection. The analogy in the case of open-ground birds where both sexes are alike, as a rule, strengthens the directive interpretation. Further, if we are right in assuming that the male is the more vigorous and the leader of bird movements, then there is ground for believing that white markings, even though intensified in the male, are directive in some sense. That such a relation exists among warblers was the belief of Dr. Coues when he wrote the following paragraph descriptive of the warbler family:

“Some travel true to the meridian in hours of darkness, stopping at daybreak from their lofty flights to rest and recruit for the next stage of the journey. Others pass more leisurely from tree to tree in a ceaseless tide of migration, gleaning as they go. The hardier males in full song and plumage lead the way for the weaker females and yearlings.”

DIRECTIVE MARKINGS OUTSIDE THE ORDER
PASSERIFORMES.

An instance of revealing coloration outside the order Passeriformes seems worth citing since the very existence of a principle of directive coloration has been questioned (Thayer, 1900). The wings of the nighthawks, both eastern and western species, are, as is well known, marked with a single white spot in each. Far from tending to merge the bird's contour with anything in the background, these spots easily reveal and characterize the bird to observers. Even were there need for the nighthawks in their swift, crepuscular flights to be hidden from winged pursuers, it is hardly credible that the spots should serve this purpose. The Texas nighthawk (*Chordeiles acutipennis texensis*) is known to have a habit which gives revealing effect to the white throat-patch, as well as that on the wing. This throat patch is concealed as the bird takes its daytime rest in the open; but when surprised upon its nest it adopts the familiar wounded bird tactics to divert attention. After fluttering a short distance it faces the intruder, elevates and depresses its breast, thus appearing to make every effort to hold the attention of its enemy. Such a motion adds decidedly to the conspicuousness of the white patch. This effect of a pattern and corresponding behavior of the bird is perhaps unique, but it seems at least to establish a case of the revealing function of white.

CONCLUSION.

This paper has attempted to test the validity of the older interpretation of white markings in birds by analyzing their mode of occurrence in a single order, and to harmonize it, if valid, with a newer and apparently contradictory interpretation. It has shown that there is good ground for believing that flight-exposed markings, whatever their mode of evolution, are of actual utility to birds as sight-clues, whether occurring in the comparatively uniform rear markings of the open ground species, or the varied top patterns of the arboreal. It has called attention to a decided correlation of the markings with the habit of

flocking, as well as with that of open ranging. It has shown that sexual selection can only have operated in producing a more sharply defined pattern in the male, but cannot account for the existence of the pattern itself. Recent views as exemplified in Thayer (1909) as to the concealing effect of white markings have been regarded as greatly simplifying the problem and aiding our understanding of the possible meaning of the patterns. This newer view, however, is found to be in perfect accord with the older one known as the Theory of Directive Markings. It restricts the application of the latter, however, to patterns that can be shown to be conspicuous.

These considerations cannot be regarded as affording evidence in an ultimate sense. They lead at best to the provisional modification of an interpretation that was open to criticism, and tend to check over-emphasis upon the concealing principle in animal coloration. Doubtless they fall short of reaching the full meaning of the white or bright patterns of passeriform birds. Possibly the interpretation of diverse coloration as having developed under conditions of comparative immunity, from such sources of attack as those to which terrestrial animals are subject needs greater emphasis than has been given it.

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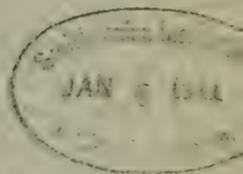
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THE CYCLOSTOMATOUS BRYOZOA
OF THE WEST COAST OF
NORTH AMERICA

BY

MALICE ROBERTSON



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THE CYCLOSTOMATOUS BRYOZOA OF THE
WEST COAST OF NORTH AMERICA.

BY

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This paper is the third of the series by the writer treating of the bryozoa of the Pacific coast of North America, and includes the *Cyclostomata* found in the present collections of the University of California and the University of Washington.

The sub-order *Cyclostomata* is characterized by great simplicity of structure. The zoœcia are calcareous tubes with circular apertures, but without accessory markings, or appendages, such as we find in the *Chilostomata*. This very simplicity of structure makes it difficult to find suitable taxonomic characters. Waters ('84), in his discussion of the classification of the fossil *Cyclostomata*, mentions the importance of the ovicell as a diagnostic mark, but regrets its frequent absence, or mutilation among fossils. Fortunately, among recent and living *Cyclostomata*, the ovicells, or œcia, are frequently numerous, and when they are present they form a satisfactory character because of their constancy of form. Harmer ('91, '96, '98) has used the shape and position of the œcium, and especially of its aperture, to determine the species of three large genera of the Cyclostomes: *Crisia*, *Tubulipora*, *Lichenopora*. This method has proved most satisfactory in identifying the present collection, and œcial characters have been used as far as possible in the determination of all species. It remains true, however, that in some cases when œcial characters were not available, characters which are considered less stable have been used. Thus, in *Idmonca*, *Entalophora*, *Mesenteripora* and *Heteropora*, mode

of growth, arrangement of zoëcia, etc., have had to be taken into consideration, rather than the position or form of the ovicell, or of its aperture, since in these genera either the ovicell or its aperture, or both, are unknown, or known to a limited degree.

Since the ovicell is so important a feature of the cyclostomatous colony it may be well at this time to give a general description of it. The fullest and most complete account of it in certain typical cases may be obtained from the work of Harmer already referred to. That investigator ('91) has shown conclusively that in one genus, *Crisia*, the oëcium is a modified zoëcium. At a definite place in an internode a zoëcium becomes inflated (pl. 18, fig. 2, *oe.*) and acquires a tubular aperture which may remain circular in shape or become more or less compressed. In the genus *Tubulipora*, the same investigator ('98) has shown that the oëcium is an inflated zoëcium which, however, may grow large and cover a considerable portion of the surface of a colony by extending into the spaces between the rows of zoëcia (pl. 21, fig. 25, *oe.*). In *Lichenopora*, Harmer ('96) describes the oëcium as a complex structure "whose growth is intimately connected with the development of the external features of the colony." That is, it begins to form when the colony contains but three or four zoëcia and increases in size as new zoëcia arise, there being but one oëcium to each colony. In matured colonies this ovicell occupies a central position, it being the "free central area" of Hincks ('80). It is further characterized by some writers, e.g., Busk ('75), and Waters ('90), as possessing *cancelli*. These cancelli are the reticulations which may be seen in the ovicell of a full grown colony of *Lichenopora* (pl. 25, fig. 48, *oe.*). This reticular appearance is due to secondary thickenings or bars supporting or strengthening the roof of the ovicell which forms around the zoëcia and over the spaces between them, as well as over the central space of the colony from which the first or oldest zoëcia radiate (pl. 25, fig. 48, *cen. can.*).

The cyclostomatous ovicell in all cases observed, belongs to one or other of the two kinds briefly described above. That is, it is either an enlarged zoëcium, *gonocium* of Hincks ('80), or what is often spoken of as an inflation of the surface of the colony, *gonocyst* of Hincks. Even in the latter case, according to Harmer, the ovicell arises in, or is in close connection with a

fertile zoëcium which gives rise to the ovum from which the embryos are developed. Unlike the *Chilostomata*, few of the zoëcia of the *Cyclostomata* produce ova, and the number of ovicells of a given colony correspond to the number of fertile zoëcia. While relatively few ovicells may be produced, the number of larvae to which a colony may give rise, however, is by no means small. This is due to the interesting process of polyembryony which occurs quite generally throughout this sub-order. As has been shown by the present writer (:03), not only are relatively few ova produced, but of these still fewer come to maturity. Each ovum which matures does so in an ovicell or zoëcium, in which it develops into an embryo of relatively enormous size. The outline of such an embryo not yet of full size is shown on pl. 18, fig. 4, *emb.* This, instead of forming a single larva, proceeds to bud, or fragment, each bud, or secondary, or even tertiary embryo giving rise to a larva. Thus, each egg produces a large number of embryos, as many as 150, or more. These secondary embryos remain within the sheltering walls of the ovicell until they acquire cilia and are able to live a free existence, when they are set free, each one capable of producing a new colony. In the large zoëcium of *Lichenopora*, the large embryo may often be found sending its arms, or branches, into the vacant spaces between the rows of zoëcia. The larvae escape from the zoëcium by an opening which has been found to be characteristic and to be useful in diagnosis. For this zoëcial aperture Harmer has devised a terminology which has been adopted throughout the descriptions of species in this paper. The opening from the zoëcium, *i.e.*, the passage by which the larvae escaped from the ovicell, is the *zoëciostome*. This may or may not possess a tube or funnel. If a tube is present through which the larvae must pass before reaching the outside this is simply known as the tube of the zoëciostome. Its external opening is known as the *zoëciopore*. Sometimes the tube is absent and zoëciopore and zoëciostome coincide. The tube of the zoëciostome frequently resembles a zoëcium in shape and size, and in the case of large ovicells which include numerous zoëcia it may be almost indistinguishable from a zoëcium. It may usually be detected, however, by the size and number of the pores piercing its wall. The tube of the zoëciostome being a direct continuation

of the wall of the oecium possesses pores similar to those of the oecium, and the wall of the oecium is easily seen to possess more numerous and larger pores than does the wall of the zoecia.

There are included in this report three families, eight genera, and twenty-one species. Of these, one genus and eight species are new to science. The new genus, *Crisulipora*, has puzzled the writer from the fact that it possesses characters which relate it to two families, to both the *Crisiidae* and to the *Tubuliporidae*. Its zoecial and oecial characters, however, seem to relate it more closely with the *Tubuliporidae*, where it is accordingly placed. The remaining new species are formed strictly upon oecial features described above, and in conformity with the investigations and judgment of the later bryozoologists. Of the species reported, twelve are restricted to this coast, five are cosmopolitan, two are circumpolar, while two are reported from Australian waters. As in the case of some of the *Chilostomata*, a few of the species seem to follow the coast line of America, being reported from the eastern shore of South America as well as from our shores, and if search were made for them, it is probable they would be found also on the west coast of South America.

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PHYLUM MOLLUSCOIDA Milne-Edwards.

Class **Bryozoa** Ehrenberg.Sub-Class **Ectoprocta** Nitsche.Order **Gymnolaemata** Allman.Sub-Order II. **CYCLOSTOMATA** Busk.

Gymnolaemata with calcareous, tubular zoecia possessing a plain, inoperculate orifice. Ova matured in special chambers called oecia, or ovicells which are sometimes modified zoecia, sometimes inflated portions of the surface of colony or internode.

Crisiidae Busk.*Les Crisics* Milne-Edwards, 1838.*Crisidae* d'Orbigny, 1850-52.*Crisiac* Smitt, 1865.*Crisiidae* Busk, 1875.*Crisiidae*, Hincks, 1880.

Zoarium dendroid, calcareous, composed of segments united by corneous joints. *Zoecia* tubular, disposed in one or two series. *Oecium* an enlarged zoecium.

As in the preceding papers of this series, the classification and method used by Hincks ('80) have been adopted wherever possible, together with synonymy, and in many cases diagnoses, with such changes as the present state of our knowledge demands.

Crisia (part) Lamouroux.*Sertularia* (part) Linnaeus, 1758.*Cellularia* (part) Pallas, 1766.*Cellaria* (part) Ellis and Solander, 1786.*Crisia* (part) Lamouroux, 1816.*Crisia*, Milne-Edwards, 1838.*Crisia*, d'Orbigny, 1850.*Crisia*, Smitt, 1865.*Crisia*, Busk, 1875.*Crisia*, Hincks, 1880.*Crisia*, Harmer, 1891.

Zoecia in a single series or in two alternate series.

The genus *Crisia* is easily identified by the shape and arrangement of its zoecia. The whole number of species falls into two

groups: those in which the arrangement is predominantly uniserial, and those in which it is biserial. In species of the uniserial type, the branches consist of internodes which typically possess a single zoëcium, this bearing a branch on each side, giving to the colony the appearance of being composed of triangular masses of zoëcia (pl. 18, fig. 2). While this arrangement of zoëcia is predominant in the uniserial type found here, there is more or less variation, especially in the younger portions of the colony. Internodes sometimes occur which contain four or five zoëcia which assume a more or less alternate arrangement. Moreover, the oëcial internode always consists of at least three members, the position of the oëcium being definite and constant.

In *Crisias* of the biserial type, the arrangement of the zoëcia is extremely regular, and the general appearance of branches and internodes is so similar that it is impossible to identify species upon either zoarial, or zoëcial characters alone, as has been commonly attempted by many of the older writers. Here as throughout the *Cyclotomata*, oëcial characters are of most importance, *i.e.*, position and shape of ovicell, and especially of its aperture. In addition, other characters have been studied and are considered useful. As Harmer ('91) has suggested, the number of zoëcia in an internode together with the character of the branching are worth considering and are frequently useful for diagnostic purposes. In our species the nature of the branching in the oëcial internode has been found especially characteristic, and is offered as another useful character of perhaps greater importance than the method of branching as a whole. It is found that in four species, three, and sometimes four branches occur on the oëcial internode; also, that a definite relation exists between the position of the ovicell in the internode and the positions of the branches in the same internode. For example, if the ovicell is the third member of an internode (pl. 20, fig. 20, *oc.*) the first branch will either be absent, as is commonly the case, or arises on the first zoëcium; the second branch will then appear on the fourth zoëcium (*br.* 2), and the third on the seventh zoëcium (*br.* 3). If the ovicell is the fifth member (pl. 19, fig. 12), then the first branch (*br.* 1) will occur on the third zoëcium; the second branch (*br.* 2) on the sixth

zoëcium; the third branch (*br. 3*) on the ninth. If the ovicell is the seventh member (pl. 20, fig. 18), then the first branch usually occurs on the third or fifth zoëcium; the second branch on the eighth, and the third branch on the eleventh zoëcium, although instances are found where the ovicell is the seventh member, and the branching has taken place on the third, sixth and ninth zoëcia of the internode. The rule is, however, this: the two upper branches, the second and third, keep a definite relative distance above the ovicell; the second pairing with it on the opposite side of the internode, and the third occurring on the fourth zoëcium above it, and hence on the same side of the internode but on a zoëcium adnate to the dorsal surface of the ovicell. Further, the oöcial internode frequently curves in such a way that the third branch begins immediately above the median line of the ovicell, and the axis of the ovicell follows the axis of the third branch rather than the axis of the internode in which it belongs, while the remaining zoëcia of this internode continue in the original axis, and, carrying the zoarial tuft upward, may send off a fourth branch considerably above the ovicell. In their profuseness of branching these species show a relation to *C. ramosa* Harmer, the oöcial internode of which may give rise to six branches.

In all the *Crisias* each zoëcium in which a branch or internode originates, consists of two parts separated by a flexible articulation: a lower conical portion known as the *basis rami* (pl. 18, fig. 2, *ba. r.*) adnate to the zoëcium from which it originates, and an upper cylindrical portion which is more or less free. These two parts are not independent but form integral parts of the zoëcium, the contained polypide when retracted passing freely downward into the *basis rami*, and when expanded passing as freely upward through the chitinous joint. The oöcium (*oe.*), or ovicell and its contained embryos are clearly examples of change of structure as adaptations to changed function. The ovicell originates as does a zoëcium, its place in the internode being, as a rule, definite for a given species, and in correlation with the zoëcia of the internode. The tissue within the zoëcium is as clearly a modified polypide. This can be shown by an investigation of the growing tips of branches where are found

the masses of cells or buds which are destined to make both the future polypides and the contents of ovicells. At certain early stages these are indistinguishable, (:03), but later some of these masses of cells change into polypides, others surround an ovum and become inclosed by an ovicell. Just what the impulse is which causes the bud in one case to transform into an ordinary polypide, and in the other into a nutritive follicle surrounding a developing ovum, is not known.

KEY TO THE SPECIES OF CRISIA.

- | | |
|--|-----------------------------|
| 1. Zoecia typically uniserial | 2 |
| 1. Zoecia biserial | 5 |
| 2. Oœcia concave on the ventral side | 3 |
| 2. Oœcia not concave | 4 |
| 3. Oœciostome opening on the dorsal side of the oœcium below the summit; oœciopore circular, directed somewhat backward and upward | <i>Crisia edwardsiana.</i> |
| 3. Oœciostome opening on the ventral side of the oœcium at the summit; oœciopore circular, directed somewhat backward and upward | <i>Crisia franciscana.</i> |
| 4. Oœciostome opening at the summit of the oœcium, tube curved forward; oœciopore elongated, slit-like and opening ventrally; or circular and opening upward | <i>Crisia geniculata.</i> |
| 5. Oœcial internode possessing two, three, or more branches, one of which occurs just above the summit of the oœcium | 7 |
| 5. Oœcial internode not possessing more than three branches, and never possessing one at the summit of the oœcium | 6 |
| 6. Oœciostome covered by a cap or operculum | <i>Crisia operculata.</i> |
| 6. Oœciostome not covered by a cap or operculum | 7 |
| 7. Tube of oœciostome bent forward | 8 |
| 7. Tube of oœciostome not bent | 9 |
| 8. Tube of oœciostome short; oœciopore flattened from right to left | <i>Crisia pacifica.</i> |
| 8. Tube of oœciostome long, either flattened or circular | <i>Crisia pugeti.</i> |
| 9. Oœciostome opening slightly dorsally behind the summit of the oœcium, its tube short and of the same diameter throughout; oœciopore opening upward | <i>Crisia occidentalis.</i> |
| 9. Oœciostome opening slightly dorsally behind the summit of the oœcium, its tube short, wider below than above; oœciopore opening not directly upward but inclining ventrally | <i>Crisia maxima.</i> |

84. *Crisia franciscana* sp. nov.

Pl. 18, figs. 1, 2, 3, 4.

Crisia occidentalis Robertson, 1903.

Zoaria composed of numerous, delicate, branching tufts 15 to 20 mm. in height; found at low tide on rocks and on seaweed, attached by flexible rootlets (pl. 18, fig. 1). *Internodes* (fig. 2, *int.*), consisting of a single zoæcium giving rise to a branch (*br.*) on each side. Each *branch* arising in a *basis rami* (*ba. r.*) adnate to the zoæcium giving origin to it. *Joints* (*j.*) light-colored at the growing tips, but becoming black with age, a clump of this species having a distinctly speckled appearance even to the naked eye. *Zoæcia* (*zoe.*) consisting of rather long, slender, calcareous tubes, usually slightly curved or concave on the ventral side; sparsely punctate, the distal end having a slightly ringed appearance. *Oæcia* (*oe.*) elongated, narrowed below, much inflated above. *Oæciostome* (*oest.*) large, its tube (*oest. t.*), prominent, bent backward. *Oæciopore* (*oep.*), circular, directed backward and slightly upward. *Oæcial internode* consisting typically of three members, the first being an ordinary zoæcium, z^1 , arising in a *basis rami*; the second being the oæcium (*oe.*), arising on z^1 in a slender cone (*oe. c.*), larger than, but corresponding to a *basis rami*; the third member being a non-flexible zoæcium, z^3 , adnate to the oæcium throughout its whole length.

The zoarium of *Crisia franciscana* has a very distinctive appearance due in part to its coarse, dense growth, but in larger part to the great number and regularity of its black joints. It is this species whose embryology was investigated by the present writer (:03) under the name of *C. occidentalis*. That name being preoccupied, (Trask '57), the specific name *franciscana* is now given it, since the region where it is most abundant is on the shores of San Francisco Bay.

In the discussion of the phenomena of the embryology of this and related species, mention was made of a structure first noted in the ovicell of *C. franciscana*, and afterwards found to be present in the ovicells of both *C. edwardsiana* and *C. geniculata*.

This consists of a ring or septum (fig. 2, *sep.*) which occurs within the oœcium at the same place relatively where the flexible joint (*j.*) does, which separates the *basis rami* from the distal tubular portion of a zoœcium. This septum is visible through the calcareous wall of the ovicell, especially if the specimen is slightly stained, or is simply cleared in glycerine, or oil. It separates, as will readily be seen, the inflated portion of the ovicell from the long conical portion (*oc. c.*). After the septum forms, section of the ovicell in any stage of growth shows that it is formed in this species by a thickening of the inner chitinous layer of the oœcial wall. This is shown in fig. 3, which represents a section through the lower portion of a young ovicell. At some distance below the embryo (*emb.*), the chitinous wall thickens and grows inward forming a circular shelf (*sep.*). This chitinous shelf is broader and thicker in older ovicells (fig. 4, *sep.*) but it seems never to close entirely. In all cases observed in this species it does not form a continuous floor, but remains open in the middle. In close connection with it, and with the cellular tissue surrounding the embryo, a delicate chitinous tube, (*chi. t.*), is seen extending, as shown in figs. 3 and 4, downward toward the base of the oœcial cone. The position and mode of formation of the septum relates it with the flexible joints of ordinary zoœcia, if not making the two structures homologous. The lower portion of the ovicell, what I have called the oœcial cone, would then be homologous with a *basis rami*, and the inflated portion with the distal tubular part of the zoœcium.

In *C. geniculata* a similar structure is seen (fig. 7, *sep.*). This in cross-section is seen to be formed in virtually the same manner as in *C. franciscana*. The projecting shelf is thicker somewhat, and from it there depends a delicate, chitinous tube more apparent than is that of *C. franciscana*. Above the septum there is an added structure in the form of a delicate, chitinous arch continuous with the tissue of the tube and attached to the septum.

If *C. edwardsiana* is viewed in optical section, the same dark ring is discernible as is seen in the two species just mentioned (pl. 19, fig. 10, *sep.*). On investigation the darkening is found to be due not to a thickening of the chitinous wall, but to a thickening of the cellular wall. At the same point relatively at which

the chitinous septum occurs in the oœcium of *C. franciscana*, a cellular septum occurs in *C. edwardsiana* formed by a layer of high columnar cells which as are seen in cross-section spread in a fan shape forming a semicircle (pl. 18, fig. 5, *sep.*). From it there depends, as in other cases, a delicate, chitinous tube, and above it there extends from side to side a continuation of this chitinous tissue forming a chitinous floor (*chi. fl.*). Whether this floor is perforated or not has not been ascertained.

The function of this septum, either chitinous or cellular, is not clear. It can hardly be said to be for the purpose of strengthening the oœcial wall at that point, since the species whose ovicell appears most to need support has merely a cellular septum. Its function seems to be most closely related with that of the inner chitinous tube, and in two species, with the chitinous floor, acting as the means of attachment and support for it. Thus, by reducing the size of the opening into the oœcial tube in *C. franciscana*, and by supporting a chitinous floor in *C. geniculata* and *C. edwardsiana*, the septum may directly in the first case, indirectly in the other two cases, prevent the larvae in their circulation through the ovicell from passing into a *cul de sac* from which they might be unable to extricate themselves.

C. franciscana is abundant between tide marks at Fort Point and Lands End, San Francisco; also at Dillons Beach, Navarro, and Pacific Grove, California. Found also at low tide at Puget Sound, the colonies of more delicate appearance than are those obtained further south; also at Orea, Alaska, growing on worm tubes. Found on the shore rocks at Ballast Point, Coronado, California, and dredged at numerous stations on the coast of Southern California in depths ranging from 2 to 19 fathoms.

85. *Crisia geniculata* Milne-Edwards.

Pl. 18 and 19, figs. 6, 7, and 8.

Crisia geniculata Milne-Edwards, 1838, vol. 9, ser. 2, p. 197, pl. 6, figs. I^a, I^b, I^c.

Filicrisia geniculata, d'Orbigny, 1851, p. 604.

?*Crisidia gracilis* Trask, 1857, p. 113, pl. 5, fig. 3.

Crisia cornuta a, *sine cornibus*, Smitt, 1865, pp. 115 and 126, pl. 16, figs. 2, 3.

Crisia cornuta, var. B, *geniculata*, Busk, 1875, p. 3, pl. I, figs. 1-4.

Crisia cornuta, var. A, *geniculata*, Hineks, 1880, p. 419, pl. 56, fig. 4.

Crisia geniculata, Harmer, 1891, p. 170, pl. 12, figs. 7 and 8.

Zoaria composed of numerous delicate branching tufts, sometimes stiff and straight, sometimes forming rather loose masses of elongated zoæcia, 15 to 25 mm. in height (pl. 18, fig. 6); found at the roots of other bryozoa, on seaweed at low tide attached by jointed rootlets. *Internodes* consisting typically of a single zoæcium (fig. 7, *zoc.*), each zoæcium giving rise to a pair of branches, each branch arising on the side of a zoæcium in a *basis rami* (*ba. r.*) adnate to the zoæcium which gives origin to it. *Joints* (*j.*) light colored in the younger portions of the colony, growing brown or black in the older parts. *Zoæcia* long, slender, slightly curved, if at all; divided into two portions by the flexible joint. *Oæcia* (*oe.*) elongated, straight, narrowed below, slightly inflated above. *Oæcial internode* consisting typically of three members of which the oæcium is the second; the third z^3 being an elongated slender tube adnate to the dorsal side of the oæcium and extending above it; consisting sometimes of five members (pl. 19, fig. 8), with the oæcium as the third member and two zoæcia adnate to its dorsal surface, z^1 and z^2 . *Oæciostome* (fig. 7, *ocst.*) large, its tube bent sharply forward. *Oæciopore* (*oep.*) narrow and slit-like; in a few instances the tube of the oæciostome upright, and oæciopore circular.

As Harmer ('91) has pointed out, this species has been considered by many of the older writers as a mere spineless variety of *Crisia cornuta*. It is true that without its spines a branch of *C. cornuta* can scarcely be distinguished from *C. geniculata*. The same is true also of *C. edwardsiana* and *C. geniculata*. Indeed, all uniserial species of *Crisia* have so similar an appearance when the zoæcia alone are considered that it is impossible to separate them with any degree of certainty on that feature only. It is only when the ovicells are compared that an adequate basis of separation is obtained. The figures of Busk ('75, pl. 1, figs. 2 and 10) show clearly the difference in the shape and internodal position of the ovicells of *C. geniculata* and *C. cornuta* respectively. Likewise, a comparison of Harmer's figures (pl. 12, figs. 7 and 8, and fig. 9) should convince one of the specific difference in these two forms. *C. cornuta* does not occur on this coast to my knowledge. Hincks ('84) reports it from Queen Charlotte Islands, but gives neither verbal description nor plate of the

species he found there, and in view of the abundance of related or somewhat similar, though not identical species on this coast, there is reason to doubt his identification. The spiny species of *Crisia* which occurs on the Pacific coast is *C. edwardsiana* (pl. 19, fig. 10). Without a close comparison of ovicells, *C. cornuta* and *C. edwardsiana* might very easily be mistaken for each other. The fact, then, that *C. geniculata* occurs here in company with *C. edwardsiana* is additional proof of its specific distinctness, and strengthens the view that it is not permissible to rank it as a variety, nor even as a sub-species, of any other form. That the species found here is *C. geniculata* is undoubtedly true, since the shape and size of the oecium, the position and shape of the tube of the oeciostome and the position of the oecium in the internode agree with the diagnoses given for this species obtained elsewhere.

An irregularity of growth is shown in this species, especially in some material obtained from a southern station (pl. 19, fig. 8). This is a tendency to form internodes of more than one zoecium, and is a variation which characterizes both the ordinary internodes and the oecial internodes. In the drawing (fig. 8), the oecial internode is shown to consist of five zoecia, the oecium being the third member of the internode.

Crisidia gracilis Trask ('57) may refer to this species. No account of the ovicell is given by that investigator and only a meager description of the species, so that identification of his species must remain a matter of conjecture.

C. geniculata is found in considerable abundance between tide marks at Lands End and Fort Point, San Francisco Bay, at Pacific Grove, Monterey Bay, and at Dillon's Beach, California; also at Deadman's Island, San Pedro, and on the rocks of the breakwater at Zuniga Point, Southern California. Dredged at numerous stations from San Pedro to Point Firmin, Southern California, in depths ranging from 2 to 30 fathoms.

86. *Crisia edwardsiana* (d'Orbigny) Busk.

Pl. 19, figs. 9, 10.

Crisidia edwardsiana d'Orbigny, 1839, p. 8, pl. I, figs. 4-8.

Crisia edwardsiana, Busk, 1875, p. 5, pl. 2, figs. 5-8.

?*Crisia cornuta*, Hineks, 1884, p. 203.

Crisia edwardsiana, Jullien, 1888, p. 81.

Crisia cornuta, Robertson, 1900, p. 328.

Zoaria composed of numerous, delicate, branching, spiny tufts curving at the tips and growing 15 to 20 mm. in height; found at low tide, on seaweed, at the roots of other bryozoa, and on the underside of rocky ledges attached by numerous jointed rootlets (pl. 19, fig. 9). *Internodes* consisting typically of a single zoæcium (fig. 10, *zoc.*) each zoæcium giving rise to a branch on each side. *Branches*, consisting either of a zoæcium, or of a long jointed spine (*sp.*), arising in a *basis rami* (*ba. r.*). An internode, *i.e.*, a single zoæcium, sometimes giving rise to two lateral zoæcia, sometimes to a zoæcium and a spine, or again, to two lateral spines. Distal ends of branches frequently possessing internodes of two, three, four, or five zoæcia arranged alternately. *Zoæcia* (*zoc.*) consisting of long, slender, curved tubes whose distal ends are smooth, hyaline, marked by delicate rings. *Oæcia* (*oe.*) pearshaped in general outline, curving inward on the ventral surface, *i.e.*, concave on the ventral side as are the zoæcia. The *oæcial internode* consisting of at least three members, of which the first is an ordinary zoæcium, z^1 ; the second being the oæcium (*oe.*) arising in an oæcial tube on the side of z^1 ; the third, z^2 , arising from the oæcium and adnate to it for half its length, the distal free portion giving rise to one or two lateral branches which carry the zoarial tuft upward. *Oæciostome* (*oest.*) large, situated on the dorsal surface of the oæcium below the summit, possessing a short, straight, or slightly bent tube. *Oæciopore*, circular, opening upward and directed either backward or upward.

C. edwardsiana is fairly abundant on the coast of California. Fig. 10 represents its method of internodal growth as it occurs on the shores of San Francisco Bay and northward. Here the internodes are almost constantly uniserial. On the southern coast internodes more frequently consist of several zoæcia as figured by d'Orbigny ('39) and Busk ('75). The ovicell of this southern form is less inflated than is that represented in the figure and the tube of the oæciostome is often bent almost at right angles so that the oæciopore opens directly upward. On examination, the same colony is often found to contain the two sorts of internodes, the uniserial type abounding in the older portions, the multiserial in the younger portions.

This species occurs between tide marks in company with other species of *Crisia* at Fort Point and Lands End, San Francisco; at Deadmans Island, San Pedro, and at La Jolla, California. It has also been obtained between tide marks at Sitka, Juneau, Yakutat, and Orea, Alaska; and at low tide on Channel Rocks, Puget Sound. Dredged also off San Diego in depths ranging from 16 to 30 fathoms.

87. *Crisia occidentalis* Trask.

Pl. 19, figs. 11, 12.

Crisia occidentalis, Trask, 1857, vol. I, p. 113, pl. V, fig. 4.

Crisia eburnea, Robertson, 1903, p. 116.

Zoaria forming dense tufts whose branches curve inward especially in those colonies bearing ovicells; colonies from 20 to 25 mm. in height (pl. 19, fig. 11), growing on seaweed, on rocky ledges, on other bryozoa, attached by numerous jointed rootlets. *Internodes* in the lower and older portion of a colony consisting of three, four, or five zoæcia; in the younger and larger portion of the colony seven being the prevailing number, although internodes of nine or more zoæcia occur. *Branching*, as a rule, alternate; usually but one branch in an internode, arising commonly from the third zoæcium. *Joints* light-colored, yellow in the older parts, white in the younger. *Basis rami* (*ba. r.*) except of the first zoæcium of an internode, not wedged in, but simply applied to the side of the zoæcium from which it originates. *Zoæcia* connate through almost their whole length, somewhat abruptly curved forward at their anterior end, often possessing a pronounced denticle (*d.*) or projection on the outer side of the aperture. *Oæcia* (*oe.*), tapering at the origin, growing broader somewhat suddenly so that the upper two-thirds is of the same diameter throughout; the third, fifth, or seventh member of its internode; adnate to its dorsal surface are several zoæcia, often four, one of which, the fifth, seventh, or ninth, depending upon the place in the series occupied by the oæcium (see page 230), extending above it, curving forward, and opening beside the oæcial aperture. *Oæciostome* smaller in diameter than the aperture of a zoæcium, opening a little below the apex of the ovicell on the dorsal side; *tube* of *oæciostome* short, but rising above the summit of the ovicell, delicate, hyaline. *Oæciopore* (*oep.*) circular, opening directly upward.

Zoarial branching in this species is fairly regular. As has been said, seven is the characteristic number of zoœcia in an internode, with a branch arising from the third zoœcium. When there are more than seven zoœcia in an internode, there will usually be more than one branch in that internode, or if but one branch it will occur higher up than the third zoœcium, *e.g.*, on the fifth. *C. occidentalis* is dioecious. Oœcial colonies never produce testes. Male colonies are abundant and never produce ovicells. The branches of male colonies characteristically close their growth at the distal end with a long spinous process. Such colonies do not present the curled appearance of oœcial colonies, so that the practiced eye soon detects the difference between them even when no ovicells are visible.

This species was formerly regarded as identical with *C. eburnea*. In some respects it shows relationship with both *C. eburnea* and *C. denticulata*. Although both species have been reported from this coast, a study of typical *C. eburnea* and *C. denticulata*, and a careful comparison with this species shows marked differences especially in the ovicell and its aperture, and in the branching of the oœcial internode. *C. occidentalis* shows some resemblance to *C. sinclairensis* Busk ('75) but Busk says nothing of the ovicell, and identification is impossible. The present identification is made not so much upon the description and figure furnished by Trask, as upon the fact that it has been obtained in great abundance in the type locality, *viz.*, San Francisco Bay, where it is the only biserial species of *Crisia* found.

C. occidentalis is abundant between tide marks at Lands End and Fort Point, San Francisco; in smaller quantity at low tide on Deadmans Island, San Pedro; between tide marks at Mendocino City and at Navarro, California; obtained also in small quantity at San Juan County, Washington. Dredged in ten fathoms off Santa Cruz Lighthouse; dredged also off San Pedro in from 2 to 6 fathoms of water.

88. *Crisia operculata* sp. nov.

Pl. 19, figs. 13, 14, 15.

Zoaria composed of delicate, brittle, straggling tufts from 12 to 20 mm. in height, attached by hairlike, flexible rootlets. *Internodes* of a varying number of zoœcia: the lower internodes

of a colony containing three or five zoëcia and rootlets; the upper, and terminal internodes, from eleven to nineteen zoëcia, and even twenty-two and twenty-eight or more. *Branching* alternate, the longer internodes possessing two branches. In internodes of seven zoëcia or fewer, branches arising on the third or fifth zoëcium; in longer internodes, branches arising from the seventh or ninth, hence branching begins high up in the internode. *Basis rami* (pl. 19, fig. 13, *ba. r.*), long, tapering, not wedged in. *Joints* light colored, yellow or amber. *Zoëcia* extremely long and slender, connate throughout their whole length; aperture circular, hyaline, slightly constricted and bent forward. *Oëcium* (*oe.*) elongated, connate throughout its length, the fifth or seventh member of the internode. *Oëcial internode* usually long, giving rise to two branches, one below the ovicell, the other originating on the zoëcium which pairs with it. *Oëciostome* (*oest.*) at the summit of the ovicell; the dorsal wall of the oëcium extending upward and forward covering the oëciostome as with a lid or cap, the *operculum* (fig. 14, *op.*). *Oëciopore* (*ocp.*) a semicircular slit, opening ventrally.

C. operculata differs from the other biserial *Crisias* of this coast in the oëcial aperture as well as in the branching of the oëcial internode. Although the quantity of material on which this diagnosis is made is small, yet there were seven perfect ovicells all possessing the peculiar covering over the oëciostome for which the species is named. Fig. 15, which represents the front wall of the ovicell as broken away, shows clearly the mode of formation of the operculum, and the manner in which the oëciopore is formed. In all the other biserial *Crisias* described in this paper, at least one of the zoëcia adnate to the dorsal surface of the oëcium gives rise to a branch. In this species none of the zoëcia adnate to the dorsal surface of the oëcium produces a branch.

C. operculata has been obtained with ovicells at one station on the Southern California coast, depth not known; probably abundant without ovicells.

89. *Crisia pacifica* sp. nov.

Pl. 20, figs. 16, 17.

Zoarium forming large bushy tufts from 20 to 25mm. in height and often 25 to 30mm. in diameter (pl. 20, fig. 17) attached to seaweed, or sponge, or entangled with other bryozoa, by means of flexible rootlets. *Internodes* long, consisting of between 13 and 28 zoæcia; the shorter internodes having only one branch; those of 19 or more zoæcia possessing two; the first branch arising from the third, fifth, or seventh zoæcium. *Joints* yellow, passing to deep amber or brown. *Basis rami* (*ba. r.*) short and stout, wedged in between the zoæcium which gives rise to it and the one next below. *Zoæcia* connate, sharply curved forward at the anterior end, surrounded by a narrow rim or peristome slightly contracted. *Oæcium* (*oc.*) large, adnate throughout the whole length, slightly flattened dorso-ventrally, the axis inclining in the direction of the branch (*br.*) which forms above it, rather than with the remainder of the oæcial internode (*oc. int.*); the third, fifth, or seventh member of the internode, or sometimes higher; usually situated low in the internode, i.e., as low as the third or fifth. *Oæcial internode* possessing two or three branches in close relation with the ovicell depending upon the position of the ovicell; if it is high, as high as the fifth, or higher, three branches develop about it; if it is low, as in the present instance, then but two branches are formed (*br.*² and *br.*³); the remainder of the oæcial internode continuing the zoarial tuft upward, and often developing a fourth branch. *Oæciostome* large, its tube usually curving forward, sometimes only slightly inclined forward, flattened. *Oæciopore* (*oep.*) flattened from right to left, opening either ventrally or upward.

This species is one of the two found on the coast of Southern California which is distinguished for the large size of the oæcia. Unfortunately a typical case of branching in the oæcial internode was not chosen for the figure given (pl. 20, fig. 16). In this figure the ovicell occupies a position low in the internode. It is here the third member, and no branch develops below it. The two branches which form in the internode occupy the places

relatively of the second, (br^2 .) and third branches (br^3 .) of a more typical internode.

C. pacifica has been obtained in the San Diego region only, dredged in depths ranging from 15 to 30 fathoms.

90. ***Crisia maxima*** sp. nov.

Pl. 20, figs. 18, 19.

Zoaria consisting of coarse, stiff, brittle, rather straggling tufts 20 to 25 mm. in height (pl. 20, fig. 19) fastened by numerous rootlets to roots of kelp, to sponge, etc. *Internodes* long, consisting of eight, ten, or eleven zoæcia in the lower portion of the colony, to forty in the upper portion; most commonly of 15 to 17 zoæcia, and giving rise to one or two branches; very long internodes possessing three branches; the first or lowest branch arising from the fifth zoæcium most commonly, but frequently from the third, seventh, or ninth; the second branch originating anywhere between the ninth and twenty-second, occurring most frequently on the ninth, tenth, sixteenth, and eighteenth. *Joints* dark brown, never black. *Basis rami* (*ba. r.*) not wedged in. *Zoæcia* long, slender, connate, except the terminal portion which curves forward. *Oæcia* (*oc.*) numerous, occurring on both main stems and side branches, of great size, adnate throughout their whole length, the dorsal surface not curved, the ventral surface prominent, and the summit truncate; the main axis always in a line with that of the branch (br^3 .) which is given off at the distal extremity; high in the internode, being the fifth, seventh, ninth, or thirteenth member. *Oæcial internode* possessing three branches, the relations between them and to the oæcium being identical with those described on page 230. *Oæciostome* at the summit of the dorsal surface; *tube of oæciostome* delicate, hyaline, inconspicuous, rising only slightly above the truncate summit and not always easily detected. *Oæciopore* (*ocp.*) small, and usually directed forward.

This species, like *C. pacifica*, is remarkable for size, especially of the ovicells. The shape of the ovicells as of their apertures in the two species is very different. A side view of that of *C.*

pacifica shows it to be flat dorso-ventrally with a distinct slope downward from the edge of the œciostome. In *C. maxima*, the ovicell in side view is seen to be ventricose, its dorso-ventral axis being much greater than that of *C. pacifica*, while the top of the ovicell is flattened.

This species has been obtained between tide marks at Escondido, Deadmans Island, and Whites Point, California; also dredged off shore from San Pedro to Coronado in depths ranging from 4 to 30 fathoms.

91. *Crisia pugeti* sp. nov.

Pl. 20, figs. 20, 21.

Zoaria composed of stiff, straggling, brittle tufts attached by jointed rootlets. *Internodes* long, consisting of eleven zoœcia, more or less, in the lower part of the colonies, and quickly increasing to 15, 17, and 39, or more, in the upper part of the branches of a colony; the shorter internodes bearing two or three branches; longer ones often having four branches arranged alternately; the first or lowest branch of an internode arising most commonly from the third or ninth zoœcium, but sometimes from the fifth or seventh. *Joints* inconspicuous, light colored, or brown. *Basis rami* (pl. 20, fig. 20 *ba. r.*) sometimes wedged in, sometimes not. *Zoœcia* long, slender, often connate throughout their whole length, more usually free at the distal extremity and bent forward. *Oœcia* (*oc.*) numerous, very long and slender, varying in length between rather wide limits, depending apparently on the place occupied by the œcium in the internode; if high in the internode, then, as a rule, the œcium is longer than if low in the internode; adnate throughout the whole length, the main axis in a line with the branch (*br*³.) always given off at its distal extremity; often the third member of the internode, but sometimes the fifth, seventh, ninth, or eleventh. *Oœcial internode* possessing three or four branches; depending on the place occupied by the œcium; if the œcium is the third member of the internode (fig. 20) then no branch develops below it and the internode will possess but three branches; if it is high in the internode, then there may be four branches, three sustaining the same relation to the œcium as that represented in fig. 18.

Oœciostome (*oest.*) at the summit of the oœcium, circular; *tube of oœciostome* (fig. 21, *oest. t.*) typically a relatively long pipe, bent forward at right angles and inclined somewhat to one side of the longitudinal axis of the oœcium. *Oœciopore* sometimes circular (fig. 21, *oep.*) sometimes flattened (fig. 20, *oep.*).

In this species we find considerable variation both in the length of the ovicell, and in the shape of its aperture. Observation of twenty-five cases shows that, typically, the oœcium occurs low in the internode. It is then relatively short, and the tube of the oœciostome is distinctly a small pipe-like stem projecting from the top of the ovicell as shown in fig. 21 or fig. 20. In cases where the oœcium is the ninth or eleventh member of an internode, it often attains a great length, sometimes being twice as long as in cases where it is the third member of its internode. The oœcial aperture in these longer oœcia is often short and bent forward very little, sometimes opening directly upward.

No complete colonies of *C. pugeti* were obtained. The material though abundant was brittle and broken. Dredged at Friday Harbor, San Juan County, Puget Sound; depth not known.

Tubuliporidae.

- Tubuliporidae* Fleming, 1828.
les Tubulipores, Milne-Edwards, 1837.
Tubuliporidae (part) Johnston, 1847.
Sparsidae, d'Orbigny, 1850-52.
Tubuliporidae, Busk, 1859.
Tubuliporidae, Smitt, 1866.
Tubuliporidae, Hincks, 1880.

Zoarium entirely adherent, or more or less free and erect, multiform, often linear, or flabellate, or lobate, sometimes cylindrical. *Zoœcia* tubular, disposed in contiguous series, or in single lines. *Oœcium* an inflation of the surface, or a modified zoœcium.

KEY TO THE GENERA OF TUBULIPORIDAE.

- | | |
|--|---------------|
| 1. Zoarium a circular, or fan-shaped, or lobed expansion, usually adnate | 6 |
| 1. Zoarium not adnate, except in some young stages | 2 |
| 2. Zoarium erect, branched | 3 |
| 2. Zoarium erect, growing in tortuous, bilaminate expansions | |
| | Mesenteripora |

- | | |
|---|--------------------|
| 3. Branches cylindrical, zoëcia opening on all sides | 4 |
| 3. Branches flattened, zoëcia opening on the ventral side only..... | 5 |
| 4. Apertures on surface of branches of approximately equal size | |
| | Entalophora |
| 4. Apertures on surface of branch of unequal size | Heteropora |
| 5. Branches flexible, possessing chitinous joints | Crisulipora |
| 5. Branches without chitinous joints | Idmonea |
| 6. Oœcia modified zoëcia; numerous in each colony | Tubulipora |

Tubulipora Lamarek

- Tubulipora* Lamarek, 1816.
Tubulipora, Lamouroux, 1821.
Tubulipora, Johnston, 1847.
Tubulipora, d'Orbigny, 1852.
Tubulipora, Busk, 1859.
Tubulipora, Busk, 1875.
Tubulipora, Hincks, 1880.
Tubulipora, Harmer, 1898.

Zoarium with a distinct basal lamina, adnate or erect, beginning as a pyriform or flabelliform colony, which may become lobed by the division of the terminal membrane or growing edge. Lobes short and adherent, or longer and dichotomously divided once or more often, sometimes becoming erect. *Zoëcia* with a free cylindrical, terminal portion; or connate in obliquely transverse series separated by flat septa corresponding with the intersection of two cylindrical zoëcia; series arranged alternately on opposite sides of the axial line of the lobe, transverse arrangement usually becoming radial in the distal part of the fertile lobes. *Oœcium* an enlarged zoëcium, which extends into the intervals between the parallel or radial series of zoëcia.

The above diagnosis is taken almost bodily from Harmer ('98), that writer having made a detailed study of the growth and embryology of this genus and his definition being exact and complete. According to Harmer and also to Hincks ('80), and as may be readily seen on inspection of youthful stages, a colony of *Tubulipora* arises in a circular disk (pl. 21, fig. 25, *dk.*), the calcified remains of the larva which gives rise to the colony. From this the first zoëcium develops, and then a second. These two zoëcia usually bend away from each other in opposite directions, while between them a third zoëcium forms. In this way a fan-shaped or lobed expansion arises, the final shape of the

colony depending upon whether or not the growing edge (*gr. ed.*) or limiting membrane remains intact. In well-formed colonies the sides may bend so far outward and downward as to inclose the circular disk, which then becomes the center approximately of a large circular colony (fig. 26). In some species the colony may become erect and take on an *Idmonca*-like form. Oœcia are usually abundant on well-formed colonies and in the four species reported here the oœcial opening is distinctive.

KEY TO THE SPECIES OF TUBULIPORA.

- | | |
|--|------------------------|
| 1. Zoarium directly adnate, circular, or flabelliform, or lobed..... | 2 |
| 1. Zoarium not directly adnate, but adherent by dorsal teeth, lobed | 8 |
| 2. Tube of oœciostome long | 3 |
| 2. Tube of oœciostome short | 6 |
| 3. Tube of oœciostome bent, often at right angles | 4 |
| 3. Tube of oœciostome straight, or slightly inclined | 5 |
| 4. Oœciopore compressed, smaller than aperture of oœcium | |
| | T. flabellaris. |
| 5. Oœciopore compressed, its long diameter greater than the diameter of the oœciostome | T. occidentalis |
| 6. Oœciostome opening at right angles to oœcial wall | 7 |
| 6. Oœciostome not opening at right angles to oœcial wall | 8 |
| 7. Oœciopore circular, compressed or flaring widely, funnel-shaped, its diameter twice that of a zoœcium | T. pacifica. |
| 8. Oœciopore circular or compressed, only slightly, if at all, larger than the diameter of a zoœcium. | T. pulchra. |

92. *Tubulipora flabellaris* Fabricius.

Pl. 21, figs. 25, 26.

Tubipora flabellaris Fabricius, 1780, p. 430.*Tubulipora flabellaris*, Smitt, 1866, p. 401, pl. 9, fig. 6.*Tubulipora flabellaris*, Harmer, 1898, p. 99, pl. 8, fig. 4.

Zoarium adnate, more or less fan-shaped, or circular in form in well-developed colonies. *Zoœcia* sub-erect, single, free, or in connate series two, three, or four in a single or double row. *Oœcium* (pl. 21, fig. 25, *oc.*) lobed, large. *Tube of oœciostome* (*ocst. t.*) arising freely from the wall of the oœcium, flattened and curving forward. *Oœciopore* (*ocp.*) elongated radially, more or less slit-like; both tube and oœciopore smaller than a zoœcium and its aperture.

The list of synonyms given for this old species is shorter than that given by many of the older writers, but there is

included here only those specific names which undoubtedly belong to this species based upon the criteria of Harmer ('98). The species of *Tubulipora* are in a sad state of confusion, and for the purposes of this report, as well as in the interests of clearness, it seems best to consider only that synonymy about which there can be no doubt.

The colony represented in fig. 25 is a youthful one possessing only one adult ovicell (*oe.*) and two immature ones (*im. oe.*). On older colonies, ovicells are usually abundant as many as seven being found on a single colony. The oœcia bulge very decidedly and are usually two-lobed, the oœciostomal tube arising on the margin of the oœcium whose point of origin is in a radius of the zoarium.

This species is quite abundant on kelp growing around Channel Rocks, Puget Sound. Also obtained on shore kelp near San Pedro, California.

93. *Tubulipora pacifica* sp. nov.

Pl. 22, figs. 27, 28.

Zoarium adnate, forming well-developed fan-shaped or almost circular colonies (pl. 22, fig. 28). *Zoœcia* radiating, sub-erect, the distal half or two-thirds frequently quite erect, connate in single or double rows, sometimes interlacing (fig. 27). *Oœcia* (*oe.*) large, lobed, extending between the connate series of zoœcia. *Oœciostome* (*oest.*) large, its tube bent and flattened, and ending in a funnel-shaped expansion which may be circular, *i.e.*, may flare widely or be more or less compressed. *Oœciopore* (*oep.*) when flaring, larger than the aperture of a zoœcium (*fl. oep.*); otherwise compressed and more or less slit-like (*com. oep.*).

The general shape and appearance of a colony of this species is not unlike that of *T. flabellaris*, but close inspection reveals many differences. The zoœcia are more nearly vertical, and except in very young stages of colonial growth are connate, sometimes in single rows, frequently in double rows or in bundles of zoœcia. The tube of the oœciostome has a diameter about equal to that of a zoœcium. It seems to emerge from the side of a zoœcium at right angles to it, its distal extremity flaring suddenly, and remaining so, or becoming more or less compressed.

T. pacifica occurs on kelp, often in great abundance, a single frond being frequently covered thickly with these small white colonies. Obtained on shore kelp off San Clemente Island, and at Coronado; also dredged off the Southern California coast at various stations, in depths ranging from 5 to 18 fathoms.

94. ***Tubulipora occidentalis*** sp. nov.

Pl. 22, figs. 29, 30, 31.

Zoarium adnate, flabelliform, when young, rounded or circular, when adult and growing on flat surfaces (pl. 22, fig. 31); often incrusting stems, (fig. 30), when the colony may form a regular or irregular, contorted mass. Central part of colony depressed, surrounded by *zoæcia* which are sub-erect, and arranged in connate, radial bundles in series of two, three, or more rows (fig. 29). *Oæcium* (*oe.*) an inflation of the surface, large, involving many *zoæcia*, hence lobed, extending between the series of *zoæcia* like the fingers of a glove. *Oæciostome* small, compressed, smaller than the aperture of a *zoæcium*; *tube of oæciostome* (*oest. t.*) usually radial, arising in a depression between the bundles of *zoæcia*, and often quite separated from the *zoæcia*, though sometimes connate with a *zoæcium*; compressed, narrow below, wider above or toward the distal end. *Oæciopore* (*oep.*) slit-like, its longer diameter parallel with a radius of the colony, and as great, or greater than a diameter of a *zoæcium*; opening directly upward.

This species is easily recognized by its coarse appearance, its color, a dirty gray, its tendency to grow in rough calcareous masses around stems and over the surface of kelp. The polypide is usually of a deep purple, but in deep water the calcareous masses are often white. This species answers in some respects to the description given by Hincks ('84) for *T. fasciculifera*, but neither from the description nor from the plate he gives can it be identified positively as such, although this species is probably closely related to the Queen Charlotte form.

T. occidentalis has been found in considerable abundance at various localities. Obtained between tide marks at Whites Point, near San Pedro, and at Monterey Bay, California, investing stems of coralline; also at Channel Rocks, and at San Juan County, Puget Sound, Washington; dredged at several stations off the coast of Southern California in depths ranging from 4 to 32 fathoms.

95. *Tubulipora pulchra* MacGillivray.

Pl. 23, fig. 32, 33, 34, 35.

Tubulipora pulchra MacGillivray, 1885, vol. XXI, p. 94, pl. 2, fig. 1.*Tubulipora fimbria* Lamareck, forma *pulchra* MacG., Waters, 1887, ser. 5, vol. XX, p. 258, pl. VII, figs. 1, 2, 3.

Zoarium small, delicate, white, in younger stages fan-shaped, in form not unlike other colonies of *Tubulipora*, usually becoming divided into three or four elongated lobes radiating from a center, each lobe wider at the distal end than where it arises (pl. 23, fig. 33); originating in a circular disk (fig. 34, *dk.*) surrounded by minute quadrangular teeth (*t.*). Triangular *teeth* visible from the upper side of the colony on many of the lateral zoæcia, and at irregular intervals on the sides of the lobes of the zoarium similar teeth occur (fig. 32, *lat. t.*); numerous large structures of a similar character on the dorsal or under side of the colony (fig. 35 *dor. t.*) *Oæcium* (*oe.*) an inflation of the surface, often lobed. *Oæciostome* large, opening beside, often in front of, a zoecium; *tube of oæciostome* (*oest. t.*) low, widening somewhat upward, compressed. *Oæciopore*, (*oep.*) considerably larger than the oæciostome, compressed, the rim somewhat higher in the middle than at the sides, then sloping downward and outward.

This species is more delicate, and its zoæcia more slender than those of either of the Tubuliporidae described on the preceding pages. It is conspicuously white, and its graceful, delicate colonies are easily recognized growing among the coarse, grey colonies of *T. occidentalis* on fronds, stems, or holdfasts of kelp. A very striking feature of these colonies are the calcareous projections from the sides of the lateral zoæcia. These may be readily detected with very slight magnification. They are larger on the oldest zoæcia, and are sometimes much larger relatively than represented in the drawings. On the dorsal side of most of the zoæcia of a colony occur calcareous projections (fig. 35 *dor. t.*) which resemble feet in having a broad sole by which the colony is fastened to the substratum. These arise as hollow processes in a manner similar to spines, but instead of growing

to a point as do spines, they flatten and expand into two lateral blunt processes (*dor. pro.*). Those on the lateral zoëcia expand more to one side than the other (*lat. t.*) so that they are plainly visible on surface view. Very often considerable debris lies between the lower surface of a colony and the substratum. The dorsal processes slightly raise the colony, or that portion of it which they underlie, supporting it on tiptoe, as it were. The loose attachment of these colonies is apparent in the ease with which they are removed.

As Waters ('87) remarks, the contraction of the apertures of the zoëcia which MacGillivray makes so prominent a character is not very apparent and might well be overlooked. However, it often occurs especially in those zoëcia which show other irregularities of form.

T. pulchra is obtained at several localities on the coast of Southern California: on the shore kelp at San Diego and dredged at various localities off shore in depths ranging from 11 to 32 fathoms.

Mesenteripora Blainville.

- Mesenteripora* Blainville 1834.
Diastopora Milne-Edwards, 1837.
Bidiastopora (part), d'Orbigny, 1847.
Ditaxia (part), Hagenow, 1851.
Mesenteripora, Wood, 1844.
Mesenteripora, Busk, 1849.
Mesenteripora, d'Orbigny, 1850-52.
Mesenteripora, Busk, 1875

Zoarium erect, bilaminar. *Zoëcia* opening on both surfaces. *Oëcia* an inflation of the surface.

96. *Mesenteripora meandrina* (Wood) Busk.

Pl. 23, figs. 36, 37, 38.

- Diastopora meandrina* Wood, 1844, vol. xiii, p. 14.
Mesenteripora meandrina, Busk, 1859, p. 109, pl. 17, fig. 2; pl. 18, fig. 4; pl. 20, fig. 2.
Mesenteripora meandrina, Busk, 1875, p. 29.

Zoarium bilaminar, forming a contorted, convoluted mass loosely enveloping stems and roots, especially the holdfasts of kelp; sometimes forming a tangled mass with the narrow fronds of seaweed (pl. 23, fig. 37); beginning as a simple, primitive

disk from which there grow tubular zoæcia curving in opposite directions, and forming a fan-shaped expansion similar to any young tubuliporidian colony. The two-layered condition results from the ridges which occur at irregular intervals over the unilaminar sheet, sometimes in a longitudinal, sometimes in a transverse direction, and which growing upward form the erect, bilaminar layers (fig. 38) the laminae becoming highly convoluted. Zoæcia tubular, alternate, the older zoæcia of a colony sub-erect (fig. 36), the younger arising near the growing edge (*gr. ed.*) and elevated but slightly, if at all, above the surface of the zoarium. Oæcium (*oe.*) an inflation of the surface of the colony and involving a number of zoæcia. Oæciostome? Oæciopore?

In adult colonies the ovicell is frequently found, but unfortunately it has been impossible to distinguish its aperture. It frequently occupies a space in the hollows formed by the folding of the laminae, near the upper or growing edge.

M. meandrina has been obtained at three stations on the coast of Southern California; growing on the roots of kelp at Whites Point, also dredged off shore at San Pedro in from 17 to 32 fathoms, and again off Coronado Islands in depths ranging from 18 to 21 fathoms.

Idmonea Lamouroux.

Idmonea Lamouroux, 1821.

Idmonea, Smitt, 1865.

Idmonea, Busk, 1875.

Idmonea, Hineks, 1880.

Idmonea, Harmer, 1898.

Zoarium ramose, erect; branching dichotomous or irregular, free or anastomosing. Zoæcia tubular, immersed for most of their length, orifice frequently projecting; disposed on one side of the branch only, in parallel, transverse, or oblique rows on each side of a median line.

As Harmer ('98) has pointed out, considerable confusion exists in regard to the generic differences between *Tubulipora* and *Idmonea*, and in his critical discussion of the species of *Tubulipora* that investigator removes at least one species of *Idmonea* to the genus *Tubulipora*, viz., *I. serpens*. The chief difference between the two genera, according to most writers, is

in the erect habit of growth of the adult form of *Idmonca*. Thus Hincks ('80) p. 451, says, "in their adult state the *Idmoncae* are attached by a somewhat expanded base, the surface of which is lined or striated; but their earliest stage is, I believe, identical with that of *Tubulipora*." As an illustration of this statement he uses *I. serpens* which Harmer has later shown to be a true *Tubulipora*. I recognize the difficulty, as I have said before, of establishing a genus on mere habit of growth, and yet I hesitate to ignore the genus *Idmonca* since the species here regarded as *Idmonca* is so distinctly different from those forms identified as *Tubulipora*. Unfortunately, though having searched diligently through a large quantity of material, I have not found the ovicell.

97. *Idmonca californica* d'Orbigny.

Pl. 23, figs. 39, 40, 41.

Idmonca californica d'Orbigny, 1852, p. 732.

Idmonca californica, Conrad, 1855, vol. vii, p. 441.

Idmonca californica, Gabb and Horn, 1862, p. 168, pl. 21, fig. 56.

Idmonca californica, Busk, 1875, p. 16.

Zoarium erect, composed of numerous dichotomously branching stems (pl. 23, fig. 41) which in many colonies anastomose, forming a rounded, reticulated mass of stems seven or more centimeters high and as many broad. Branches one, two or three millimeters wide, the zoecia opening on the one side only. *Zoecia* tubular, long, extending one behind the other, so that in cross-section there are three or four transverse rows of openings of different sizes representing cross-sections of zoecial tubes at different levels; zoecial orifices six or more in a transverse row, sometimes directed straight forward, more often half of them slightly more inclined to one side than to the other, so that while a median line is not as distinct as in some species, it is more or less apparent (fig. 39); often bent at right angles to the surface, projecting prominently, the tubular projection being more delicate than the ordinary zoecial wall and without the pores; marked by circular lines. *Oecia*?

There is much variation in the width of the branches and the mode of branching in specimens brought from different

depths. Some colonies (fig. 40) have relatively broad branches and show little, if any, anastomosis. These colonies were obtained in relatively deep water. From shallower water and from the shore come large masses of complexly anastomosing colonies (fig. 41). Wherever two branches touch each other apparently, or where they touch a hard substance, as a shell, they grow fast.

This species is very abundant, especially in deep water, being frequently taken in the dredge off shore between Santa Catalina Islands and Coronado Islands in depths ranging from 150 fathoms to 6 fathoms.

37. *Crisulipora* gen. nov.

Zoarium dendroid, calcareous, composed of segments or internodes united by chitinous joints. *Zoæcia* tubular, disposed in several alternate rows. *Oæcium* an inflation of the surface of an internode.

This genus is unlike other genera of the Tubuliporidae in possessing chitinous articulations between the branches, and in being attached by flexible rootlets. In these two respects it resembles *Crisia*. In the form and arrangement of its zoæcia, however, and more especially in the formation of its oæcium, this genus resembles members of the family Tubuliporidae. In some respects it seems to be allied with *Filisarsa* Waters, or *Tervia* Jullien. But the differences between it and either of these genera seem to warrant its erection into a new genus.

98. *Crisulipora occidentalis* sp. nov.

Pl. 21, figs. 22, 23, 24.

Zoaria forming large, stiff, brittle masses, from 25 to 30 mm. in height (pl. 21, fig. 23) attached by a few rootlets extending from the lower zoæcia, some of which possess a hook or clasp (fig. 24, *h.*) by which the colony is anchored; others possessing a long, stolon-like process (*sto.*) entangled in sponge, masses of hydroids, other bryozoa, etc. *Internodes* long, typically from 6 to 8 mm., consisting of a varying number of zoæcia, from 10 to 30 or more; each internode beginning in two zoæcia (fig. 22) which spread widely; between these other zoæcia arising, the rows in the fertile internode (*fer. int.*) at least, increasing to

seven or eight, then gradually narrowing again to two zoœcia. Branching extremely irregular, following no particular method; arising both from lateral and ventral zoœcia at any point of an internode and becoming more profuse toward the distal ends of the branches. *Basis rami* (*ba. r.*) often of great length, and as in *Crisia* being merely the proximal portion of those zoœcia which have developed a non-calcified, somewhat thickened chitinous ring in the wall, serving as a flexible joint. *Joints* (*j.*) large, light-colored, yellow or amber. *Zoœcia* long, slender, connate for part of their length, curving sharply forward, and projecting frequently half their length; proximal portion scantily punctate, distal portion less distinctly punctate; number in an internode not constant, arrangement more or less alternate, except in the oœcial internodes where it is regularly alternate. *Oœcial internodes* always longer and broader than those that do not produce ovicells; growing rather suddenly broader by an increase in the number of rows of zoœcia at the point where the ovicell begins, and growing narrower toward the distal extremity. *Oœcia* (*œ.*) found on the younger internodes, numerous, large; formed by an inflation of the ventral wall, extending partially over and between the zoœcia whose distal extremities project through the oœcium, but unaffected apparently by its growth around them; beginning about one-fourth the length of the internode from the joint, and occupying its middle half; embryos numerous. *Oœciostome* below the summit of the ovicell; *tube of oœciostome* (*œst. t.*) prominent, arising beside a zoœcium near the distal end of the ovicell, adnate to it for part of its length, then growing smaller than a zoœcial tube and curving freely forward. *Oœciopore* (*œp.*) circular, directed upward.

Adult ovicells frequently possess a large number of larvae in all stages of development. Owing to the spindle-shape of the ovicell, its interior is divided into long, narrow passages which are the spaces between the zoœcia; in these the embryos develop in long, narrow chains, or strands, resembling beads strung on a string. In reality they are held together by strands of tissue which form a network that holds the larvae in a chain and holds the chains together more or less closely. The question

of embryonic development in this species is one of interest which the writer hopes to investigate in the future. Enough has been seen to establish the fact of embryonic fission similar probably to that already known for *Crisia* and for several genera of the Tubuliporidae.

Crisulipora occidentalis may be obtained at low tide almost anywhere on the coast of Southern California. It is abundant at Deadmans Island, San Pedro; at various places in and around San Diego Bay: near Point Loma, at Ballast Point, and on the piles on the water front. It has been dredged off the coast, from San Pedro to San Diego in depths ranging from 2 to 17 fathoms.

Entalophora Lamouroux.

- Entalophora* Lamouroux, 1821.
Pustulopora Blainville, 1834.
Pustulopora, Milne-Edwards, 1838.
Pustulopora, Busk, 1859.
Pustulopora, Busk, 1875.
Entalophora, Hincks, 1880.

Zoarium erect, simple or branched, rising from a more or less expanded base, composed of decumbent tubes, or from a circular base; branches cylindrical. *Zoæcia* tubular, opening on all sides of the branches and main stem, their apertures of approximately equal diameter.

99. *Entalophora raripora* d'Orbigny.

Pl. 24, figs. 42, 43.

- Entalophora raripora* d'Orbigny, 1847, p. 267.
Pustulopora proboscidea, Milne-Edwards, 1838, vol. IX, ser. 2, p. 219, pl. 12, fig. 2.
Entalophora raripora d'Orbigny, 1850-'52, vol. v, p. 787.
Entalophora santonensis d'Orbigny, 1850-'52, vol. v, p. 787, pl. 623, figs. 15-17.
Pustulopora proboscidea, Busk, 1875, p. 21, pl. xvii A.
Pustulopora proboscidea, Waters, 1879, vol. iii, ser. 5, p. 274.
Entalophora raripora, Waters, 1884, vol. xl, p. 686.
Pustulopora proboscidea, Busk, 1884-'86, vol. xvii, p. 19, pl. iv, fig. 1.

Zoarium erect, branched or unbranched, consisting of a number of long, tubular zoæcia whose proximal extremities are united for part of their length into a calcareous column or stem, and whose distal portions are free and curve outward at almost right

angles to the column. *Zoecia* relatively few in number, frequently but four, projecting in four directions at any given level of the stalk or branch. *Oecia* unknown.

The colonies here described are simple and unbranched. No ovicells are found, this and their lack of branches being perhaps due to their youth.

E. raripora was obtained at Monterey, California, in 90 fathoms.

100. *Entalophora capitata* Robertson.

Pl. 24, figs. 44, 45.

Entalophora capitata Robertson, 1900, vol. 2, p. 328, pl. XXI, fig. 12, not 11, 13.

Zoarium arising from a flattened or incrusting base and growing from 5 to 6 or 8 mm. in height (pl. 24, fig. 44). *Zoecia* tubular, uniting in a short, stout column terminating in a broad somewhat rounded head; distal ends free, usually extending for a considerable distance beyond the general surface of the colony, both of the supporting column and of the head. *Oecium* an inflation of the surface of the head (fig. 45, *oe.*) *Oeciostome* and *oeciopore* coinciding (*ocp.*), slightly compressed, opening beside the zoecial aperture.

E. capitata obtained on shore rocks at Orca, Prince Williams Sound, Alaska, at low tide; also dredged at Juneau, Alaska, in 10 fathoms.

Heteropora Blainville.

Heteropora Blainville, 1834.

Heteropora, Lonsdale, 1845.

Heteropora, Busk, 1859.

Heteropora, Waters, 1879.

Heteropora, Busk, 1879.

Heteropora, Whiteaves, 1882.

Zoarium erect, branching. *Branches* cylindrical, in well-grown colonies frequently anastomosing; surface furnished with openings of two sizes, the larger being the orifices of zoecia, the smaller, the openings of the interstitial canals or tubes.

According to Busk ('79) *Heteropora* is an ancient genus well known among fossil Bryozoa as far back as the Cretaceous. The characteristic feature of this genus, as the name indicates,

is the presence on the surface of the colony of pores of different sizes (pl. 24, fig. 53). These pores are either zoæcial apertures (*zoc. ap.*) or the apertures of other smaller tubes, the so-called interstitial canals (*inter. can.*) occurring between the zoæcia. Busk describes the surface of a colony or branch as *even*, meaning doubtless, that it is not roughened by projecting tubes. This is the usual appearance except in portions where the surface may be protected from contact with other objects. In such protected places the zoæcial tubes extend a considerable distance beyond the general surface (fig. 55, *zoc.*) the zoæcial projection being non-porous, frequently annulated, expanding sometimes as it rises. This extension of the zoæcia beyond the surface is mentioned also by Whiteaves ('82) as characteristic of the Vancouver form. The smaller pores are apertures of relatively minute tubes whose function, as Busk suggests, may be to afford means by which fluid may permeate the colony. The walls of both zoæcia and interstitial canals are porous, as are the zoæcia throughout the Cyclostomata.

If one examines the growing tips of a branch, the tubular openings found there are for the most part those of the zoæcia in various stages of maturity. Between them, formed by minute triangular spaces where the walls of zoæcia do not come into contact, are the interstitial spaces. These, which at first are triangular or quadrangular, soon become circular. As growth proceeds, both zoæcia and interstitial canals curve outwards, and although at the growing tips these tubes are parallel to the axis of the branch, when adult they curve almost at right angles with the axis of a branch and the apertures open laterally, the larger zoæcial apertures being surrounded with a circle of small interstitial openings (fig. 53).

101. *Heteropora pelliculata* Waters.

Pl. 25, figs. 51, 52, 53, 54, 55.

Heteropora pelliculata Waters, 1879, vol. 2, pl. 15, figs. 1, 2, 3, 4, and 7.

Heteropora ncozcalanica Busk, 1879, vol. 14, p. 725, pl. 15, figs. 1-4.

Heteropora sp.? Whiteaves, 1882, ser. 3, vol. 24, p. 279.

Entalophora capitata Robertson, 1900, vol. 2, 328, pl. XXI, figs. 11 and 13, not fig. 12.

Zoarium erect, composed of short, divergent, cylindrical branches, frequently dividing dichotomously and terminating in blunt rounded extremities. When the branches closely approximate each other, they frequently coalesce, giving the whole colony a complexly reticulated appearance (pl. 25, figs. 51 and 52). *Zoœcial* aperture (fig. 53, *zoc. ap.*) circular, large, surrounded by numerous (6-8) smaller, variously shaped pores, the openings of the interstitial canals (*inter. can.*). Surface, except toward the tips of the branches, covered with a delicate calcareous layer which hides the interstitial pores (fig. 54) but which except in the oldest parts of the colony leaves the zoœcial apertures unimpeded.

Living *Heteropora* has been reported from comparatively few localities, viz., from the neighborhood of Japan and Australia by Waters, from New Zealand by Busk, and from Vancouver Island by Whiteaves. Busk has expressed the opinion that *H. neozelanica* may prove to be identical with the Japanese species, *H. pelliculata*, and Whiteaves regards the species found on Vancouver Island as similar in all respects to the Japanese species. In our collection *Heteropora* has been obtained from several localities from Alaska southward. One specimen found on Channel Rock, Puget Sound, was a clear lemon yellow when living, the color soon disappearing when placed in alcohol. This colony, in a perfect state, was about five centimeters high and somewhat broader, and is remarkable for the complexity of its branching, the anastomosis which has taken place giving it a highly reticulated appearance (fig. 51). The surface is covered by a thin calcareous layer (fig. 54) so that the pores of the interstitial canals are not discernible over most of the surface. On the inner protected portions of the surface the zoœcial tubes project to a marked degree, but on the exposed portions they are almost level with the surface of the branch. The other colonies obtained are of a somewhat stouter habit of growth and show less anastomosis, as a rule (fig. 52). In all of these the polypides and the tissue lining the zoœcia and interstitial canals are purplish, and the colonies after long immersion in alcohol are of a dark color.

H. pelliculata is probably abundant on the western coast of America.

A specimen obtained at Juneau, dredged in ten fathoms and formerly identified as an *entolophora* (:00, p. 328) is now thought to be a young colony of *H. pelliculata*. Obtained also on Channel Rocks, Puget Sound, at extreme low tide; dredged at San Juan County, Puget Sound, from a depth unknown, and obtained at an unknown locality farther south, probably on the coast of northern California.

Lichenoporidae Smitt.

Lichenoporidae Smitt, 1866.

Discoporellidae Busk, 1875.

Lichenoporidae, Hincks, 1880.

Zoarium discoid, adnate or partially free. *Zoœcia* tubular, erect or suberect, disposed in series which radiate from the center; central part of a colony cancellated or porous, the cancelli or pores extending into the spaces between the series of zoœcia, partially immersing them.

Lichenopora Defrance.

Lichenopora Defrance, 1823.

Discoporella Gray, 1848.

Discoporella, Smitt, 1866.

Discoporella, Busk, 1875.

Lichenopora, Hincks, 1880.

Lichenopora, Waters, 1890.

Lichenopora, Harmer, 1896.

Zoarium disk-shaped, flat on the under surface by which it is attached to the substratum to which it closely adheres, more or less convex on the upper surface; originating in a primitive disk, the calcified larval body, from which grow the tubular zoœcia curving right and left, forming a fan-shaped, then a circular expansion. *Zoœcia* in radiating rows either in single series, or in several connate series. *Cancelli* numerous in the central portion of the disk as well as between the radiating rows of zoœcia. *Oœcium* an inflation of the surface; *oœciostome* distinctive for each species.

In size, habitat, and superficial appearance colonies of *Lichenopora* closely resemble those of *Tubulipora*. The difference, which is easily detected upon slight magnification, lies in the cancelli which appear in the spaces between the series of zoœcia and over the central space between the bases of zoœcia.

These cancelli, or alveoli as they are variously called, are formed by secondary, calcareous thickenings or septa which begin to form very early in the history of the colony, and according to Harmer ('96) bear a close relation to the growth of the ovicell. This investigator says "the presence of cancelli between the rows of zoecia is an indication that the ovicell is developing, even although no other evidence is obtained of its presence." According to the same authority, each colony of *Lichenopora* possesses but one ovicell, the aperture of which is formed secondarily. A second characteristic is frequently shown in the shape of the zoecial apertures, which frequently end in a tapering point either single or bifid.

There are three species of *Lichenopora* on the Pacific coast distinguished in the key given below partly by their habit of growth, partly by the oecial aperture.

KEY TO THE SPECIES OF LICHENOPORA.

- | | |
|---|------------------------|
| 1. Zoecia in single rows; oecial aperture flaring | 2 |
| 1. Zoecia not in single rows; oecial aperture not flaring | 3 |
| 2. Rows of zoecia radiating regularly in alternating single series | <i>L. radiata</i> |
| 2. Rows of zoecia radiating irregularly, in more or less alternating series | <i>L. verrucaria</i> |
| 3. Zoecia in connate bundles, irregularly radiating; oeciopore smaller than the aperture of a zoecium | <i>L. californica.</i> |

102. *Lichenopora californica* (d'Orbigny) Conrad.

Pl. 25, figs. 48, 49.

Unicavca californica d'Orbigny, 1852, p. 972.

Lichenopora californica, Conrad, 1855, p. 44.

Lichenopora californica, Gabb and Horn, 1862, p. 176.

Discoporella californica, Busk, 1875, p. 32, pl. 30, fig. 5.

Lichenopora californica, Waters, 1890, p. 283, pl. 15, fig. I.

Zoarium discoid, adnate, adhering to kelp, eel grass, etc.; colonies small, oval or circular (pl. 25, fig. 49). *Zoecia* connate in radiating series, one, two, or three rows of zoecia in each series (fig. 48) erect, almost vertical, throughout more than half their length, the central part of the colony and the portions between the zoecia, therefore, much depressed. *Oecium* (*oe.*) an

inflation of the surface, beginning on the cancelli (*cen. can.*) of the central portion and extending into the various depressed portions between the connate series of zoæcia. *Oaciostome* situated to one side of the center. *Oaciopore* (*oep.*) circular or compressed, smaller than the aperture of a zoæcium.

This species is reported by d'Orbigny from Lower California, and by Conrad from San Diego and San Pedro, California. Neither of these writers gives more than a meagre description of the species, and this identification is based on the description and plate of Busk ('75) who reports it from the neighborhood of San Diego and San Pedro, the region in which our specimens were obtained. *L. californica* might, perhaps, be identified on its habit of growth, since it is the only *Lichenopora* known from this coast which possesses zoæcia in *connate* radiating series.

L. californica has been obtained in rather small quantity growing on eel grass dredged near Ballast Point, San Diego Bay, in from 5 to 8 fathoms.

103. *Lichenopora radiata* (Audouin) Hincks.

Pl. 24, fig. 46, 47.

Melobesia radiata Audouin, 1826, t. 1, p. 235, pl. 6, fig. 3.

Unicavca radiata, d'Orbigny, 1851, p. 971.

Discoporella radiata, Busk, 1875, p. 32, pl. 34, fig. 3.

Lichenopora radiata, Hincks, 1880, p. 476, pl. 68, figs. 9, 10.

Zoarium circular, adnate, forming conspicuous white patches on kelp, varying in size from six to eight millimeters in diameter (pl. 24, fig. 47). *Zoocia* radiating from the center in single connate rows. In older colonies the radiating rows of zoæcia alternately longer and shorter; raised slightly at the distal end, the upper margin of each zoæcium frequently terminating in a single, or bifid process. *Cancelli* numerous, (fig. 46 *can.*) *Oacium* (*oc.*) large, occupying the central space as well as the spaces between the rows of zoæcia. *Oaciostome* (*ocst.*) circular, about the size of a zoæcial aperture; *oaciopore* (*oep.*) large, circular, sometimes somewhat compressed, but always larger in diameter than a zoæcial aperture.

According to Hincks ('80) *L. radiata* may have as many as

three apertures to one ovicell, while according to the observations of Harmer ('96) we should not expect to find more than one oœciopore in the oœcium of this genus. In my study of the specimens of *L. radiata* it has often been found extremely difficult to decide among the numerous and variously shaped openings on the surface of a colony whether or not there may be more than one oœciopore, and if not, which one is the oœciopore. In most cases, however, if examined very closely with a Zeiss binocular, the true oœciopore could be detected, and other apparent openings of the ovicell could be referred to thin places in the roof of the ovicell, or to the apertures of zoœcia. The drawing (fig. 46) represents a young colony, one in which no doubt can be entertained as to its possession of a single oœcial aperture. This always occurs, as far as I can judge, near the outer edge of the central area of the colony near the base of a zoœcium. I have never been convinced that what may have resembled an oœciopore occurring in the radii between the series of zoœcia, or toward the outer edge of the colony, was really one.

L. radiata is found rather abundantly on the sea weed near shore. It occurs apparently only on the southern shores, having been obtained at San Diego both on the fronds and the holdfasts of kelp, and dredged in depths ranging from 17 to 32 fathoms. Obtained also at Avalon, Santa Catalina Island.

104. *Lichenopora verrucaria* (Fabricius) Hincks.

Pl. 25, fig. 50.

?*Madrepora verrucaria* Linnaeus, 1758, ed. 10, p. 793.

Madrepora verrucaria, Fabricius, 1780, p. 430.

Discoporella verrucaria, Smitt, 1866, p. 405, pl. X, figs. 6-8; pl. XI, figs. 1-6.

Discoporella verrucaria, Busk, 1875, p. 31, pl. 28, figs. 2, 3.

Lichenopora verrucaria, Hincks, 1880, p. 476, pl. lxiv, figs. 4, 5.

Zoarium subcircular, very convex, at times subconical (pl. 25, fig. 50). *Zoœcia* stout, slightly raised, disposed more or less regularly in radiating lines, not connate; zoœcial aperture obliquely elliptical, the margin often prolonged into a single, or double process. *Oœcium* (*oe.*) an inflation of the surface of the disk, occupying all of the central portion of the colony and

extending between the radiating rows of zoœcia. *Oœciopore* (*ocp.*) flaring.

This species is usually ascribed to Fabricius and doubtfully to Linnaeus. It seems to be a strictly Arctic form, and the only specimens in this collection were found growing on *Flustrella* from Pribilof Islands, Behring Sea, collected on shore at low tide.

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Wellesley, Mass., August, 1909.

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ABBREVIATIONS USED.

<i>ba. att.</i> —basal attachment.	<i>int.</i> —internode.
<i>ba. r.</i> —basis rami.	<i>inter. can.</i> —interstitial canal.
<i>br.</i> —branch.	<i>im. oe.</i> —immature oœcium.
<i>can.</i> —cancelli.	<i>j.</i> —joint.
<i>cen. can.</i> —central cancelli.	<i>lat. t.</i> —lateral tooth.
<i>chi. fl.</i> —chitinous floor.	<i>oe.</i> —oœcium.
<i>chi. t.</i> —chitinous tube.	<i>oe. c.</i> —oœcial cone.
<i>com. oep.</i> —compressed oœciopore	<i>oe. int.</i> —oœcial internode.
<i>d.</i> —denticle.	<i>oep.</i> —oœciopore.
<i>dk.</i> —disk.	<i>ost.</i> —oœciostome.
<i>d. j.</i> —double joint.	<i>oest. t.</i> —oœciostomal tube.
<i>d. w.</i> —dorsal wall.	<i>op.</i> —operculum.
<i>dor. pro.</i> —dorsal process.	<i>r.</i> —rootlet.
<i>dor. t.</i> —dorsal tooth.	<i>sep.</i> —septum.
<i>emb.</i> —embryo.	<i>sp.</i> —spine.
<i>fer. int.</i> —fertile internode.	<i>sto.</i> —stolon.
<i>fl. oep.</i> —flaring oœciopore.	<i>t.</i> —tooth.
<i>gr. ed.</i> —growing edge.	<i>z. or zoe.</i> —zoœcium.
<i>h.</i> —hook.	<i>zoe. ap.</i> —zoœcial aperture.

EXPLANATION OF PLATES.

As far as possible all figures made with the aid of a camera lucida.

PLATE 18.

Fig. 1. *Crisia franciscana* sp. nov. Habit sketch. $\times 1$.

Fig. 2. *C. franciscana*. A portion of a colony showing method of branching, and formation of ordinary and of oœcial internodes. The ordinary uniserial internode consisting of a zoœcium (*zoc.*) giving origin to two other zoœcia (*br.*). The oœcial internode consisting of the zoœcium (*z¹.*) the first member of the internode, the oœcium (*oc.*), the second member, the zoœcium (*z³.*), a third member. Arising from a basis rami (*ba. r.*) on the third zoœcium is a fourth zoœcium (*z⁴.*), which serves to continue the branch upward. The prominent oœcium (*oc.*) having a well developed tube (*ocst. t.*) at its summit, bent slightly backward and upward. $\times 36$.

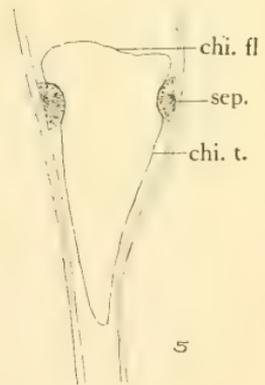
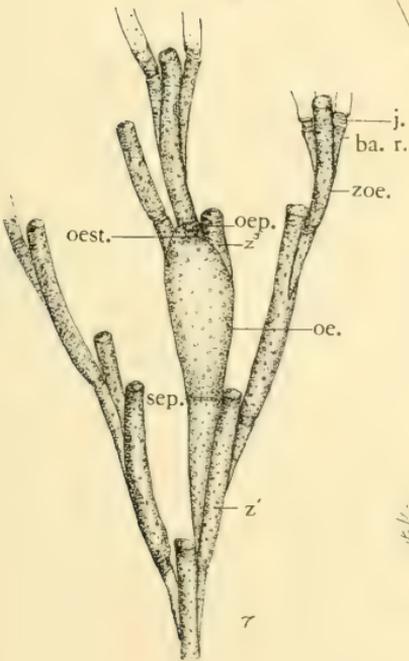
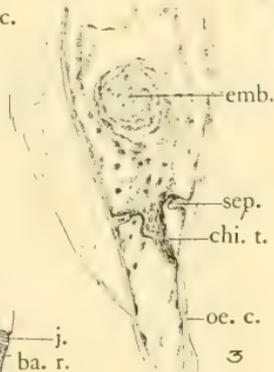
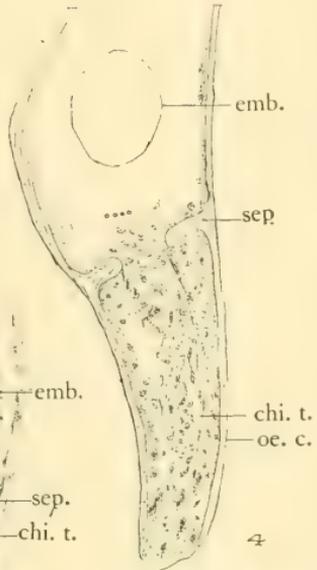
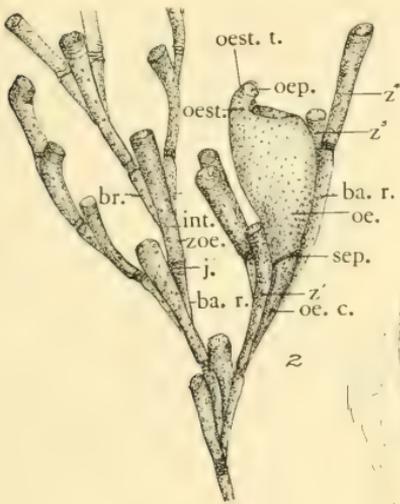
Fig. 3. *C. franciscana*. A cross-section of an ovicell containing a developing embryo in a young stage (*emb.*) and showing, also, an early stage in the growth of the septum (*sep.*).

Fig. 4. *C. franciscana*. Cross-section of an ovicell in an older stage of growth, showing a relatively large embryo (*emb.*) and a septum (*sep.*) whose growth is about completed. The chitinous tube (*chi. t.*) growing down into the oœcial cone (*oc. c.*) shows only at intervals in this section.

Fig. 5. *C. edwardsiana*. Diagrammatic representation of a cross-section of the ovicell of *C. edwardsiana* showing the cellular septum (*sep.*) with the chitinous tube (*chi. t.*) and chitinous floor (*chi. fl.*).

Fig. 6. *Crisia geniculata*. Milne-Edwards. Habit sketch, natural size. $\times 1$.

Fig. 7. *C. geniculata*. A portion of a colony showing method of branching, etc. This, with position of ovicell and abbreviations, are in all essential respects what have just been given for *C. franciscana*, fig. 2. $\times 36$.



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PLATE 19.

Fig. 8. *C. geniculata*. A portion of a branch showing œcial internode containing five zoœcia, the œcium (*œc.*) being the third member of the internode, instead of the second member as in Fig. 7. $\times 36$.

Fig. 9. *Crisia edwardsiana* (d'Orbigny) Busk. Habit sketch. $\times 1$.

Fig. 10. *C. edwardsiana*. A portion of a colony showing method of branching and formation of ordinary and œcial internodes. Ordinary internodes consisting sometimes of a single zoœcium (*zoœ.*) sometimes of a spine (*sp.*) originating as does a zoœcium in a basis rami (*ba. r.*). The œcial internode consisting of three members the œcium (*œc.*) being the second. Separating the inflated portion of the œcium from the slender conical portion is the septum (*sep.*). $\times 36$.

Fig. 11. *Crisia occidentalis* Trask. Habit sketch. $\times 1$.

Fig. 12. *C. occidentalis*. A portion of a colony showing branching, especially of the œcial internode. In this, the œcium (*œc.*) is the fifth member of the internode; the first branch (*br. 1*) arising in a basis rami (*ba. r.*), not wedged in, but attached to the side of the third zoœcium; the second branch (*br. 2*) arising on the side of the sixth zoœcium, the zoœcium which pairs with the œcium; the third branch (*br. 3*) arising on the ninth zoœcium just above the summit of the ovicell. The distal portion of the œcial internode carrying the zoarial growth upward. $\times 36$.

Fig. 13. *Crisia operculata* sp. nov. A portion of colony showing the branching of the œcial internode. Here the first branch (*br. 1*) arises in a slender basis rami (*ba. r.*) attached to the third zoœcium; the second branch (*br. 2*) arises on the sixth zoœcium which pairs with the ovicell, the fifth member of the internode. The distal portion of the œcial internode (*œc. int.*) continues the zoarial tuft upward in a line with the axis of the œcium. $\times 36$.

Fig. 14. *C. operculata*. The distal portion of the œcium showing the operculum (*op.*) and the œciopore (*œp.*) at higher magnification. About $\times 80$.

Fig. 15. *C. operculata*. The same as Fig. 14. with a portion of the front, or ventral wall of the ovicell broken away to show the formation of the operculum (*op.*) as a continuation of the dorsal wall (*d. w.*). About $\times 80$.

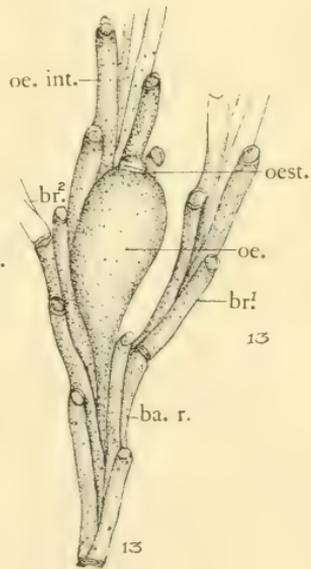
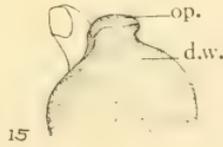
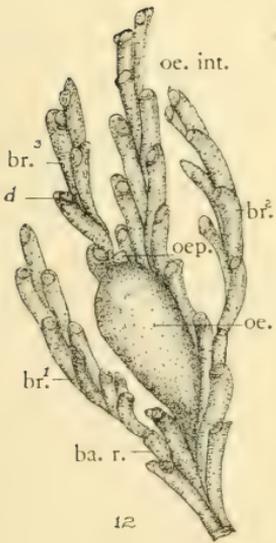
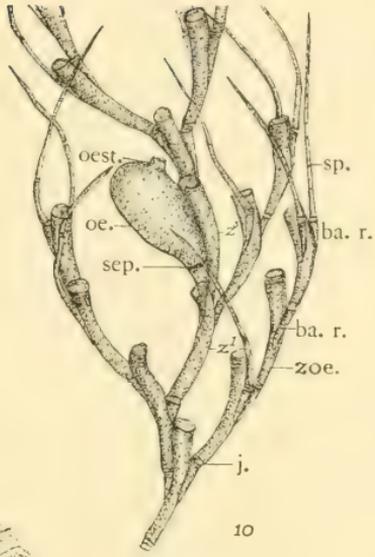
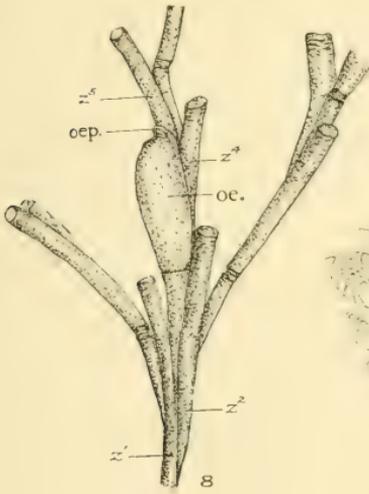


PLATE 20.

Fig. 16. *Crisia pacifica*, sp. nov. A portion of a young tip of a branch showing the method of branching when the oœcium is low in the internode, the third member (*oe.*). The first branch of this internode corresponding to the second branch of a typical internode, occurs on the fourth zoœcium, the zoœcium alternating with the oœcium (*br. 2*), while the next branch occurs on the seventh zoœcium (*br. 3*), its origin being almost hidden by the oœcial aperture. $\times 36$.

Fig. 17. *C. pacifica*. Habit sketch. $\times 1$.

Fig. 18. *Crisia maxima* sp. nov. A portion of a branch showing a typical case of the relation between the position of the oœcium and the branching of the oœcial internode. The oœcium being the seventh member of the internode, the first branch (*br. 1*) occurs on the fifth zoœcium, the second branch (*br. 2*) on the eighth zoœcium, that member of the internode which pairs with the oœcium; the third branch (*br. 3*) on the eleventh zoœcium, its joint appearing just behind the oœcial aperture (*oep.*). $\times 36$.

Fig. 19. *C. maxima*. Habit sketch. $\times 1$.

Fig. 20. *Crisia pugeti* sp. nov. A portion of a branch showing the oœcium (*oe.*) with the long flattened tube of the oœciostome and the oœciopore (*oep.*). $\times 39$.

Fig. 21. *C. pugeti*. The upper part of another ovicell from the same colony as that from which fig. 20 was taken, showing a variation in the shape of the tube of the oœciostome (*oest. t.*) and the circular oœciopore (*oep.*) $\times 36$.

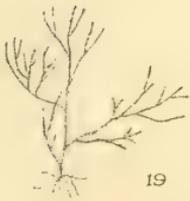
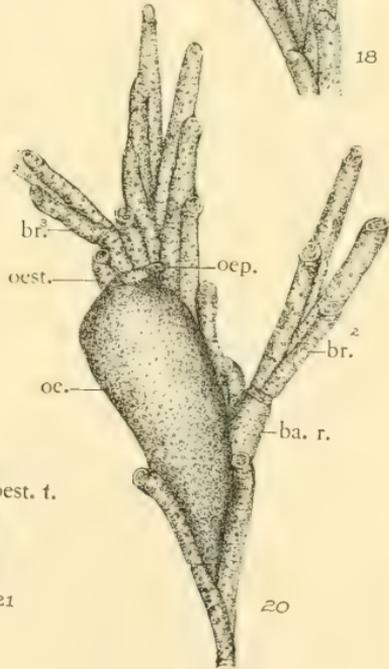
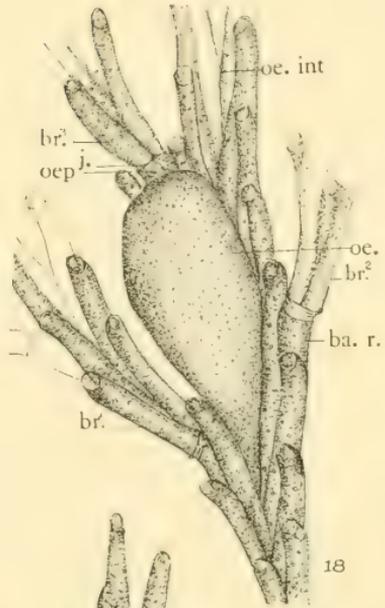
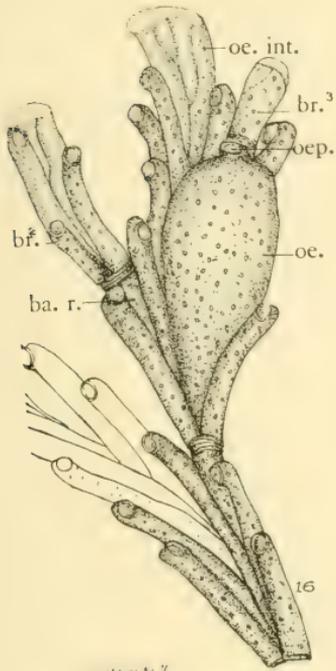


PLATE 21.

Fig. 22. *Crisulipora occidentalis* sp. nov. An oœcial internode, showing its origin in two zoœcia in whose walls the first chitinous joint (*j.*) occurs, and the mode of formation of three branches; also, the oœcium (*oe.*) distinguished by its coarsely punctate wall, with the tubular aperture (*oest. t.*) and circular oœciopore. The tubes at the distal extremity of the internode, the proximal portions of which only are shown, give rise to another internode. $\times 20$.

Fig. 23. *Cr. occidentalis*. Habit sketch. $\times 1$.

Fig. 24. *Cr. occidentalis*. A portion of the lower part of a colony showing a rootlet (*r.*) which grows long, penetrating masses of other material; another which is shorter and possesses a hook (*h.*) or process which has laid hold of a grain of sand or a pebble; and a stolon-like process (*sto.*) which grows horizontally sending up zoœcia at intervals which produce new branches. From the first zoœcium (*zo.*) there arise two tubes one of which gives rise to a double joint (*d. j.*) giving off branches at an angle to each other and hence in different directions.

Fig. 25. *Tubulipora flabellaris* Fabricius. A small colony showing its origin in a primary disk (*dk.*) and containing one complete ovicell (*oe.*) with typical oœciostomal tube (*oest. t.*) and compressed oœciopore (*oep.*); showing also two immature ovicells (*im. oe.*). $\times 40$.

Fig. 26. *T. flabellaris*. An older colony than that shown in fig. 25, showing an older stage of growth. $\times 16$.

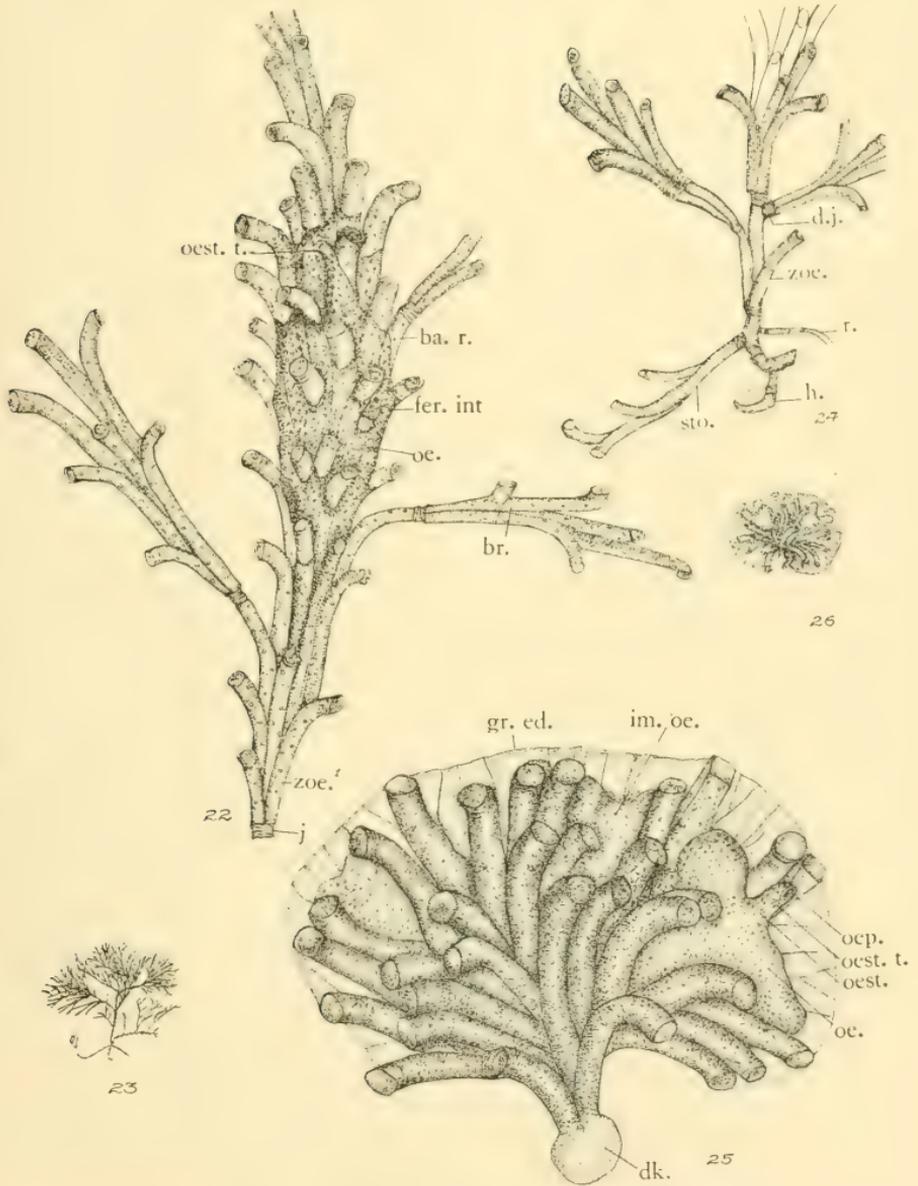


PLATE 22.

Fig. 27. *Tubulipora pacifica* sp. nov. A small colony showing the arrangement of the zoëcia and the shape and position of two oëcia; one oëcium with flaring oëciopore (*fl. oep.*), the other with a somewhat compressed oëciopore (*com. oep.*). $\times 40$.

Fig. 28. *T. pacifica*. Habit sketch. $\times 8$.

Fig. 29. *Tubulipora occidentalis* sp. nov. A portion of a colony to show the arrangement of the zoëcia in bundles and the position of an oëcium with typical oëcial tube (*oest. t.*) and oëciopore (*oep.*) $\times 25$.

Fig. 30. *T. occidentalis*. A colony growing round a stem. $\times 1$.

Fig. 31. *T. occidentalis*. A colony growing on a flat surface. $\times 1$.

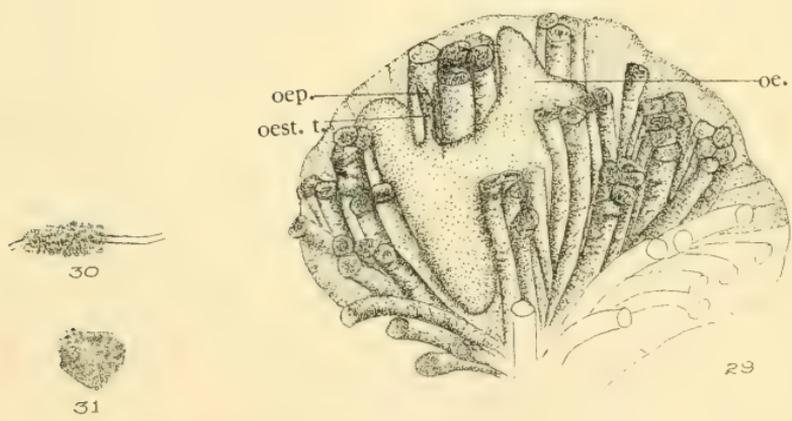
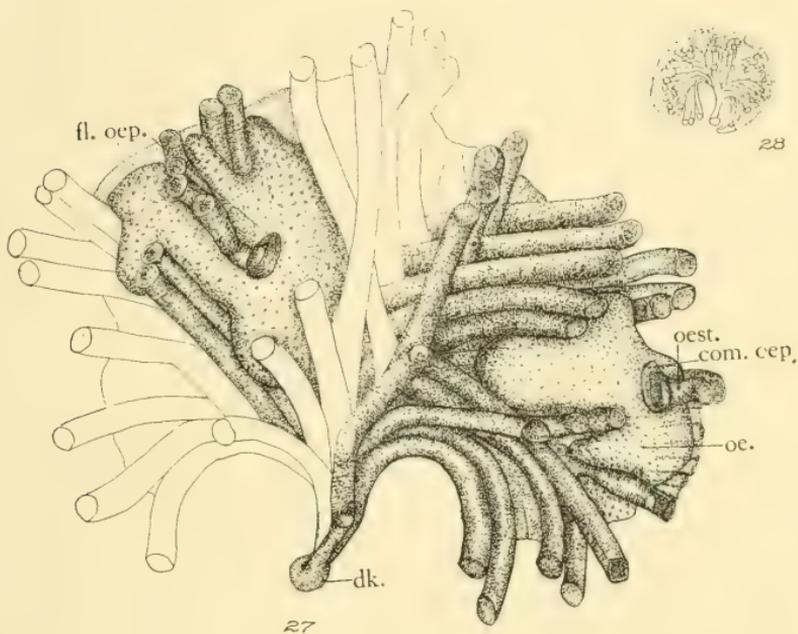


PLATE 23.

Fig. 32. *Tubulipora pulchra* Macgillivray. The distal extremity of a lobe of a colony showing an ovicell (*oe.*) with characteristic aperture (*oest.*) and oeciopore (*oep.*). $\times 40$.

Fig. 33. *T. pulchra*. Habit sketch. $\times 1$.

Fig. 34. *T. pulchra*. The primary disk (*dk.*) surrounded with a row of teeth (*t.*); also the proximal extremities of two zoecia with lateral teeth (*lat. t.*). $\times 100$.

Fig. 35. *T. pulchra*. A portion of the dorsal side of a colony showing the dorsal teeth (*dor. t.*) and dorsal processes (*dor. pro.*) $\times 100$.

Fig. 36. *Mesenteripora meandrina* Wood. Portion of a colony showing its bilaminate formation, the terminal membrane or growing edge (*gr. ed.*) and an oecium (*oc.*). $\times 10$.

Fig. 37. *M. meandrina*. Habit sketch. $\times 1$.

Fig. 38. *M. meandrina*. Habit sketch. $\times 1$.

Fig. 39. *Idmonca californica* d'Orbigny. Portion of a branch to show the form and arrangement of the zoecia. $\times 25$.

Fig. 40. *I. californica*. Habit sketch of a specimen brought from deep water. $\times 1$.

Fig. 41. *I. californica*. Habit sketch of a shore form showing anastomosis. $\times 1$.

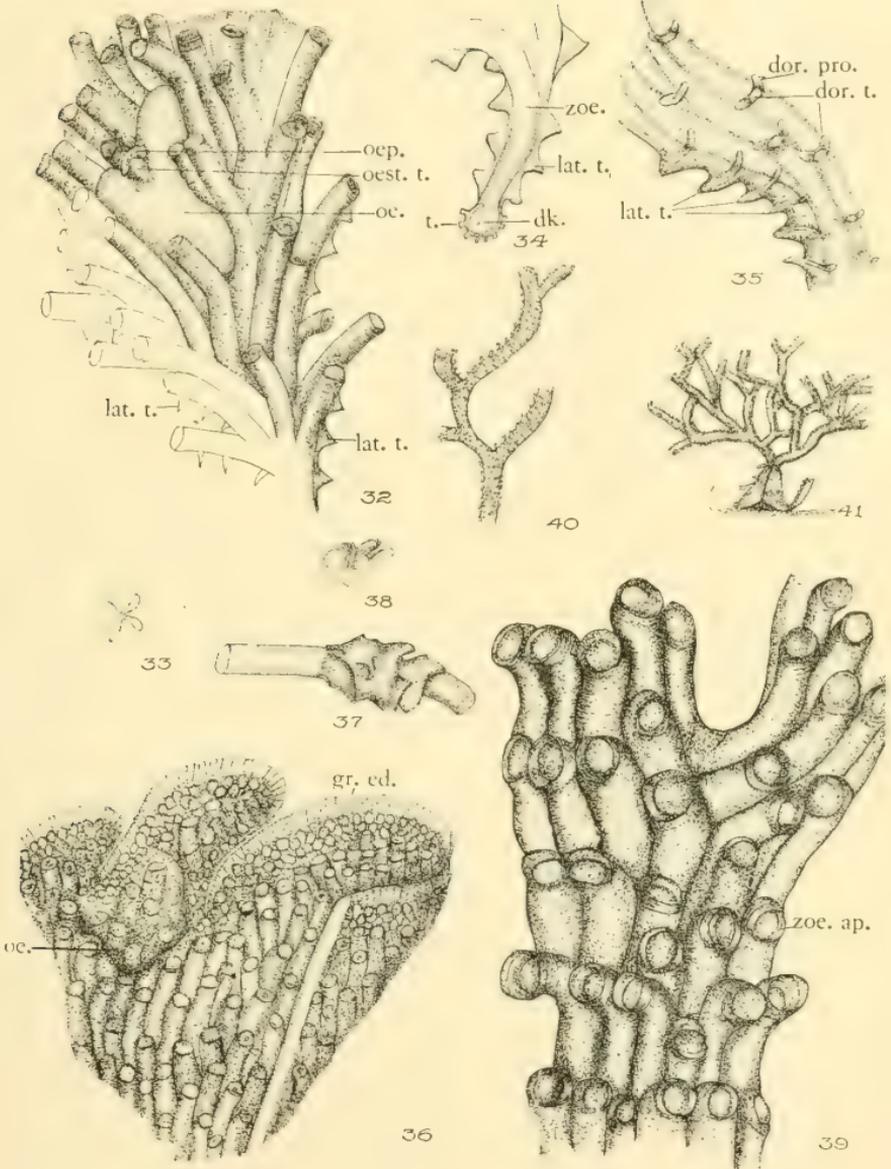


PLATE 24.

Fig. 42. *Entalophora raripora* d'Orbigny. A young colony without branches, showing the mode of growth of the zoæcia. $\times 10$.

Fig. 43. *E. raripora*. Habit sketch. $\times 1$.

Fig. 44. *Entalophora capitata* Robertson. A colony incrusting a stem. $\times 1$.

Fig. 45. *E. capitata*. The colony shown in fig. 44 showing oecium (*oe.*), and oeciopore (*oep.*). $\times 7$.

Fig. 46. *Lichenopora radiata* (Audouin) Hincks. A portion of a colony showing arrangement of zoæcia, the oecium (*oe.*) covering not only the central area, but also the spaces between the zoæcia; oeciostome (*ocst.*) and oeciopore (*oep.*). $\times 60$.

Fig. 47. *L. radiata*. An entire colony. $\times 18$.

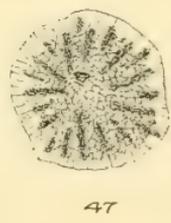
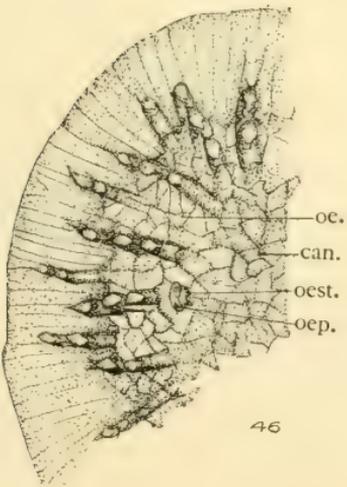
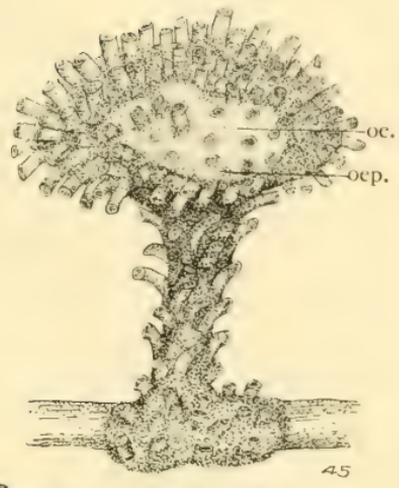


PLATE 25.

Fig. 48. *Lichenopora californica* (d'Orbigny) Conrad. A small colony showing arrangement of zoecia in connate bundles, oecium (*oe.*) and oeciopore (*oep.*) $\times 20$.

Fig. 49. *L. californica*. Habit sketch. $\times 1$.

Fig. 50. *Lichenopora verrucaria* (Fabricius) Hincks. Portion of a colony showing arrangement of zoecia and the oecium (*oe.*) with its oeciopore (*oep.*) $\times 25$.

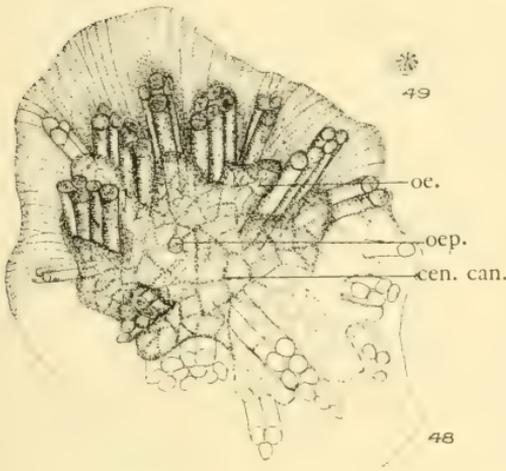
Fig. 51. *Heteropora pelliculata* Waters. Habit sketch. $\times 2$.

Fig. 52. *H. pelliculata*. Habit sketch. $\times 2$.

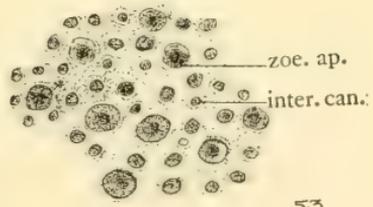
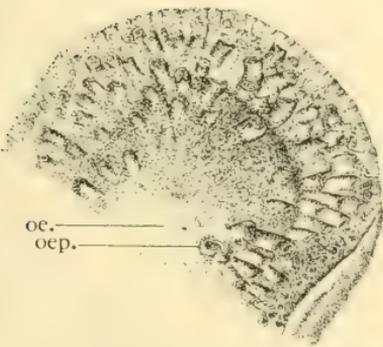
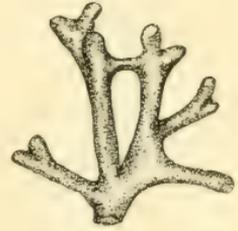
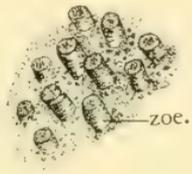
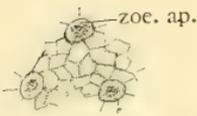
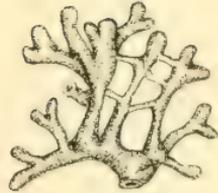
Fig. 53. *H. pelliculata*. Portion of the surface of a branch showing the zoecial apertures (*zoe. ap.*) and the apertures of the interstitial canals (*inter. can.*). $\times 40$.

Fig. 54. *H. pelliculata*. Portion of the surface of a colony in which the interstitial canals are covered by a delicate calcareous layer, the zoecial apertures only visible (*zoe. ap.*). $\times 40$.

Fig. 55. *H. pelliculata*. Portion of the surface of a colony showing the projection of the zoecial tubes beyond the surface (*zoe.*) when in a sheltered position. $\times 40$.



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OF THE
MARINE BIOLOGICAL ASSOCIATION OF SAN DIEGO

XXXIII

THIRD REPORT ON THE COPEPODA OF
THE SAN DIEGO REGION

BY
CALVIN OLIN ESTERLY

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CONTRIBUTIONS FROM THE LABORATORY
OF THE
MARINE BIOLOGICAL ASSOCIATION OF SAN DIEGO.

XXXIII*

THIRD REPORT ON THE COPEPODA OF
THE SAN DIEGO REGION

BY
CALVIN OLIN ESTERLY.

The animals described in this paper were all taken with the "000" or "10" plankton nets at stations and depths which are given under "occurrence" after the description of each species. In most cases only one sex has been taken and where a description deals only with the male or female it may be understood that the other sex is unknown. The nets were open, unless otherwise stated.

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All the figures were drawn with the aid of a camera.

Family CALANIDAE.

Genus *Aetideopsis* Sars.

Aetideopsis, Sars (1903), p. 159, supp. pls. 4, 5.

Faroella, Wolfenden (1904), p. 117, figs. 26, 27, 28.

The genus resembles *Actideus* Brady in that the rostrum is heavy, strong and bifurcate, and the sides of the last thoracic segment acutely produced. The main difference between the two genera is that in *Actideopsis* the fourth and fifth segments of the thorax are separated at least by a distinct line. The posterior maxillipeds are more slender in *Actideopsis* than in *Actideus*.

Actideopsis also resembles *Chiridius* Giesbrecht in the general form of the appendages, but *Chiridius* has a weakly developed rostrum and as in *Actideus* the fourth and fifth thoracic segments are not visibly separated.

There are some points about the two species I have recorded as belonging to *Actideopsis* Sars, in which they do not agree with the descriptions of Sars, but I can see no valid reason for not including the San Diego specimens in that genus.

***Actideopsis pacifica*, n. sp.**

Pl. 28, figs. 24, 25, 30; pl. 31, figs. 86, 103; pl. 32, fig. 113.

Adult female. The head is smoothly rounded and the rostrum is strong and heavily chitinised (pl. 28, figs. 24, 25). The prongs of the rostrum do not curve backward very much and are set close together at the base; they do not diverge much from the base (pl. 28, fig. 30).

The sides of the last thoracic segment are produced into sharp projections and the head is fused with the first thoracic segment; the fourth and fifth thoracic segments seem to be fused, though there is a very distinct line visible between them everywhere (pl. 28, fig. 24). This is shown better in fig. 31, which is of *A. divaricata*. The abdomen is 4-segmented and, with the furca, is between one-fourth and one-fifth as long as the cephalothorax; the first segment is longer than any of the others and the second segment is about as long as the third and fourth together.

The anterior antennae are 23-jointed and do not extend back to the end of the cephalothorax. The posterior antennae and mouth parts do not show any peculiarities, unless the slender form of the posterior maxillipeds, which is characteristic of the genus, is mentioned (pl. 32, fig. 113). The first foot (pl. 31, fig. 86), has a 3-jointed outer ramus, each joint with an outer marginal spine. The inner ramus of the second foot is 2-jointed; that of the third and fourth feet is 3-jointed. The teeth on the serrate bristle of the outer rami in the second to fourth pairs of feet are characteristically arranged (pl. 31, fig. 103).

Length: 3.18 mm.

Coloration: Opaque white in formalin.

Occurrence: Station 1252, tow at, and vertical from, 310 f., sounding 345 f., July 11, 1906; station 1303, tow at, and vertical from, 315 f., sounding 340 f., July 18, 1906.

Aetideopsis divaricata, n. sp.

Pl. 28, figs. 27, 29, 31, 32; pl. 31, figs. 88, 102.

Adult female. This species closely resembles the preceding one, but is easily distinguished from it by the form of the head and rostrum (pl. 28, figs. 29, 32). The rostral prongs are very long and strong; they curve backward somewhat and are set far apart at the base, from which they diverge but little (pl. 28, fig. 32). The last thoracic segment is produced laterally into strong points (pl. 28, fig. 31). This species also shows the distinct line between the fourth and fifth thoracic segments (pl. 28, fig. 31). The abdomen is 4-segmented and, with the furca, is from one-fourth to one-fifth as long as the cephalothorax; the genital segment is as long as the next two together, and the third and fourth segments are of equal lengths (pl. 28, fig. 31).

The anterior antennae are 24-jointed and extend back to about the middle of the abdomen. The other cephalic appendages are not unusual; the posterior maxillipeds are much like those of *A. pacifica* (pl. 32, fig. 113). The first foot has a 3-jointed exopodite, each joint with an outer marginal spine (pl. 31, fig. 88). The inner ramus of the second foot is 1-jointed but there is some indication of a line of fusion between two joints; the inner rami of the third and fourth pairs are 3-jointed. The teeth on the terminal spines of the outer rami second to fourth pairs of feet are long and more closely apposed for the greater part of their length than in *A. pacifica* (pl. 31, figs. 102, 103).

Length: 3.36 mm.

Coloration: Opaque white in formalin.

Occurrence: On the same stations as *A. pacifica*.Genus **Gaidius** Giesbrecht.**Gaidius tenuispinus** Sars.

Pl. 28, fig. 26; pl. 29, fig. 64.

Chiridius tenuispinus, Sars (1900), p. 67, pl. 18; (1903), p. 30, pl. 18 (female).

Gaidius tenuispinus, Sars (1903), p. 162, pl. 18 and supp. pl. 6.

Adult male. Similar to *G. pungens* Giesbrecht but distinguished from it by the much longer and more slender spines on

the thorax (pl. 29, fig. 64). While the San Diego specimen does not agree in all respects with the description given by Sars (1903, pp. 30 and 162), there is no apparent reason for making a separate species. The fifth feet are exactly as shown by Sars (1903, supp. pl. 6). Sars gives the length of the male as about 2 mm.

Length: 3.10 mm.

Coloration: In formalin, transparent and without pigment.

Occurrence: One male, station 1249, tow at, and vertical from, 325 f., sounding 370 f., July 11, 1906.

According to v. Breemen (1908, p. 36), *Gaidius pungens* and *G. borealis* Wolfenden (1904, p. 11), are the same as *G. tenuispinus* Sars.

Genus **Gaetanus** Giesbrecht.

Gaetanus secundus n. sp.

Pl. 26, fig. 3; pl. 28, figs. 38, 43; pl. 30, figs. 73, 84.

Adult female. The spine on the head is long, and directed forward and slightly downward, and the rostrum is short and rounded (pl. 28, fig. 43). The spines on the sides of the last thoracic segment are long and extend beyond the middle of the genital segment (pl. 28, fig. 38).

The length of the cephalothorax from the tip of the cephalic spine to the tip of the thoracic spine is over five times the length of the abdomen, including the furca. The cephalothorax and abdomen are each 4-segmented; in the latter, the genital segment is markedly convex on the ventral side and twice as long as the second and third segments together, and twice as long as the anal segment (pl. 28, fig. 38).

The anterior antennae when removed from the body are 10.9 mm. long, thus being twice the length of the body. The posterior antennae and mouth parts are of the usual forms; the posterior maxilliped has the lamella on the first basal (pl. 30, fig. 84). The swimming feet do not show any marked peculiarities except that the first basal of the fourth pair has a row of heavy spines (pl. 30, fig. 73).

Immature male. The forms that I take to be the males of this species resemble the adult females in every way except that they

have a fifth pair of feet which are not fully formed. According to Farran (1908, p. 35), the presence of a fifth pair of feet in immature animals of this genus is no evidence that they are males; but I cannot see that this is the case, at least in the available material.

Length: Adult females, 5.2 mm.

Coloration: Red pigment is found in the body between the appendages, in the eye, mouth-parts and feet, distal half of anterior antennae, and in the intestine.

Occurrence: Station 1249, tow at, and vertical from, 325 f., sounding 370 f., July 11, 1906; station 1315, tow at, and vertical from, 320 f., sounding 330 f., July 19, 1906.

Gaetanus secundus resembles *G. unicornis* (Esterly, 1906, p. 57), rather closely, but is easily distinguished by the much greater length of the antennae and the character of the spines on the basals of the fourth feet.

Genus *Undeuchaeta* Giesbrecht.

Undeuchaeta bispinosa n. sp.

Pl. 26, fig. 4; pl. 29, figs. 48, 56.

Adult female. This species resembles *U. major* Giesbrecht, but the head is not crested (pl. 26, fig. 4), and the sides of the last thoracic segments end in acute angles, not in pointed processes. The genital segment is of nearly the same shape as in *U. major*, and has the hook-like appendage at the right of the orifice, but in addition there is a spine on the right side of the segment about midway between the anterior and posterior borders (pl. 29, fig. 56); there is a second and much shorter spine at the left of the orifice. The segment carries a group of heavy spines on the left side at the posterior border, and usually the second segment is similar in that regard. The anterior antennae are as long as the cephalothorax, and the other appendages are not noticeably different from those in *U. major* Giesbrecht.

Length: Averages 4.5 mm.

Coloration: Opaque and without pigment in formalin. During life there is a small amount of reddish pigment in the basals of the maxillipeds and feet and in the anterior part of the intestine.

Occurrence: Females are common in the deep hauls; for example, station 1134, vertical from 285 f., June 26, 1906.

Undeuchaeta incisa n. sp.

Pl. 27, figs. 12, 19; pl. 28, fig. 28; pl. 29, fig. 59.

Adult female. The head is crested and has a rather prominent rostrum (pl. 27, fig. 19). The last thoracic segment is rounded on the right side and produced on the left into a process which is notched at the end (pl. 28, fig. 28; pl. 29, fig. 59). The cephalothorax is a little over four times as long as the abdomen and furca (pl. 27, fig. 12). The genital segment is markedly protuberant ventrally; there is a lamellar process at the right of the orifice, and on the right of the segment about the middle there is a wing-like extension (pl. 28, fig. 28; pl. 29, fig. 59).

The cephalothorax and abdomen are 4-segmented. The genital segment is as long as the second and third together, the second about half as long as the third and the anal half as long as the second. The furcal rami are short, broader than long, and about as long as the anal segment.

The anterior antennae extend a little beyond the end of the body. The posterior antennae are of the usual shape and the inner ramus is half the length of the outer. The maxilla has the form characteristic of the genus; the outer ramus has eleven bristles and the three middle ones are considerably shorter than the others.

The outer ramus of the first foot is indistinctly 3-jointed, the suture between the first and second joints being indicated by a line; there are two outer marginal spines. The spines of the outer margin of the outer ramus of the first foot are much longer than in the second and third feet.

Length: 6.1 mm.

Coloration: The animals are without pigment.

Occurrence: Station 1252, tow at, and vertical from, 310 f., sounding 345 f., July 11, 1906; station 1270, tow at, and vertical from, 155 f., sounding 170 f., July 13, 1906; station 1303, tow at, and vertical from, 315 f., sounding 340 f., July 18, 1906.

Genus **Euchirella** Giesbrecht.**Euchirella simplex** n. sp.

Pl. 26, fig. 10; pl. 29, figs. 50, 62.

Adult female. The head has a high and rather pointed crest (pl. 29, fig. 50), and the last thoracic segment is very broadly rounded at the sides. The head is produced below into a minute point (pl. 29, fig. 50), which can scarcely be called the rostrum.

The cephalothorax and abdomen are both 4-segmented, the abdomen with the furca is about one-sixth the length of the cephalothorax. The first abdominal segment is as long as the last three together but does not show any peculiarities. The furcal rami are widely divergent and as long as the anal segment. (Pl. 29, fig. 62).

The anterior antennae are 23-jointed and when folded back reach a little beyond the last thoracic segment. The posterior antenna has the outer ramus two and one-half times the length of the inner. The outer ramus of the maxilla has ten bristles, the inner ramus three large bristles; the second basal has three bristles of which two are very small, and the outer marginal lobe has seven.

The outer ramus of the first foot is 3-jointed with three spines on the outer margin. In the second foot the outer marginal spine of the second joint of the outer ramus is long and curved and reaches a little beyond the tip of the first outer marginal of the second joint. The first basals of the fourth feet are without the spines usually found in this genus, there being only the plumose bristle.

Length: 6.36 mm.

Coloration: The mouth-parts and region are a very deep red; the basal halves of the anterior antennae are light red, and the plumose bristles on the posterior antennae are orange. The first pair of feet are the color of the mouth-parts, while the thorax and remaining pairs of feet are light red.

Occurrence: Station 1303, tow at, and vertical from, 315 f., sounding 340 f., July 18, 1906.

Euchirella simplex differs from all other species in lacking the spines on the first basal of the fourth foot, but it approaches the genus so closely in other respects that I have not removed it. *E. curticauda* Giesbrecht is also cristate and non-rostrate.

Euchirella propria n. sp.

Pl. 27, figs. 14, 20; pl. 30, figs. 67, 83; pl. 31, fig. 85.

Adult male. The head is uncrested and smoothly rounded, with a short, stout rostrum (pl. 27, figs. 14, 20). The cephalothorax is 4-segmented and three and one-half times as long as the abdomen with the furca. The abdominal segments are of about equal lengths except for the anal segment which is so short as to be almost invisible.

The first foot (pl. 31, fig. 85) has a 2-jointed outer ramus and the first joint is provided with two tiny spines. The fifth feet are of the usual structure (pl. 30, fig. 83), and the outer ramus of the right foot is about four and a half times as long as the greatest breadth of the second basal joint.

Length: 5.6 mm.

Coloration: The sides of the thorax, the abdomen, and mouth-parts are red.

Occurrence: Station 1315, tow at, and vertical from, 320 f., sounding 330 f., July 19, 1906; station 1318, tow at, and vertical from, 170 f., sounding 330 f., July 19, 1906; station 1342, tow at, and vertical from, 150 f., sounding 330 f., July 21, 1906.

This species was found in the collections with *E. curticauda*, *pulchra*, *simplex*, *galcata* and *rostrata*, but I can discover no other evidence for its being the male of an old species and have therefore placed it in a species by itself.

Euchirella rostrata Claus.

Pl. 29, fig. 52; pl. 30, fig. 66; pl. 32, fig. 116.

Euchaeta hessci (male), Brady (1883), p. 63, pl. 20, figs. 1-13;
pl. 23, figs. 11-14.

Euchirella rostrata (male), Cleve (1900), p. 4, pl. 2, figs. 1-14.

Adult male. While the males resemble the females in the general form of the body, the presence of the fifth pair of feet will distinguish the former from the latter; these organs in *E. rostrata* are quite unlike those in any other species (pl. 32, fig. 116). Both feet are biramous; the inner ramus of the right foot is nearly twice as long as that of the left. The former is of a peculiar shape, being bent at the end so that a hooked process extends proximally. The outer ramus of the right foot is more

than four times as long as the second basal is wide. The outer ramus of the left foot terminates about as in the other species (pl. 30, fig. 66), but the third joint ends in a sharp point.

Length: 3 mm.

Coloration: The posterior half of the body is orange, there being no pigment anterior to the first pair of feet; there are flecks of coloring matter in the thoracic segments and basals of the feet.

Occurrence: Station 1140, vertical from 60 f., June 27, 1906; station 1177, vertical from 160 f., June 30, 1906; station 1134, vertical from 285 f., June 26, 1906.

Females are a good deal more common than males.

***Euchirella truncata* n. sp.**

Pl. 26, fig. 5; pl. 28, fig. 35; pl. 29, fig. 63; pl. 30, fig. 71; pl. 31, fig. 104.

Adult female. The head is regularly rounded in profile, without a crest and with a rostrum (pl. 28, fig. 35) of characteristic shape. The last thoracic segment is very broadly rounded laterally (pl. 29, fig. 63), and almost square when seen from above. The abdomen is very short, being (with the furca), a little more than one-sixth the length of the cephalothorax. The cephalothorax and abdomen are each 4-segmented (pl. 26, fig. 5). The genital segment is longer than the last three (pl. 29, fig. 63), and the two middle segments are of about equal lengths; the anal segment is about three-fifths the length of the third. The furcal rami are about as broad as long, widely divergent and provided with four bristles richly plumose to their ends and of equal lengths.

The anterior antennae are 23-jointed and when folded back reach beyond the end of the furca. The posterior antennae are of the usual form and the inner ramus is half as long as the outer. The outer ramus of the maxilla has eleven long bristles, the inner ramus four large bristles and one small, and the second basal two large and one small; the outer marginal lobe has eight bristles.

The outer ramus of the first foot is 2-jointed (pl. 31, fig. 104), with three outer marginal bristles; the first basal of the fourth foot has one long heavy spine near the plumose bristle (pl. 30, fig. 71). In the second foot, the outer marginal spines of the

outer ramus are of about equal lengths, but the spine of the second joint does not reach the base of the first spine of the third joint.

Length: 6.6 mm.

Coloration: The intestinal contents are red, the first three thoracic segments are outlined in red and the last segment is entirely so. The furcal bristles are bluish red and highly iridescent; those of the posterior antennae are somewhat iridescent, and there are two plumose orange bristles at the base of the anterior antenna.

Occurrence: Station 1303, tow at, and vertical from, 315 f., sounding 340 f., July 18, 1906; station 1306, tow at, and vertical from, 150 f., July 18, 1906; station 1516-2, vertical from 250 f., June 30, 1908.

Genus **Euchaeta** Phillipi.

Euchaeta diegensis n. sp.

Pl. 28, fig. 37; pl. 29, figs. 49, 55; pl. 31, fig. 92.

Adult female. The rostrum is very long and curved and the frontal eminence is prominent, though it does not protrude very much (pl. 28, fig. 37). The abdomen and genital segment resembles *E. media* Giesbrecht, but the genital convexity and the protuberances about the orifice are different; the right side of the segment as seen in outline is more irregular, with a smaller knob-like protrusion near the posterior margin of the segment (pl. 29, figs. 49, 55).

The anterior antennae are about as long as the cephalothorax. The maxilla has eight bristles (one very minute) on the first lobe of the outer margin, one on the second lobe of the inner margin, two on the second basal and four on the fused second and third joints of the inner ramus.

In the outer ramus of the second foot, the middle spine of the outer margin reaches two-thirds of the distance from its base to the base of the third outer marginal spine (pl. 31, fig. 92); in *E. media* the spine is longer. The third outer marginal is half as long as the middle one (in *E. media* it is about one-third as long). The outer marginal of the second joint is twice as long as the first of the third joint.

Length: 4.22 mm.

Coloration: Translucent and without pigment.

Occurrence: Station 1140, vertical from 60 f., June 27, 1906.

While this species resembles *E. media* Giesbrecht in some respects, the shape of the rostrum, the bristling of the maxilla, and the outer ramus of the second foot separate the two sharply.

***Euchaeta acuta* var. *pacifica* n. var.**

Pl. 32, fig. 115.

Euchaeta acuta, Giesbrecht. (Esterly, 1905, p. 157, fig. 23).

Adult male. The fifth feet closely resemble those of *E. acuta*, as shown by Giesbrecht (1892, pl. 16, figs. 18, 19), but the process on the second joint of the outer ramus of the left foot is not pyramidal and pointed, and in addition the inner ramus of the right foot is broadened at the distal end and carries a flap-like appendage (pl. 32, fig. 115). There are no other noticeable differences, yet the process mentioned is usually a well-marked character in the differentiation of species. So it seems as if the San Diego form should at least be made a variety.

Occurrence: Station 1099, vertical from 35 f., June 20, 1906.

***Euchaeta solida* n. sp.**

Pl. 26, fig. 2; pl. 28, fig. 34; pl. 30, fig. 78.

Adult male. The shape of the body is shown in fig. 2; the rostrum is heavy and straight, and pointed directly down (pl. 28, fig. 34); the frontal protuberance is not very marked.

The main point about the species is the shape of the toothed process on the second joint of the outer ramus of the left fifth foot; it is scoop-like and expanded distally (pl. 30, fig. 78).

Length: 5.22 mm.

Coloration: Somewhat opaque and whitish in formalin.

Occurrence: Station 1315, tow at, and vertical from, 320 f., sounding 330 f., July 19, 1906.

This species occurred with females of *E. spinosa*, *tousa* and *diegensis*, but it does not seem to me that that alone is evidence enough to ally it with one of them.

Genus ***Xanthocalanus*** Giesbrecht.

***Xanthocalanus tectus* n. sp.**

Pl. 28, fig. 33; pl. 29, fig. 53; pl. 31, fig. 95.

Adult female. The head is smoothly rounded but with a very slight crest (pl. 28, fig. 33), and the forehead protrudes

so that the rostral filaments are covered. The filaments are delicate, not situated on a prominence, and widely separated at the base. The last thoracic segment ends in a small, pointed projection (pl. 29, fig. 53). The cephalothorax is 4-segmented, the head being fused with the first thoracic segment. The abdomen is 4-segmented; the genital segment is as long as the second and third together and the anal is very short (pl. 29, fig. 53).

The anterior antennae are 24-jointed and from one-fifth to one-sixth of their length longer than the body. The outer ramus of the posterior antennae is one and one-half times the length of the inner ramus. The anterior maxillipeds have eight vermiform appendages. The first four pairs of feet are of the usual form; the second joint of the inner ramus in the second, third and fourth pairs has a proximal row of three or four long spines and a few short ones, and a distal row of from three to five short spines; the joints of the outer rami are not spinose on the flat surfaces. The fifth foot (pl. 31, fig. 95), is 3-jointed, the terminal joint with four heavy spines, two of which are on the distal margin of the foot.

Length: 4.25 mm.

Coloration: Whitish and translucent in formalin.

Occurrence: Station 1468, vertical from 290 f., sounding 330 f., June 19, 1908.

Xanthocalanus pulcher n. sp.

Pl. 29, figs. 60, 61; pl. 31, fig. 91.

Adult female. The head has a long, low crest, and the rostrum consists of two slender filaments (pl. 29, fig. 61). The last thoracic segment ends laterally in a small, sharp projection (pl. 29, fig. 60). The genital segment of the abdomen (pl. 29, fig. 61), has a slight ventral convexity, and the segment is as long as the third and fourth together; the second and third segments are of equal lengths, and the fourth is the shortest of all.

The anterior antennae are 23-jointed and as long as the cephalothorax. The maxilla has nine bristles on the outer ramus, five on the second basal, eight on the inner ramus and four on the second lobe of the inner margin. The anterior maxillipeds have six vermiform and two pectinate appendages.

The first foot has a 3-jointed outer ramus, the first joint without a spine on the outer margin. None of the feet are heavily spinose on the faces; the largest spines are on the inner ramus of the second foot and there are none at all on the fourth foot. The fifth foot (pl. 31, fig. 91), is 3-jointed, broader at the distal end than at the proximal, and with three spines on the terminal joint.

Length: 3.42 mm.

Coloration: Translucent, with orange pigment in the basals of the feet, in the mouth-parts, anterior antennae and abdomen.

Occurrence: Station 1134, vertical from 285 f., June 26, 1906.

The structure of the fifth feet and the presence of a-crest are distinctive characters for this species.

Genus *Onchocalanus* Sars.

I refer the following species to the above genus on account of the resemblance of the anterior maxilliped to *Xanthocalanus* (*Onchocalanus*) *similis* (Esterly, 1906, p. 69, pl. 12, fig. 60). *X. similis* closely resembles *X. cristatus* Wolfenden, and that species is transferred to the genus *Onchocalanus* by Farran (1908, p. 49). I found no trace of a fifth pair of feet in my specimen but that was through mutilation in dissecting.

Onchocalanus latus n. sp.

Pl. 29, fig. 47; pl. 30, fig. 70; pl. 31, fig. 97.

Adult female. The body is rather strongly depressed. The head is rounded both in dorsal and side views and the last thoracic segment is rounded at the sides. The cephalothorax is widest just behind the suture between the head and thorax (pl. 29, fig. 47). The abdomen is 4-segmented; the genital segment is about twice as long as the second, which is as long as the third; the anal segment is about one-third as long as the preceding one.

The anterior antennae are as long as the cephalothorax and 24-jointed. The inner ramus of the posterior antenna reaches about to the distal end of the second basal of the latter. The anterior maxilliped has one vermiform and six pencillate appendages; of the latter, four are slender and two very heavy (pl. 30, fig. 70).

The outer rami of all the feet are 3-jointed and in the first foot each joint has a spine on the outer margin. The outer rami are not spinose on the surfaces, but in the third and fourth feet the second joint of the inner ramus has groups or rows of heavy spines (pl. 6, fig. 97).

Length: About 4 mm.

Coloration: Translucent and unpigmented.

Occurrence: Station 1134, vertical from 285 f., June 26, 1906.

Genus *Scolecithrix* Brady.

Several species of Copepoda are found in the San Diego region which differ in important respects; these forms would belong to a number of different genera if one were to follow the classification of Sars or of Wolfenden. But as I stated in another paper (Esterly, 1906, p. 64), it does not seem to me that the separation of the large genus *Scolecithrix* into other well-defined genera is possible; at least, I find it difficult to do so with the San Diego forms. So I shall describe these specimens under the genus *Scolecithrix*, even if it should be found desirable later to change the classification.

Scolecithrix vorax n. sp.

Pl. 27, figs. 15, 21; pl. 29, fig. 45; pl. 30, fig. 68; pl. 31, figs. 93, 96, 99.

Adult female. The head is smoothly rounded and the rostrum is bifid, the prongs being stout, long and somewhat divergent (pl. 27, fig. 15). The last segment of the thorax is rounded and the margin is indented above and below the middle (pl. 29, fig. 45). The cephalothorax is 5-segmented and six and one-half times as long as the abdomen and furca; the abdomen is 4-segmented, the genital segment being more than twice the length of the others together; the second and third are of equal lengths and the anal is longer than the preceding one (pl. 27, fig. 21; pl. 29, fig. 45).

The anterior antennae are 23-jointed and, as carried on the body, do not reach back to the first segment of the thorax. The outer ramus of the posterior antenna is one and one-half times as long as the inner ramus and the bristles are very long and richly plumose. The anterior maxilliped has eight of the appendages so characteristic of the genus; but some of them are of a type

that is new so far as I am aware. Three are vermiform, four end in daisy-like expansions, and the other one is relatively of enormous size and terminates in a set of structures like tentacles (pl. 30, fig. 68). There is a central core in the larger appendage (not shown in the figure) that is surrounded by the tentacles. The four smaller flower-like appendages seem to have a similar structure.

The first foot has a 3-jointed outer ramus with three outer marginal spines, and a 1-jointed inner ramus. The inner ramus of the second foot is 2-jointed, that of the third and fourth feet is 3-jointed (pl. 31, fig. 93); the posterior surfaces of the rami are covered with spines of various sizes. The terminal spines of the three posterior pairs of feet are somewhat peculiar in having a row of small holes inside the serrated margin, as shown in plate 31, fig. 99. The fifth feet (pl. 31, fig. 96), are 2-jointed, the end joint with two heavy spines of which the outer one is the shorter.

Length: 1.6 mm.

Coloration: A brownish pigment is generally distributed through the body.

Occurrence: Station 1252, tow at, and vertical from, 310 f., sounding 345 f., July 11, 1906.

This species is distinct in the shape of the head and thorax, and in the character of the appendages of the anterior maxilliped.

***Scolecithrix angusta* n. sp.**

Pl. 28, fig. 42; pl. 29, figs. 46, 51; pl. 31, fig. 101.

Adult female. The head has a long, low crest, and the rostrum is heavy and stiff; it is somewhat peculiar in the abruptness with which the slender terminal part originates from the heavier basal part (pl. 29, fig. 51). The cephalothorax is 5-segmented, the fourth and fifth segments being separated from each other; the last segment ends in a point and below this is a deep notch (pl. 29, fig. 46). The abdomen is 4-segmented and with the furca is about one-fifth the length of the cephalothorax (pl. 28, fig. 42); the genital segment is as long as the second and third together (these are of equal lengths) and about four times as long as the anal segment (pl. 28, fig. 46).

The anterior antennae reach back to the posterior border of the genital segment; the anterior maxillipeds have eight vermiform sensory appendages. The fifth feet are phyllous, 2-jointed, and the distal joint has three spines (pl. 31, fig. 101).

Length: 3.14 mm.

Coloration: Opaque white in formalin.

Occurrence: Station 1527, vertical from 500 f., sounding 640 f., July 11, 1908.

The shape of the head and thorax will serve to distinguish this species sharply from others.

Family CENTROPAGIDAE.

Genus **Pleuromamma** Giesbrecht.

Pleuromamma quadrangulata Dahl.

Pl. 30, fig. 65; pl. 32, fig. 111.

Pleuromamma quadrangulata, Dahl (1893), p. 105.

Pleuromamma quadrangulata, Giesbrecht (1898), p. 109.

Those forms occur in the same hauls with *P. abdominalis* and *P. xiphias* commonly, and occasionally with *P. gracilis*. They are easily recognized by the four heavy, curved hooks on the anterior antennae (pl. 30, fig. 65). There are two hooks on the first joint, one on the second and one on the fourth; in *P. abdominalis* there is but one hooked spine and that is on the basal joint. The pigment knob in *P. quadrangulata* seems to be always on the right side. The sexes are alike in the spines of the anterior antennae, and the abdomen of the male is symmetrical. The fifth feet of the male are shown in pl. 32, fig. 111.

Length: Female, 3.48 mm.; male, 3.55 mm.

Coloration: Whitish in formalin, with a characteristic pink fleck in the mouth.

Occurrence: Rather common in all the deeper hauls, as station 1528, vertical from 500 f., sounding 640 f., July 2, 1908; none taken above 170 f.

Genus **Augaptilus** Giesbrecht.

Augaptilus lamellifer n. sp.

Pl. 26, fig. 8; pl. 28, fig. 36.

Adult female. The head and last thoracic segments are rounded (pl. 26, fig. 8); the rostral filaments are slender but

rather stiff and carried on a projecting lamella that can be seen from the side (pl. 28, fig. 36).

The cephalothorax is about three times as long as the abdomen and furca; the genital segment is somewhat longer than the second and third segments together, and the furca is as long as the genital segment and half the second one; the third segment is half as long as the genital (pl. 26, fig. 8).

The anterior antennae exceed the length of the body by their four terminal joints. The posterior maxilliped is very long and slender, the two basal joints being just one-fourth the length of the body. The other appendages do not show any noteworthy characters.

Length: 4.4 mm.

Coloration: Semi-transparent and without pigment.

Occurrence: Station 1252, tow at 310 f., sounding 345 f., July 11, 1906.

The appearance of the head and rostrum of this species is distinctive.

Genus *Disseta* Giesbrecht.

Disseta, Giesbrecht (1892), p. 63, 369; (1898), p. 112.

Disseta, Esterly (1906), p. 71.

Disseta maxima n. sp.

Pl. 29, figs. 54, 58; pl. 30, fig. 79.

Adult female. This species resembles *D. grandis* (Esterly, 1906, p. 71), but is larger. The head (pl. 29, fig. 54), is smoothly rounded, as is the last thoracic segment (pl. 29, fig. 58). The abdomen is 4-segmented; the genital segment is as long as the other three together, and the anal segment is less than one-third the length of the genital; the genital eminence is at the middle of the segment (pl. 29, fig. 58). The left furcal blade is longer than the right by about one-third the length of the latter.

The anterior antennae are very long and slender, one-fifth of their length longer than the body. The fifth feet (pl. 30, fig. 79) are of the usual form, but the spine of the second joint of the outer ramus is unusually long and heavy. It is nearly two-thirds the length of the third joint of the ramus, and from its

position on the joint reaches nearly to the distal margin of the third joint.

Length: 9.4 mm.

Coloration: Whitish and translucent in formalin, but unpigmented.

Occurrence: Station 1075, vertical from 600 f., Dec. 17, 1905.

Disseta sp. (Wolfenden).

Pl. 28, figs. 40, 41; pl. 30, figs. 76, 80; pl. 31, fig. 100; pl. 32, figs. 107, 108.

Heterorhabdus grandis, Wolfenden (1904), p. 120, pl. 9, fig. 36.

?*Disseta palumboi* Giesbrecht, (Farran, 1908, p. 67).

The figures given by van Breemen (1898, p. 228, fig. 243) of the fifth feet of the male of *Heterorhabdus grandis* Wolfenden agree closely with those of a species of *Disseta* found in this region. Farran (1908, p. 67), states that *H. grandis* Wolfenden is identical with *D. palumboi* Giesbrecht. However, so far as I am aware, the male of *Disseta* was unknown until I described the male of *D. grandis* (Esterly, 1906, p. 71), and I can see no reason for identifying *Heterorhabdus grandis* with *Disseta palumboi* in view of the few figures of the former that have been published. The length of *D. palumboi* is given as 5.7 mm., that of *H. grandis* as 6.6 mm., while the length of the specimens under discussion is 7.3 mm. In *D. grandis* Esterly the males are smaller than the females. The following is a description of the male from the San Diego region.

Adult male. The head, as seen in side view, ends in a rather abrupt angle, as do the edges of the last thoracic segment (pl. 28, fig. 40). The rostral filaments are stiff and placed so far beneath the head that they are invisible except from directly below; the sides of the cephalothorax in front seem to be prolonged so as to cover the rostrum (pl. 28, fig. 41).

The cephalothorax and abdomen are each 5-segmented and the former is twice the length of the abdomen and furca. The head is not fused with the thorax but the last two thoracic segments are fused with each other. The middle segment of the abdomen is the longest one; the first and second are of equal lengths and about four-fifths as long as the third; the fourth is three-fourths the length of the third, and the fifth is about

half as long as the third. The left blade of the furca is longer than the right.

The anterior antennae are 22-jointed and a little longer than the body; the grasping antenna is on the left side and the portion distal to the geniculation is 4-jointed. The terminal joint of the inner ramus of the second and third feet has eight bristles. The fifth feet are characteristic and shown in pl. 32, figs. 107, 108; the inner ramus of the left foot is 2-jointed.

Length: 7.3 mm.

Coloration: Whitish and transparent in formalin.

Occurrence: Station 1527, vertical from 600 f., sounding 640 f., July 2, 1908.

Genus **Augaptilus** Giesbrecht.

Augaptilus macrodus n. sp.

Pl. 27, fig. 18; pl. 29, fig. 44; pl. 30, figs. 72, 74; pl. 31, fig. 87; pl. 32, fig. 112.

Adult female. The body is exceedingly robust and the rostrum very long and heavy; the head is smoothly rounded, and the last thoracic segment (pl. 29, fig. 44) shows a peculiar indentation or bay in the posterior border. The cephalothorax is densely covered with fine spines; it is 5-segmented, the head being separated from the thorax; the head is a little longer than the rest of the cephalothorax (pl. 27, fig. 18). The abdomen is 3-segmented and, with the furca, is between one-fourth and one-fifth as long as the cephalothorax; the genital segment is about as long as the second and third together, the second half as long as the third and the furcal blades half as long as the abdominal segments (pl. 29, fig. 44).

The anterior antennae reach only to the posterior border of the head. The outer ramus of the posterior antennae is longer than the inner ramus and twice the greatest breadth of the second basal (pl. 30, fig. 72). The blade of the mandible is shown in fig. 74; it has three teeth, two of which are long and curved, the other being shorter and straighter. The bristles of the maxillipeds have the cup-like structure of this genus.

The rami of the feet are 3-jointed, but the third joint of the inner ramus of the third pair has eight bristles instead of six as

in that joint of the first, second and fourth pairs. The first pair is shown in pl. 31, fig. 87, and the outer ramus of the fifth pair in pl. 32, fig. 112.

Length: 5.31 mm.

Coloration: There is a characteristic brown fleck around the mouth; otherwise the body is exceedingly transparent.

Occurrence: Station 1249, tow at, and vertical from, 325 f., sounding 370 f., July 11, 1906.

The shape of the body in this species is characteristic so far as it is possible to compare it with figures of other species. The presence of eight bristles on the terminal joint of the inner ramus seems not to have been mentioned for other species.

Augaptilus lucidus n. sp.

Pl. 26, fig. 7; pl. 27, fig. 16; pl. 30, figs. 75, 77; pl. 32, fig. 105.

Adult male. The body is robust but the head is not so rounded as in the preceding species, and the rostral prongs are of a different shape, though heavy and stiff and expanded at the base (cf. pl. 27, figs. 16 and 18). The cephalothorax is 5-segmented and three and three-fourths times the length of the abdomen and furca; its greatest width is at a point midway between the anterior and posterior borders (pl. 26, fig. 7). The cephalothorax is densely covered with fine spines. The abdomen is 5-segmented; the genital segment is a little longer than the anal, the three middle segments are of equal lengths, and their combined length is that of the first segment. The furcal blades are as long as the fourth and fifth segments of the abdomen together (pl. 26, fig. 7).

The anterior antennae reach a little beyond the posterior border of the first thoracic segment (pl. 26, fig. 7). The rami of the posterior antennae are of equal lengths (pl. 30, fig. 77); the basal joint of the inner ramus is over half as broad as it is long. The blade of the mandible is shown in pl. 30, fig. 75; it is of the same structure as in *A. macrodus*, but the proportions are different. Both rami of all the feet are 3-jointed, but the end joint of the inner ramus of the third pair has eight bristles, while that joint in the other pairs (except the fifth) has six bristles. The fifth feet are not unusual (pl. 32, fig. 105).

Length: 5.81 mm.

Coloration: Very transparent, with a brown spot around the mouth.

Occurrence: Station 1339, vertical from 310 f., sounding 330 f., July 21, 1906.

This species appears to resemble *A. rattrayi* Scott, in the shape of the head; but the differences seem to me to be specific.

***Augaptilus pyramidalis* n. sp.**

Pl. 26, figs. 1, 9; pl. 30, fig. 69; pl. 32, fig. 106.

Adult female. As seen from above the forehead is smoothly but rather sharply rounded (pl. 26, fig. 1); in side view the forehead is pyramidal in shape and overhangs the rostrum, which is very strong and heavy (pl. 26, fig. 9). The posterior margins of the thorax are rounded (pl. 26, fig. 9). The cephalothorax is 5-segmented and the abdomen 3-segmented; the former is six and one-half times as long as the latter with the furca. The head is as long as the thorax plus the abdomen and furca (pl. 26, fig. 9). The genital segment is as long as the rest of the abdomen and furca.

The anterior antennae reach to the posterior border of the second segment of the thorax. The rami of the posterior antennae are of equal lengths; the mandibular blade is of a similar structure to that in *A. macrodus*. The bristles of the maxillipeds are well equipped with augaptiloid cups.

The rami of the first pair of feet are 2-jointed and the first joint of the outer ramus has an unusually long and heavy spine (pl. 30, fig. 69); the rami of the other pairs of feet are 3-jointed and the end joints of the inner rami have 7, 8, 8, 7, 6 bristles in the five pairs respectively.

Length: 6.68 mm.

Coloration: Very transparent and without pigment.

Occurrence: Station 1557, tow with closing net at 250 f., July 17, 1908.

The shape of the head in this species recalls that of *A. horridus* Farran (1908, p. 78, pl. 8, fig. 29), but the head protrudes more in *A. pyramidalis* and the rostrum is heavier and longer. It is interesting to note that both the species mentioned lack the brown spot around the mouth, though that is a common feature of the larger transparent forms like those described here.

Genus **Paraugaptilus** Wolfenden.**Paraugaptilus buchani** Wolfenden.

Pl. 26, fig. 6; pl. 28, fig. 39; pl. 29, fig. 57; pl. 31, figs. 94, 98.

Paraugaptilus buchani, Wolfenden (1904), p. 123, pl. 9, figs. 44, 45.

Arietellus buchani, Sars (1907), p. 26.

Paraugaptilus buchani, Farran (1908), p. 82.

Adult female. The specimens that I have agree fully with Wolfenden's description. His statement that the genus "seems to partake of some of the characters" of both *Arietellus* and *Augaptilus* seems to be correct. Sars (1907, p. 26) has transferred the forms to *Arietellus*, but it is hard to see how they can properly belong to that genus when they have the characteristic appendages of *Augaptilus* on the bristles of the maxillipeds. The fifth feet (pl. 31, fig. 94) are a good deal like those of *Arietellus* and not at all as in *Augaptilus*.

The animals are easily recognized by the lemon-yellow color when alive; it is found in the feet, the last two thoracic segments, the abdomen and mouth-parts, and in the last two joints of the anterior antenna. Another noticeable feature is the enlargement, or clubbing, of the end joint of the antenna (pl. 31, fig. 98). Other characteristic marks are shown in the figures.

Length: 3.63 mm.

Coloration: Lemon-yellow as described.

Occurrence: Station 1303, tow at, and vertical from, 315 f., sounding 340 f., July 18, 1906; station 1315, tow at, and vertical from, 320 f., sounding 330 f., July 19, 1906.

Genus **Arietellus** Giesbrecht.**Arietellus setosus** Giesbrecht.

Pl. 27, figs. 22, 23; pl. 30, figs. 81, 82.

Arietellus setosus, Giesbrecht (1892), p. 415, pl. 29, figs. 1, 3-7, 9-13; pl. 39, figs. 34-36; 1898, p. 124.

Adult male. The female has been recorded previously from this region (Esterly, 1905, p. 189). The male resembles the female in the form of the body, but the sexes can easily be separated because the male has the large pair of fifth feet (pl. 30, figs. 81, 82).

Length: 6.2 mm.

Coloration: The intestinal contents are light yellow; light rose pigment occurs in the bristles of the feet, in the maxillipeds, and there is a fleck around the mouth.

Occurrence: Station 1252, tow at 310 f., sounding 345 f., July 11, 1906; station 1315, vertical from 320 f., sounding 330 f., July 19, 1906.

The fifth feet of the San Diego specimens show slight differences as compared with the figures of Giesbrécht (1892, pl. 29, fig. 9), but they are not sufficient to warrant a specific distinction.

Genus *Phyllopus* Brady.

Phyllopus integer n. sp.

Pl. 27, figs. 11, 13, 17; pl. 31, fig. 90; pl. 32, figs. 109, 110.

The sexes are alike in conformation of the head and thorax. The head is smoothly rounded in dorsal and side views (pl. 27, figs. 13, 17). The thorax is symmetrical and there is a bay or indentation in the dorsal margin of the last segment near the tip (pl. 27, fig. 11). The rostrum is short and heavy (pl. 27, fig. 17).

The cephalothorax is 4-segmented and the greatest width is contained two and one-sixth times in the length along the mid-dorsal line. The abdomen in the male is 5-segmented, and with the furca is less than half as long as the cephalothorax. The genital segment in the female is half the length of the abdomen, the other segments being of equal lengths. Each of the three middle segments in the male is longer than the genital segment; the middle segments are of equal lengths among themselves.

The anterior antennae reach back to the posterior border of the second segment of the cephalothorax. The other appendages do not show any specific differences except in the case of the fifth feet; their structure may be understood from pl. 32, figs. 109 and 110.

Length: Female, 3.54 mm.; male, 2.64 mm.

Coloration: Whitish and somewhat translucent in formalin.

Occurrence: Among other stations, station 1249, tow at, and vertical from, 325 f., sounding 370 f., July 11, 1906; station 1339, vertical from 310 f., sounding 330 f., July 21, 1906.

Wolfenden (1904, p. 124, pl. 9, fig. 16) was the first to describe the male of *Phyllopus*, but was in error in stating that

the right foot of the fifth pair is biramous. He referred his specimens to *P. bidentatus* Brady, but said that the females in his collections did not correspond with Brady's descriptions. Later Farran (1905, p. 45, pl. 11, figs. 12-21) also referred his specimens to *P. bidentatus* Brady, but afterwards (1908, p. 83) separated them into two new species. The San Diego specimens do not have the bidentation on the last thoracic segment, and, though I have assigned an animal from this locality to the species *bidentatus* (Esterly, 1905, p. 191), I now think that the males and females occurring in the same collections belong to this new species. The most evident specific differences are found in the fifth feet of the male as compared with *P. helgae* Farran (1905, p. 11, figs. 18, 19), and this author states that he first regarded the male of this species as that of *P. bidentatus*. The fifth feet in the female of *P. helgae* (Farran, 1908, pl. 11, figs. 20, 21) resemble those of *P. integer*, yet there are differences which I think may be regarded as specific.

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Los Angeles, California, May 15, 1910.

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EXPLANATION OF PLATES.

PLATE 26.

- Fig. 1. *Augaptilus pyramidalis* n. sp. Female, dorsal. $\times 11$.
Fig. 2. *Euchaeta solida* n. sp. Male, lateral. $\times 22$.
Fig. 3. *Gaetanus secundus* n. sp. Female, lateral. $\times 22$.
Fig. 4. *Undeuchaeta bispinosa* n. sp. Female, lateral. $\times 22$.
Fig. 5. *Euchirella truncata* n. sp. Female, lateral. $\times 11$.
Fig. 6. *Paraugaptilus buchani* Wolfenden. Female, lateral. $\times 35$.
Fig. 7. *Augaptilus lucidus* n. sp. Male, dorsal. $\times 13.5$.
Fig. 8. *Augaptilus lamellifer* n. sp. Female, lateral. $\times 22$.
Fig. 9. *Augaptilus pyramidalis* n. sp. Female, lateral. $\times 22$.
Fig. 10. *Euchirella simplex* n. sp. Female, lateral. $\times 11$.

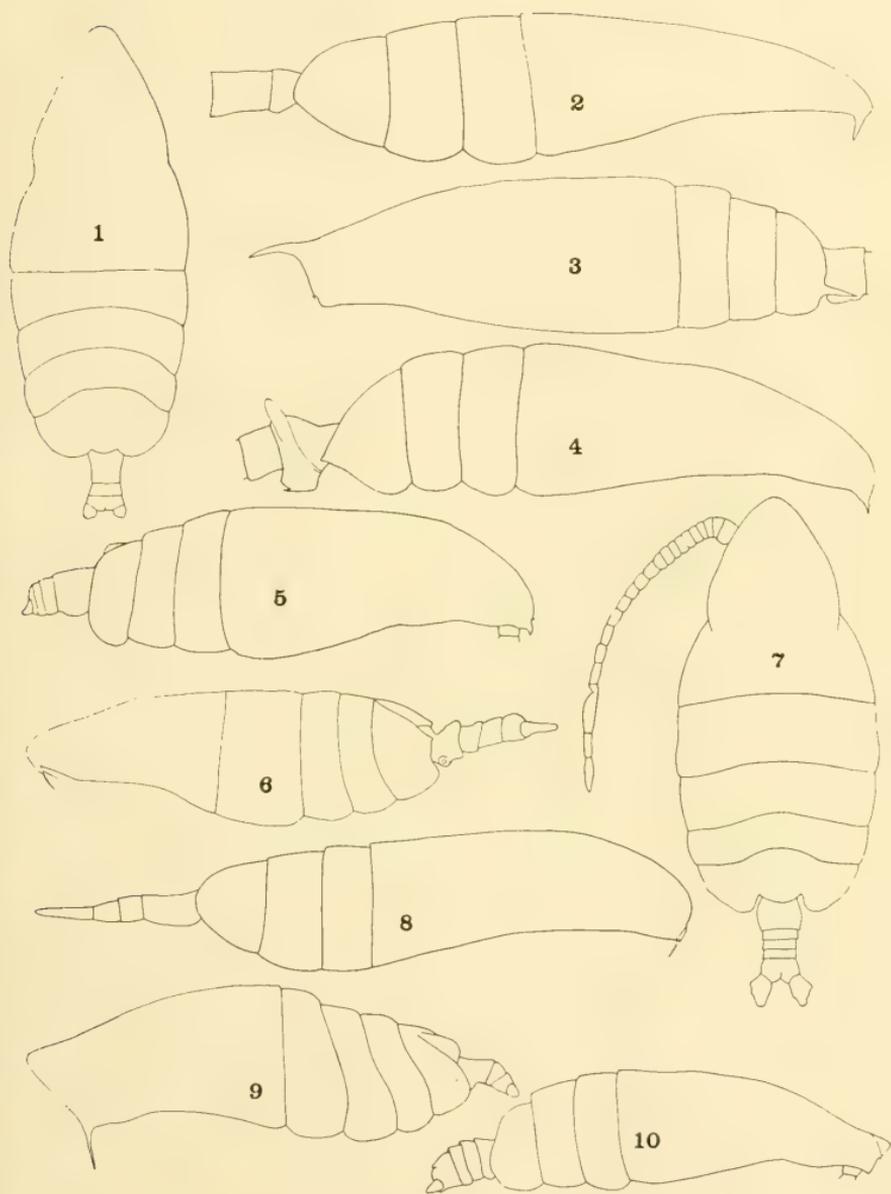


PLATE 27.

- Fig. 11. *Phyllopus integer* n. sp. Male, lateral. $\times 33$.
Fig. 12. *Undeuchaeta incisa* n. sp. Female, lateral. $\times 16.5$.
Fig. 13. *Phyllopus integer* n. sp. Male, dorsal. $\times 33$.
Fig. 14. *Euchirella propria* n. sp. Male, lateral. $\times 16.5$.
Fig. 15. *Scolecithrix vorax* n. sp. Female, head from side. $\times 105$.
Fig. 16. *Augaptilus lucidus* n. sp. Male, head from side. $\times 16.5$.
Fig. 17. *Phyllopus integer* n. sp. Male, head from side. $\times 105$.
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Fig. 19. *Undeuchaeta incisa* n. sp. Female, head from side. $\times 52.5$.
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Fig. 22. *Arietellus setosus* Giesbrecht. Male, head from side. $\times 105$.
Fig. 23. *Arietellus setosus* Giesbrecht. Male, lateral. $\times 16.5$.

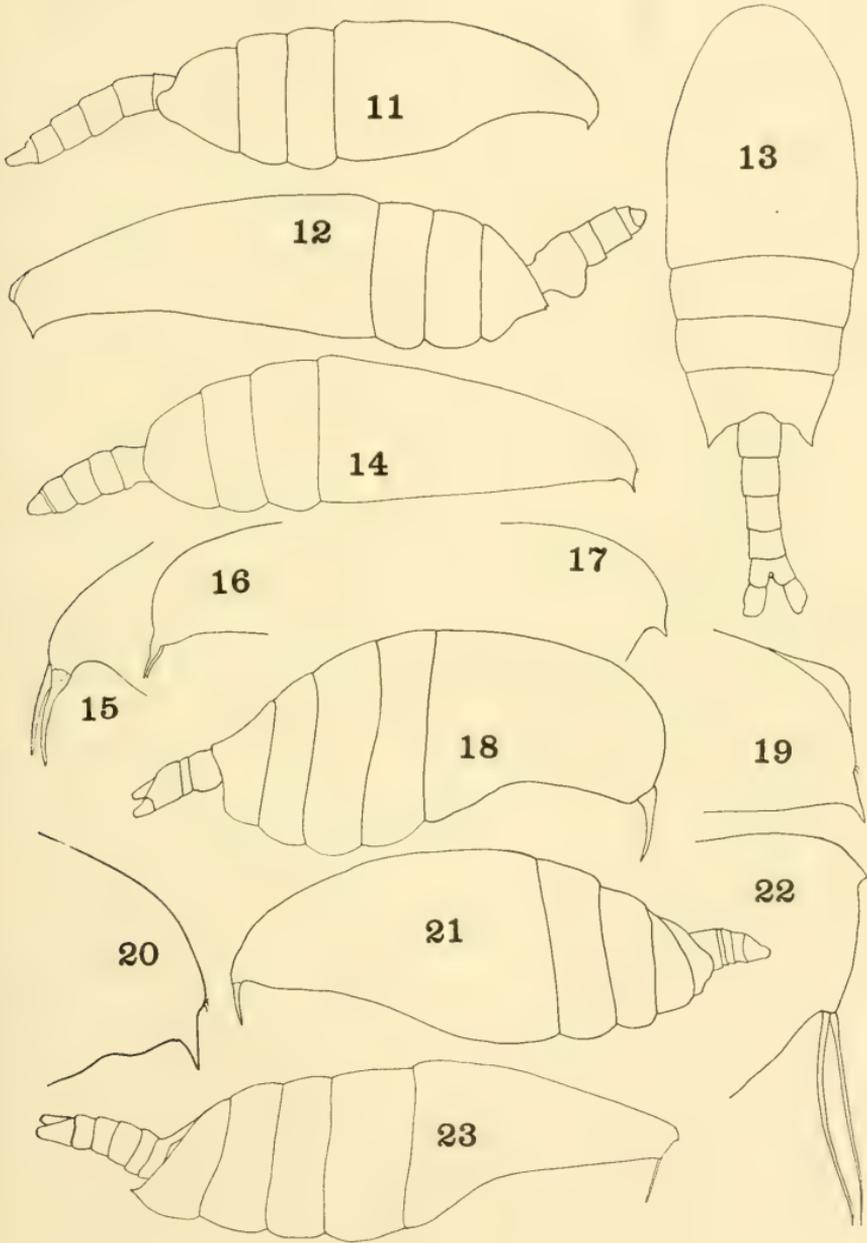


PLATE 28.

- Fig. 24. *Actideopsis pacifica* n. sp. Female, lateral. $\times 29$.
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 Fig. 26. *Gaidius tenuispinus* Sars. Male, head from side. $\times 47$.
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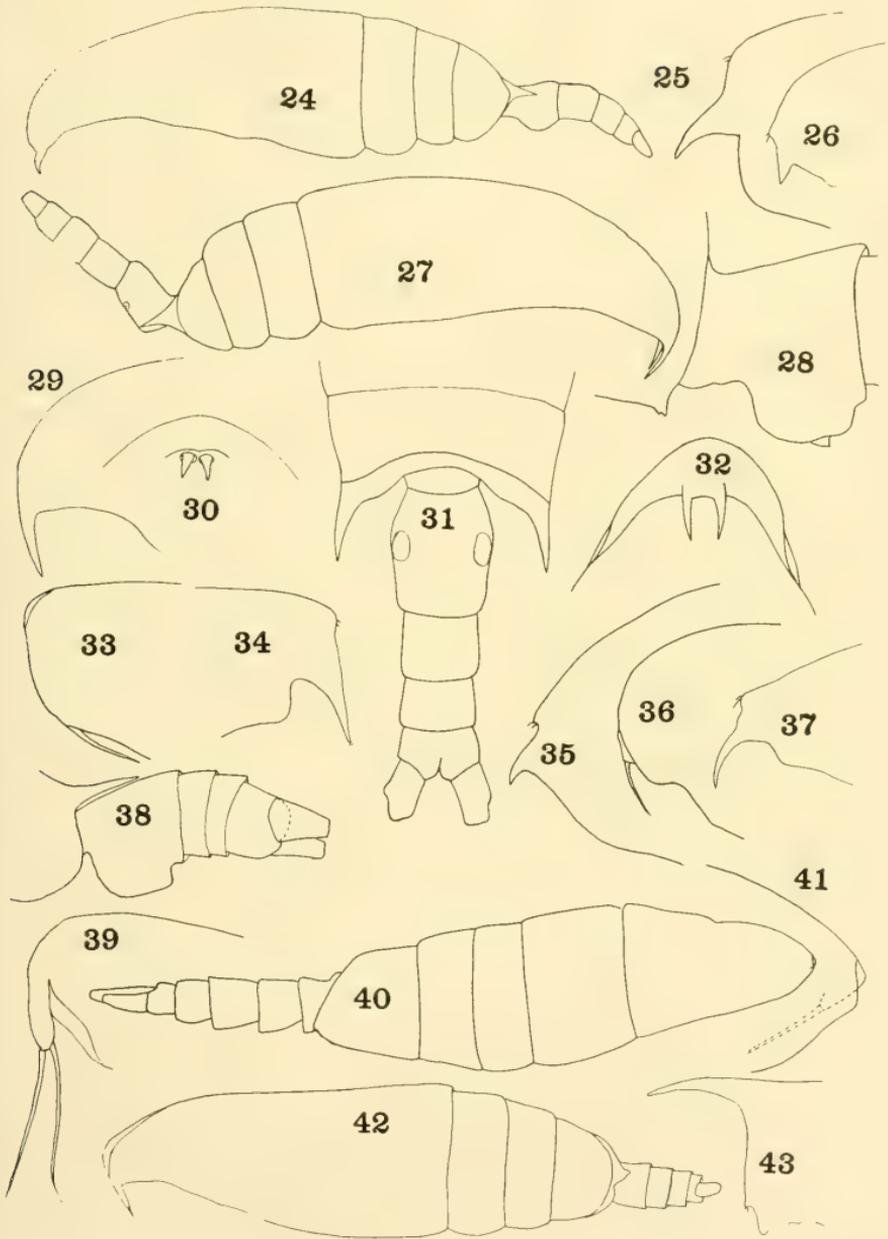


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Fig. 47. *Onchocalanus latus* n. sp. Female, head and two thoracic segments, dorsal. $\times 72.5$.

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Fig. 52. *Euchirella rostrata* Claus. Male, head from side. $\times 72.5$.

Fig. 53. *Xanthocalanus tectus* n. sp. Female, abdomen and last thoracic segments, lateral. $\times 35$.

Fig. 54. *Disseta maxima* n. sp. Female, head from side. $\times 40$.

Fig. 55. *Euchaeta diegensis* n. sp. Female, genital segment from below. $\times 72.5$.

Fig. 56. *Undeuchaeta bispinosa* n. sp. Female, genital segment, ventral. $\times 72.5$.

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Fig. 60. *Xanthocalanus pulcher* n. sp. Female, abdomen and last thoracic segment from side. $\times 72.5$.

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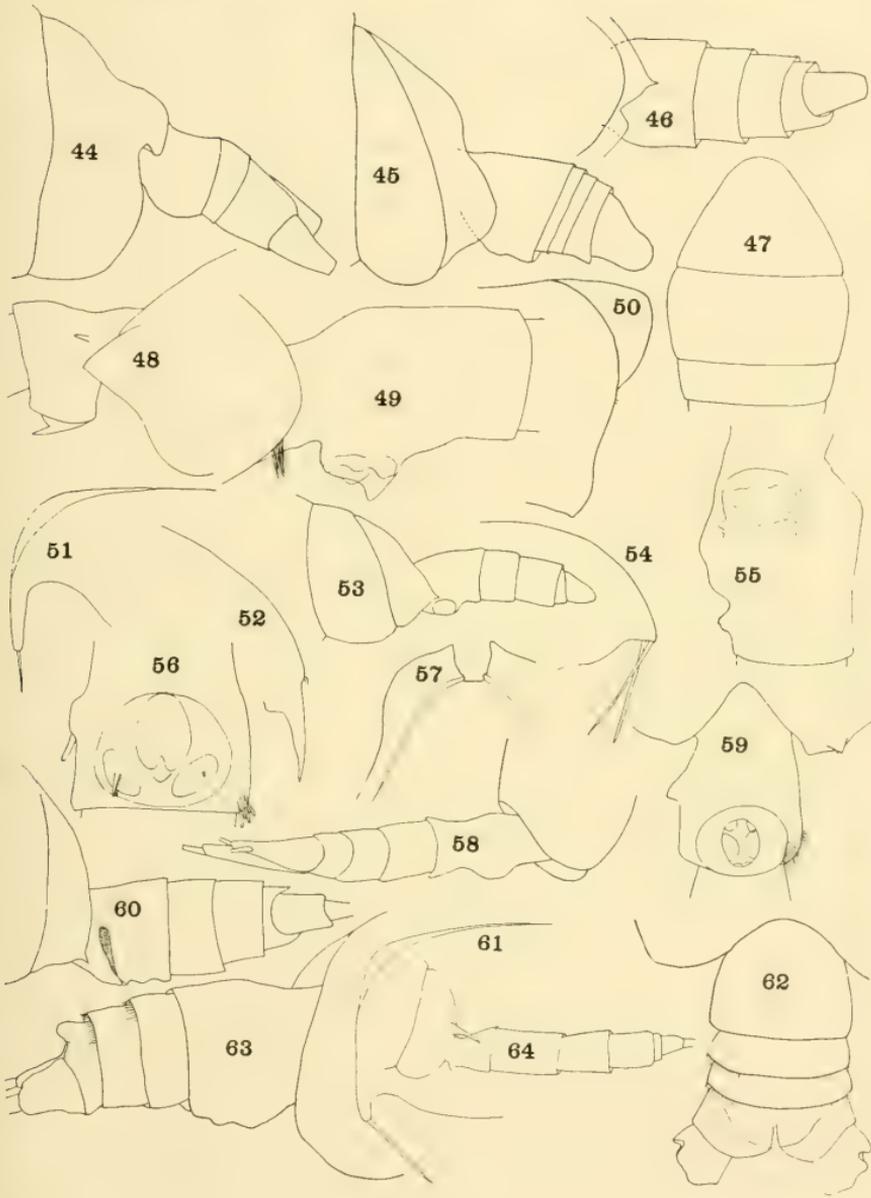


PLATE 30.

- Fig. 65. *Pleuromamma quadrungulata* Dahl. Female, first four joints of right anterior antenna. $\times 40$.
- Fig. 66. *Euchirella rostrata* Claus. Male, tip of left fifth foot. $\times 190$.
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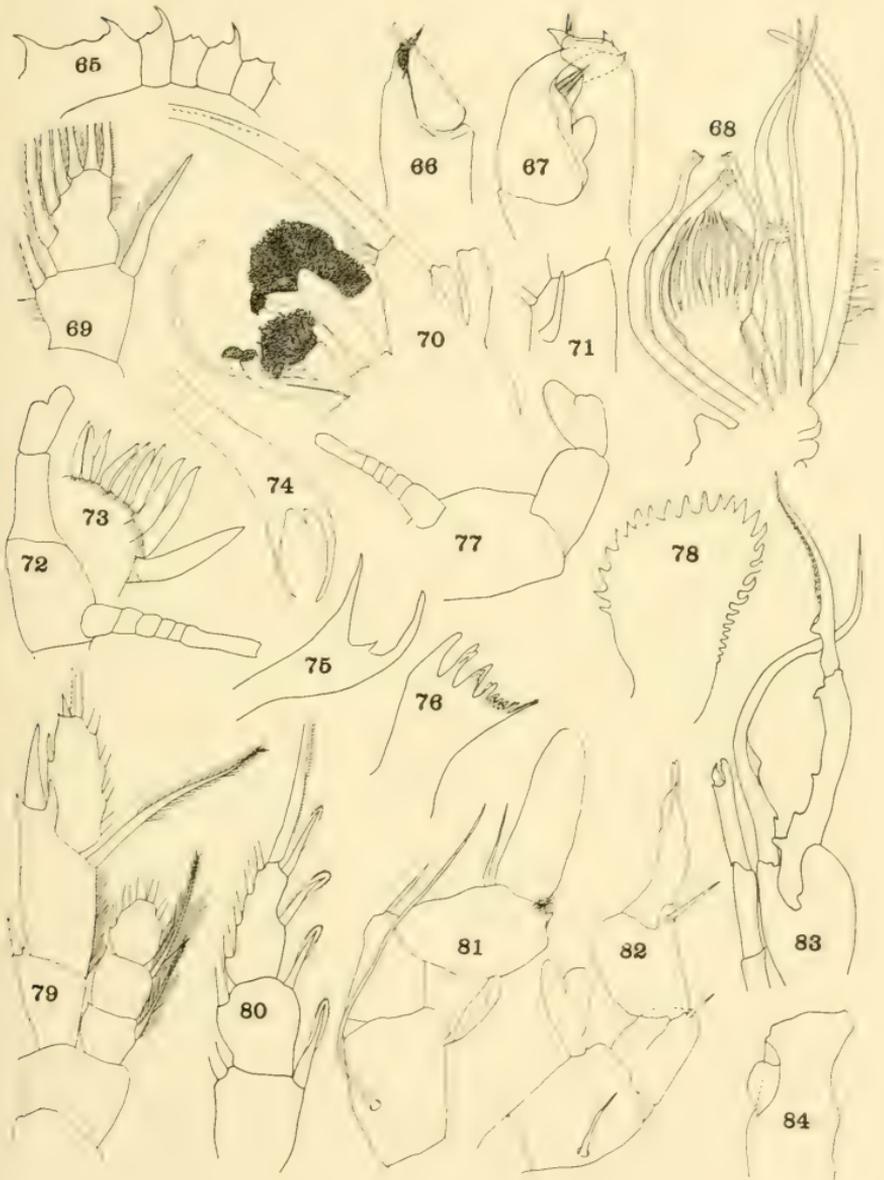


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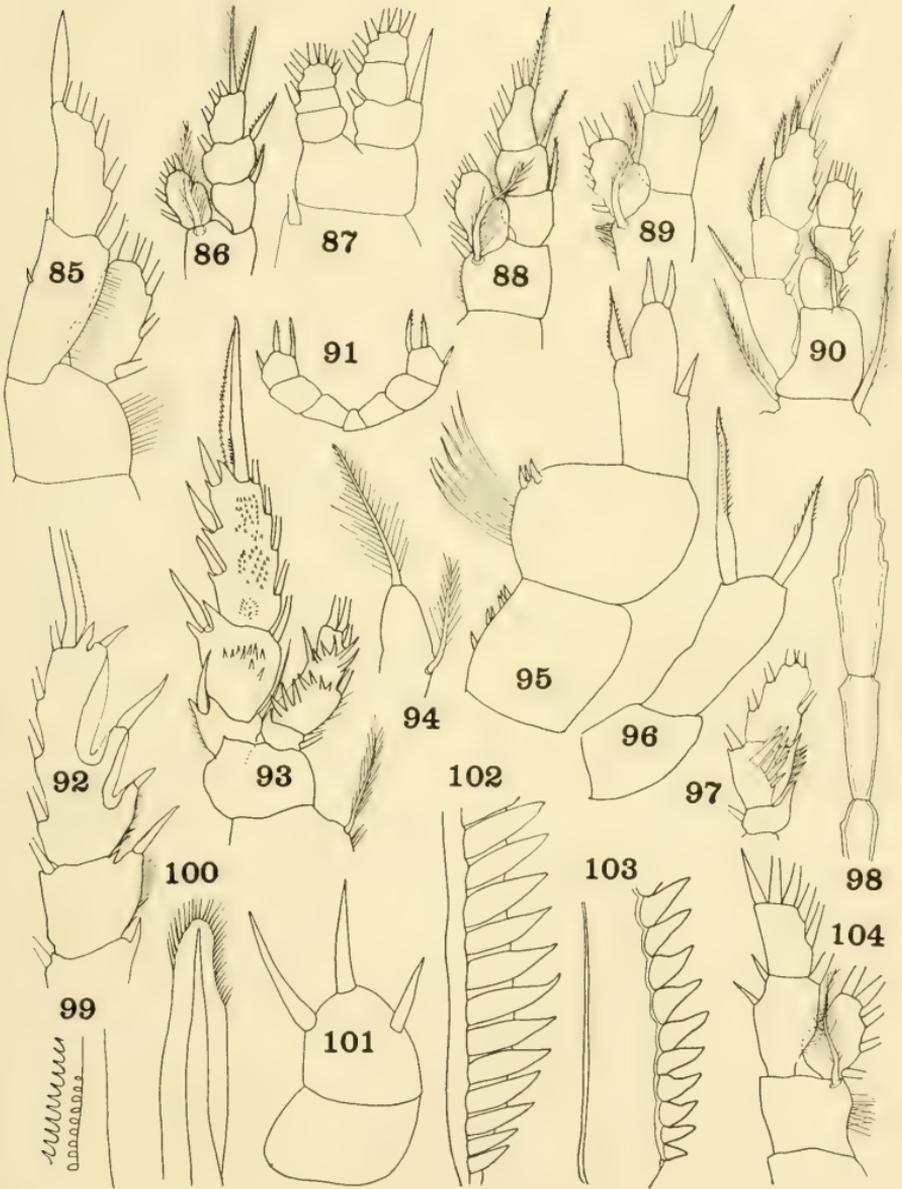
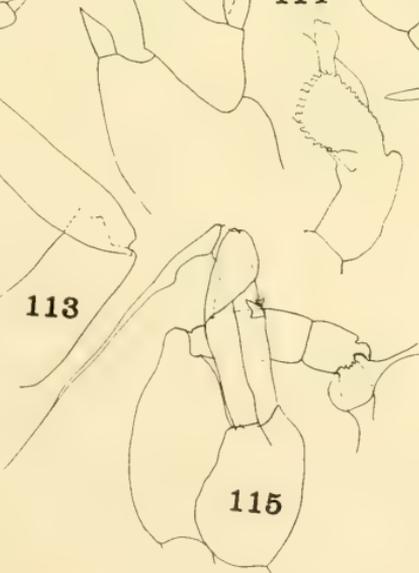
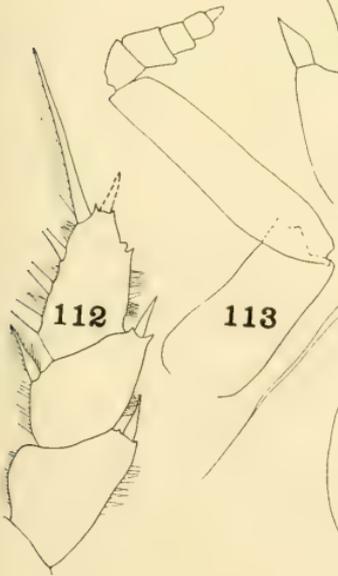
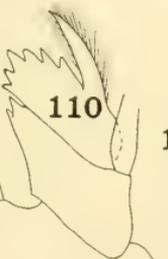
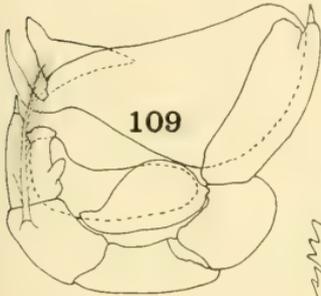
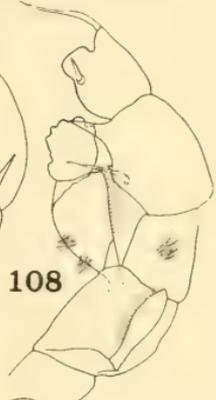
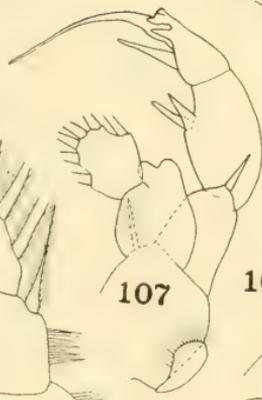
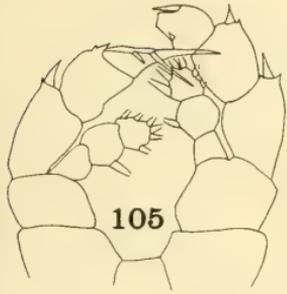


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ZOOLOGY

Vol. 6, No. 15, pp. 353-468, plates 33-48 June 17, 1911

THE GENUS *GYROCOTYLE*, AND ITS
SIGNIFICANCE FOR PROBLEMS
OF CESTODE STRUCTURE
AND PHYLOGENY

BY
EDNA EARL WATSON



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* A dissertation presented to the Faculty of the College of Natural Sciences, in the University of California, in partial satisfaction of the requirements for the degree of Doctor of Philosophy. April, 1910.

A. INTRODUCTION.

The Cestodaria (Monticelli, 1892) or monozoic cestodes (Lang, 1891), including *Amphilina*, (Rud.), *Archigetes* (Ratz) *Caryophyllaeus*, (Rud.) *Gyrocotyle*, (Diesing) and *Wageneria* (Wag.) are of peculiar interest to students of the platyhelminths. They occupy a position intermediate between the merozoic cestodes and the trematodes, being allied to the latter by the general arrangement of the reproductive organs and by their fundamentally unitary character, and distinguished from them by the absence of a digestive tract. This last characteristic allies them with the merozoic cestodes, from which they are distinguished on the other hand by their unsegmented condition and by the accompanying absence of segmental repetition of the genital organs, as stated by Monticelli (1892). The group is difficult to consider as a whole because of the remarkable diversity shown in its four well-established genera, both as to structure, life-history and host. The characters mentioned above practically exhaust those common to the group, and each genus possesses characters of such rank as fittingly to receive ordinal distinction in classification. Two of the genera, *Archigetes* and *Wageneria*, have but one species each. Two each have been assigned to *Caryophyllaeus* and *Amphilina*, and at least four are now recognized in the genus *Gyrocotyle*. The grounds on which specific distinctions have been made are far from satisfactory. These considerations indicate that the group is not only phylogenetically intermediate but composed of very old, long-established forms, on which the forces that make for speciation have long since ceased to act. The Cestodaria are either remnants of a once large and differentiated group, or they are members of a class never differentiated to any considerable extent. They are presumably of greater age than the cestodes, their hosts being invertebrates or primitive vertebrates. Cestodes are phylogenetically the youngest of the platyhelminths, since the host in the sexual period is always a vertebrate. They have been greatly and variously modified by their parasitic habit, and they present problems of structure and development of extreme difficulty. It seems probable that much help towards the solution of these can

be obtained through an exhaustive study of the Cestodaria, the nearest surviving relatives of the merozoic cestodes; and in this possibility lies the chief interest pertaining to the former group and to this investigation.

Lönnerberg (1897), in a study of the phylogeny of parasitic platyhelminths, discusses the possible phylogenetic significance of the Cestodaria and comes to the conclusion that they cannot be regarded as ancestral forms of the merozoic cestodes:

“Die jetzigen polyzoischen Bandwurmstrobilen sind natürlich aus monozoischen Formen hervorgegangen. Die noch jetzt existierenden monozoischen Cestoden können aber kaum als Stammformen der polyzoischen angesehen werden. . . . Diese [*Gyrocotyle* and *Amphilina*] sind wahrscheinlich beide ursprünglich, weichen aber in mehreren Hinsichten von den echten Cestoden recht sehr ab. *Gyrocotyle* ist durch das Erwerben von Haftorganen an beiden Körperenden, das Trichterorgan am Vorderende und das Acetabulum am Hinterende, unfähig geworden, sich weiter zu entwickeln.”

While the writer is convinced of the essential correctness of Lönnerberg's general contention, that the ancestors of cestodes must be sought, not among Cestodaria or trematodes, but among Turbellaria, it is felt that he undervalues the evolutionary significance of the Cestodaria. The merozoic cestode is probably not the descendant of any monozoic cestode now in existence; but because of the fundamental similarity between the two groups we may hope to find, in the simpler forms meeting the same problems in essentially the same way, some clue to the manner in which occurred the complicated processes by which the hypothetical turbellarian-like ancestor was transformed into the merozoic cestode. Naturally, those cestodes which are secondarily monozoic, *Archigetes* and *Caryophyllaeus* (Lönnerberg, 1897) are of little value in this sense. *Amphilina* (*Acipenser*) and *Gyrocotyle* (*Chimaera*) are primarily monozoic, inhabit hosts of great phylogenetic age, and show fundamental correspondence to the typical cestode structure in all important respects. *Gyrocotyle*, the genus with which this paper is concerned, Lönnerberg regarded as off the line of cestode evolution, side-tracked by the development of organs of attachment at both ends. The writer hopes to show that only one functional organ of attachment is present, that this is homologous to the cestode scolex, although

much simpler, and that its structure and position afford very significant indications of the origin and primitive location of the cestode scolex. The evidence of this homology and its theoretical significance will be discussed later; the point of chief interest now is that the very structural peculiarity which Lönnberg regarded as removing *Gyrocotyle* from any great phylogenetic interest is the source of its most significant and interesting contribution to the solution of the problem of cestode origins.

This investigation has been carried on in the Zoological Laboratory of the University of California and at the Station of the Marine Biological Association at La Jolla. For material I am indebted to Professor C. A. Kofoid, and through him to the United States Bureau of Fisheries and the Marine Biological Association at La Jolla; also to Professor Jacques Loeb, for privileges at the Herzstein Research Laboratory at Monterey. For substantial assistance in the preparation of drawings for publication I am indebted to Miss E. J. Rigden. For the pointing out of this line of investigation, for help in obtaining the obscure and not easily accessible literature of the subject, and for counsel and encouragement, I wish to express my debt to Professor Kofoid, under whose direction this work has been brought to its present state of completion.

B. HISTORY OF THE GENUS.

The history of the genus *Gyrocotyle* is complicated by conflicting reports as to its systematic position, its habitat, its orientation and its morphology. The genus was established by Diesing (1850), for a parasite obtained by Gueinzus in 1842 from *Antilope pygarga*, a South African ungulate. This report was an error (Diesing, 1858, p. 492), but was accepted as correct for several years, contributing in no small degree to the confusion concerning the habitat and systematic position of the genus. In 1844 Kröyer showed Diesing a parasite similar to that collected by Gueinzus, taken from inside the shell of an edible mollusk (Diesing, 1855). These two specimens were grouped in one species by Diesing (1850) under the new genus *Gyrocotyle*, and described in the following terms:

“Corpus sub-ellipticum depressum; os subterminale corpore continuum; os subterminale anticum exiguum; acetabulum unum in extremitate caudali terminale, sessile, orbiculare, disce in gyros plicata; penis ventralis superus lateralis; apertura feminea infra penem centralis; porus excretorius dorsalis supra acetabulum.” [Quoted from Braun (1889)].

The genus as thus defined contained only a single species, *Gyrocotyle rugosa*. Diesing referred the genus to the trematodes, placing it near the genus *Amphistomum* because of the posterior position of its acetabulum. In 1855, in his description of the collection of endoparasitic worms made by Natterer in Brazil, Diesing published a second description of the genus identical with the first, with five figures and a discussion of the habit and systematic affinities of the genus. He regards it as improbable that both *Maetra edulis* and *Antilope pygarga* are true hosts of *Gyrocotyle*, and believes that the report of its occurrence in *Maetra* is an error. In case *Maetra* should prove to be the true host, he concludes that *Gyrocotyle* as an ectoparasite would have to be referred to the Bdellidea. As an endoparasite of *Antilope*, he places it under the trematodes. Diesing made no attempt at a study of the internal structure of the parasite and apparently only a cursory examination of its external appearance. From his figures it seems probable that his specimens were in a state of decomposition when preserved.

In 1852 Wagener described and figured a parasite found by himself and Grube in the spiral valve of *Chimaera monstrosa*, at Nice. For this he established the genus *Amphiptyches*, containing a single species, *urna*, and referred this genus to the cestodes because of its morphological resemblance to that group. Wagener made a careful study of the internal structure of the worm, both in the living animal and preserved specimens made partially transparent by clearing. Except for confusion as to the ducts of the genital organs and in a few minor details, his figures are correct. Diesing's (1855) description and figures convinced Wagener that *Amphiptyches* was identical with *Gyrocotyle*. In a letter to Diesing (1857) he calls the latter's attention to *Amphiptyches urna*, and in his “Enthelminthica No. V.” (Wagener, 1858), he discards *Amphiptyches* as a generic name and retains it as a specific name for the form discovered by him:

Gyrocotyle amphiptyches. Diesing ("Revision der Myzhelminthen," 1858) recognizes *Amphiptyches* as a distinct genus, placing it near *Amphistomum* under trematodes, in the place occupied in his earlier paper (1855) by *Gyrocotyle*, then considered an ectoparasite of *Antilope pygarga*. He supposes *Amphiptyches* to have a mouth, digestive tract and anus, in the face of Wagener's (1852, p. 547) explicit statement to the contrary. He gives as its habitat the gills and intestinal tract of *Chimaera monstrosa*. His own genus, *Gyrocotyle*, he puts under the Bdellidea near *Malacobdella* (Diesing, 1858, p. 492). He makes certain changes in the generic description, the most important of these being in the interpretation of the ventral canal opening (proboscis of Spencer); in his description of 1850 he regards it as an excretory pore, in 1858 as the anus. The change was made in order to place the genus under the Bdellidea, where Diesing was convinced it belonged if *Mactra* was its true host. That the report of its occurrence in *Antilope* was an error Diesing had discovered in the interval between 1855 and 1858, and it was probably due to this discovery that the change in the position of the genus was made (Diesing, 1858, p. 492).

Diesing's disposition of *Amphiptyches* was apparently not satisfactory to Wagener, for in his paper "Ueber *Amphilinea foliacea*, *Gyrocotyle* Diesing und *Amphiptyches* (Grube and Wagener)" (1858), Wagener definitely withdraws *Amphiptyches*, recognizing his form to be a species of Diesing's older genus. In Diesing's "Nachträge und Verbesserungen zur Revision der Myzhelminthen" (1859), he agrees with Wagener in placing the two species under one genus, which he refers to the "Bdellidea monocotylea."

The two species are distinguished one from the other only by the absence of spines and lateral frills and the smaller size of the "tail rosette" in *Gyrocotyle rugosa*.

Diesing (1859, p. 448) regards the genus as typically ectoparasitic on marine mollusks, assuming that the species of Grube and Wagener has its normal habitat, not in *Chimaera monstrosa*, but rather on some of those mollusks whose fragments occur in the intestine of the fish. "Da *Gyrocotyle rugosa* aus einem

Mollusken, nämlich der *Maetra edulis* stammt, so ist es sehr wahrscheinlich, dass auch die von Grube und Wagener beschriebene Art ihren eigentlichen Wohnort nicht in der *Chimaera monstrosa*, sondern vielmehr in einer jener Mollusken, deren Fragmente sich im Darne des Fisches verfinden, habe."

Van Beneden and Hesse (1864), maintain the two genera and refer both to the Hirudinea as the "Malacobdellaria dioici." These authors agreed with Diesing in regarding a mollusk as the true host of *Amphiptyches*, stating explicitly that it is not to be considered a parasite of *Chimaera*, but as having been taken in by chance with the mollusk on which the fish feeds. Later Van Beneden (1869) withdrew from this position and classed *Amphiptyches* as a true parasite of *Chimaera*.

No further work was done on either of these forms until Monticelli's "Saggio di una morfologia dei trematodi" (1888) in which he excludes *Gyrocotyle* and *Amphiptyches* from the trematodes, referring *Gyrocotyle* to the bdelloides, near *Malacobdella*, following Hesse and Van Beneden. He affiliates *Amphiptyches* with the cestodes, suggesting that *Amphilina* and *Amphiptyches* are closely related forms, the latter being the simpler of the two, and together should be regarded as forms transitional between trematodes and cestodes. Shortly after this Monticelli (1889b) compared the specimens of *Gyrocotyle* and *Amphiptyches* available in the museums of Leipzig, Berlin and Vienna. As a result of the comparison he says:

"Io ho potuto stabilire con certezza la loro posizione sistematica desumendola dai loro caratteri anatomici ed embryologici. Dalle mie ricerche sono pervenuto alle seguenti conclusioni:

"1. Che l' *Amphiptyches* ed il *Gyrocotyle* devono considerarsi, come già pensavano il Wagener ed il Diesing, due specie distinte del gen. *Gyrocotyle*. Le due specie si chiameranno: *G. rugosa* Diesing e *G. urna* Grube e Wagener.

"2. Che il gen. *Gyrocotyle* deve allogarsi fra i Cestodi e riguardarsi affine all' *Amphilina*."

He goes on to say that the first conclusion rests on remarkable uniformity of structure; the sole external difference being the lack or slight development of the lateral folds in *Gyrocotyle*. The second conclusion rests on the mode of development and internal structure of both species. The similarity of cestodarian

organization to that of the cestodes is then pointed out in the musculature, the lack of a digestive tract, the arrangement of the excretory system, the general form of the nervous system, the arrangement of the genital organs, and the presence of a six-hooked embryo, in *Gyrocotyle rugosa*.

In the same year (1889e), in examining the Entozoa of the British Museum, Monticelli found an undoubted example of *G. rugosa*, taken from *Callorhynchus antarcticus* at Dunedin, New Zealand. As he points out (1890), *G. rugosa* had up to this time been reported only from *Mactra edulis*, *G. urna* only from *Chimaera monstrosa*. He summarizes his conclusion as follows:

“1. Che il genere *Gyrocotyle* è parassita proprio della famiglia delle Chimaeridae.

“2. Che i due generi finora conosciuti della famiglia (*Chimaera* e *Callorhynchus*) albergano ciascuno una specie del genere *Gyrocotyle*.

“3. Che il genere *Gyrocotyle* perviene nelle *Chimaeridae* per mezzo di molluschi bivalvi.”

Monticelli discusses the question whether *Mactra edulis* is to be regarded as the true intermediate host of *G. rugosa*, and concludes that, since the example found in the mollusk contained hooked embryos, a third host must be found to convey *G. rugosa* to *Mactra*. He suggests that possibly some of the mollusks on which *Chimaera monstrosa* feeds (probably some member of the *Cyprinidae*), may be the intermediate hosts of *G. urna*.

This work of Monticelli's definitely settles the question as to the generic identity of *Gyrocotyle* and *Amphiptyches*, and establishes two species of the genus *Gyrocotyle*, separated by three distinct characters. Further, it indicates that *G. rugosa* is a true parasite of *Callorhynchus*, though this point could hardly be considered as established by a single occurrence of the parasite in the fish.

Further evidence on this question was supplied by Spencer's (1889) report on the morphology of three specimens of *Gyrocotyle* found by him in the mouth of a specimen of *Callorhynchus antarcticus*. These Spencer referred to Wagener's *Amphiptyches urna*, but from the form of the lateral frills and the presence of hooked embryos, it seems quite clear that his species was not *G. urna*, but *G. rugosa*. (See my pl. 38, fig. 36). This

view is substantiated by Monticelli's identification of a specimen from *C. antarcticus* as *G. rugosa*, Diesing's original species, though the size, number and character of the frills of the terminal rosette as figured by Spencer do not agree with Diesing's original figure of those structures.

Braun (1889) published a careful review of the literature of the genus up to and including Monticelli's (1890) paper on the finding of *Gyrocotyle rugosa* in *Callorhynchus antarcticus*, but not including Spencer's paper. He reduces *Amphiptyches* to a synonym of *Gyrocotyle*.

Lönnerberg (1890a) mentions the finding of *Gyrocotyle* in July and August, near Bergen. He later (1890b) published a short paper. "Ueber *Amphiptyches* Wag. oder *Gyrocotyle urna* (Grube et Wagener) Diesing." In a subsequent paper (1891) he includes a detailed study of *Amphiptyches urna*, covering the questions of synonymy, systematic position, occurrence, habitat, behavior, orientation, and morphology, concluding with a comparison of *Amphiptyches* with the other genera of the Cestodaria. Lönnerberg agrees with Wagener in regarding *Gyrocotyle* as a true cestode; he considers it the most primitive of the monozoic cestodes and the most closely related to the trematodes. He does not accept the combination of *Gyrocotyle* and *Amphiptyches* in one genus, and regards the form investigated by him, from *Chimaera monstrosa*, as *Amphiptyches urna*. Aside from his careful study of this species, which will be referred to later, Lönnerberg's most important contribution to the knowledge of the genus was his description of the animal in the living condition and the various forms assumed by it. Its behavior and appearance he describes as being in the majority of cases similar to that described by Wagener, namely, pointed at one end, with marginal frills and a terminal rosette. But this typical body-form he saw transformed into a totally different one in which the worms "ganz platt und am beiden Enden gleich sind" (p. 17). (See my pl. 33, figs. 1-4). The ordinary frilled form he regards as a contracted condition of this "Ligulaähnlicher" worm; the intermediate stage between the two he describes as one in which "die Seitenränder in grossen Wellen gebogen sind und nur der äusserste Teil des Trichters in einen kleinen krausen

Kopf zusammengezogen." He describes also a third contraction stage, differing from the ordinary frilled stage even more widely than the "Ligulaähnlicher." This is the most expanded state of the worm, described by Lönnberg as follows:

"Wenn der *Amphiptyches* sich lebhafter bewegen will, verlängert er sein Körper: die Querrunzeln an der Mitte des Körpers glätten sich aus, die dichten seitlichen Krausen wandeln sich dann zuerst in weniger zahlreicher Falten um und diese gehen darauf in einige wenige grosse Wellen über, die bald auch verschwinden und die Seitenränder glatt erscheinen lassen. Der Körper ist nun im Ligulastadium, also platt und lanzettenförmig. Aber gleichzeitig hiermit vollziehen sich am Trichter und dem Halsteil grosse Veränderungen. Dieser verliert seine seitlichen Falten, wird länger und schmaler und erhält eine cylindrische Form. Jener verlängert sich unverhältnissmässig mehr und zwar in der Weise, dass er von hinten und vorwärts sich in ein cylindrisches Rohr umwandelt, der krause 'Kopf' wird immer kleiner und gleichwie vorwärts geschoben; dies geht natürlicher Weise so zu, dass nach und nach mehr von den proximalen Teilen des Trichters zur Bildung des cylindrischen Rohres angewandt werden; bald sind nur die äussersten Lippen ein wenig kraus und schliesslich werden auch diese glatt und man hat eine solche eigentümliche Form, wie fig. 36 [my pl. 33, fig. 2] zeigt, vor sich. . . . Bei höchster Ausdehnung hat dieser Cylinder, wie oben geschrieben ist, beinahe dieselbe Länge wie der ganze übrige Körper, in welchen er allmählig ohne Absatz übergeht. Es ist mir mit schnell totenden Reagentien gelungen einige Tiere in diesem Stadium zu fixieren, und wenn ich sie mit den gewöhnlichen, krausen Formen vergleiche, muss ich gestehen: hätte ich nicht selbst mit eigenen Augen die Umwandlungen gesehen und die Zwischenstadien studieren können, so würde es mir kaum klar werden können nur zwei verschiedene Kontraktionszustände vor mir zu haben." (Lönnberg, 1891, p. 17.)

These statements of Lönnberg's are in part corroborated by the observations of Professor Collett (quoted in Lönnberg, 1891, p. 17, footnote): "Dass zwei verschiedene Cestoden die Spiralklappe Chimaeras bewohnte und zwar ein platter Ligulaähnlicher und der gewöhnliche krause *Amphiptyches*." In addition Olsson (1896) reports that among thirty-three individuals he found "Deux exemplaires, longs de 30 mm, avaient la forme curieuse qui a été dessinée par Lönnberg (1891, fig. 36) et la conservent encore en alcool. La longueur du cylindre creux, qui est formé du cou et de l'entonnoir, est de près de 13 mm, celle du corps n'est que de 17 mm." (See Olsson's fig. 9, p. 509).

Braun (1894) gives a review of the Cestodaria, including *Gyrocotyle*. He recognizes two species of the genus, *G. urna*

(Gr. et Wag.) (from *Chimaera monstrosa*) and *G. rugosa* Diesing (from *Callorhynchus antarcticus*), but adds (p. 1157) that they "differiren so wenig von einander, dass es fráglich ist, ob die Unterscheidung zweier Species sich rechtfertigen lässt; möglicherweise bestehen Unterscheide in der Lage der Genitalpori." According to Lönnberg and Wagener, the vaginal opening is the most anterior and lateral to the penis; but according to Spencer, dealing with *G. rugosa*, the penis opening is anterior to the vagina and marginal.

Benham (1891) recognized the single genus, *Gyrocotyle*, "in the intestine of *Chimaera* and *Callorhynchus*."

Haswell (1902) reported a new species of *Gyrocotyle*, *G. nigrosetosa*, from a new species of *Chimaera*, *C. ogilbyi*, trawled off the Australian coast by the "Thetis." Haswell had one specimen of *G. rugosa*, and two specimens of the new species, "not in good condition for investigation." He did not study the living form. He distinguishes *G. rugosa* from *G. urna* (following Lönnberg's description of the latter) on the following grounds:

- (1) Relative positions of the apertures of the penis and vagina.
- (2) Presence of an eversible cirrus, adapted to self-impregnation, in *G. rugosa*.
- (3) Spinules lining ejaculatory duct, in *G. urna*.
- (4) Size of eggs.
- (5) Presence of hexacanth embryo in *G. rugosa*.
- (6) Shape of spines, which are simpler in *G. rugosa*.

C. GYROCOTYLE OF THE COAST OF CALIFORNIA.

I. OCCURENCE AND HOST.

As this review of the literature shows, the genus *Gyrocotyle* includes three species, *G. rugosa*, *G. urna*, and *G. nigrosetosa*, all occurring as intestinal parasites in the family Chimaeridae. The occurrence of a form of the genus in *Chimaera collicii*, found off the coast of California, has not to my knowledge been previously reported. So far as can be determined, no work has ever been done on the parasites of *C. collicii*. This is the only species

of *Chimaera* found on the Pacific coast of the United States (Dean, 1906, pp. 6, 7) and was first described by Lay and Bennet, 1839, p. 71, pl. 23, in *Zoology of Captain Beechey's Voyage*. Professor Bashford Dean (1906) bases his work largely on eggs of *C. colliei*, and gives a description of the living fish, with notes on its occurrence, habitat, food and breeding habits. It occurs in depths of from 5 to 10 fathoms, being found in shallower water in the Puget Sound region than along the California coast. The specimens examined by the writer have come from the fishing grounds off Piños buoy in Monterey Bay, mentioned by Dean (1906, p. 15); from Cabral's banks off San Diego; and to the north of San Diego, off La Jolla, in depths up to fifty fathoms.

Dean's observations (1906, p. 20) on the food habits of this species, are as follows:

“In view of the special character of the dentition of *Chimaera*, one would naturally expect its food supply to be definite in character. The examination of the contents of its gut, however, showed (*C. colliei*) singularly omnivorous habits. It is true that the broken shells of mollusks are commonly found, as well as fragments of good-sized crustaceans, as indeed the scanty literature records. Thus, in the gut of *C. monstrosa* Faber finds Crustacea and shell-fish fragments; Monticelli, quoting Lütken, *Cyprina islandica*; and Olsson, broken shells (*Leda* and *Venus*) and bits of large decapods. Olsson finds also (and his observations are the most detailed hitherto published on the feeding of *Chimaera*) chaetopods, amphipods, echinoids and polyps. In *C. colliei* observations on about a score of individuals showed a singular mixture of foods. The most numerous were vertebral columns of small isospondylous fishes, a few mollusk shells, usually greatly crushed, a quantity of sand and fine gravel, squid, nudibranchs and opisthobranchs, bits of cases, jaws and setae of annelids, and occasionally a fragment of a crustacean. In one instance the gut was filled with seaweed. One is not surprised, therefore, that this species is taken readily with various baits.”

The observations on stomach contents made by Professor Kōfoid and myself yield results agreeing in general with the above; with the addition that the stomachs contained a great quantity of echinoderm spines, plates, etc. Small fish were common, as were fragments of lamellibranchs, nudibranchs and gastropods. Cephalopod beaks were almost always found. Crustacean fragments, especially of *Hippa* and *Blepharada*, were not uncommon in the San Diego specimens. The fish is so nearly omnivorous in food habits that no definite clue as to the life-history of its parasites can be obtained from these data.

The examination of *C. collicii* for parasites has yielded the following results:

(1) The fish is almost invariably infested with a parasite belonging to the genus *Gyrocotyle*. The parasite was found in 34 of the 38 specimens examined.

(2) The parasite rarely occurs singly, but usually two individuals in one host. More than three in one fish I have never found. In four cases a single individual was found.

(3) No other adult cestodes have been found in the alimentary tract of the fish. Encysted cysticerci are common in the walls of the tract, in the mesenteries, liver, etc., especially during the summer months. Parasitic crustaceans were frequently found on the gills, and an aspidocotylean, probably belonging to the genus *Macraspis*, was found embedded in the muscles of the rectum. A distome, bearing a strong superficial resemblance to a small *Gyrocotyle* without frills, was found once in the posterior region of the rectum, and once in the body-cavity.

(4) Two distinct species of *Gyrocotyle* are found in *C. collicii*; one, the less common of the two, is closely related to and perhaps identical with, *Gyrocotyle urna*; the other differs in several characteristics from any species heretofore described. The incompleteness of the figures and descriptions of *G. urna* make it impossible to determine accurately the identity of the form first mentioned with *G. urna*. It will be referred to as *G. urna* (var.?). The second form, which, in view of its well-defined peculiarities and of the absence of any intermediate forms linking it to any described form, I regard as a new species, will be referred to as *G. fimbriata*.

***Gyrocotyle fimbriata*, sp. nov.**

Diagnosis.—Color, creamy white; length 30-55 mm, width 7-12 mm.; rosette posterior, folds complex; lateral frills 3-5 mm. deep, much folded, passing into smooth lateral fin near anterior extremity; spines numerous, distributed in definite pattern, points directed anteriorly; eggs about 0.09 mm. in average long diameter, no hooked embryos; penis opens mediad of vagina, at about the same antero-posterior level. Occurs in spiral valve of *Chimaera collicii*; can leave host and live for some days free.

These two species occur in fish from the same locality, even taken on the same trawl. Both species have never been found in the same individual. *G. fimbriata* is the more abundant of the two.

II. GROSS ANATOMY OF GYROCOTYLE.

The characteristics on the basis of which species are separated, as given in the literature of the genus, are of various degrees of usefulness and trustworthiness. This is due in great measure to the manifold changes in form and appearance of the living animal and of specimens preserved by different methods in all stages of contraction and deterioration. Before they can be intelligently considered, a brief description of the gross structure of the animal and of the external form and behavior of the living specimen will be necessary. First, the orientation adopted in this paper must be defined. The pointed acetabular end is the anterior, the rosette or canal end the posterior. The surface on which lie the uterine pore and opening of the canal is the creeping surface and the one to which the animal returns in rest. It is therefore ventral. The following description refers especially to *G. fimbriata*.

The worm when alive and attached is almost translucent. After detachment it becomes opaque, whitish-yellow in color, decidedly deeper in tone in the marginal frills and the folds of the terminal posterior rosette. The anterior end is not frilled, is highly contractile, and in the living animal is in constant motion (pl. 33, figs. 7-9). It consists of a very muscular acetabulum, whose margin can be retracted somewhat, while the whole can be drawn back into the body by the retraction of the longitudinal muscles attached to the sucker. Posterior to the acetabulum, in the median dorsal line, lies the opening of the uterus (*ut. po.*, pl. 39, fig. 42). Anterior to this, one-third of the distance between the uterine pore and the posterior margin of the acetabulum, lie the vaginal opening (*vag. op.*), on the ventral surface, and the penis opening (*p. op.*), on the dorsal surface. Both lie almost on the margin, but the penis opening is the more medial and anterior to the vaginal pore. In the median third of the body of the adult, the much coiled and distended uterus occupies

most of the space. In front and to either side of it, running forward to the posterior margin of the sucker, are the follicles of the testes. Peripheral to these, running out into the lateral folds, are the follicles of the vitellaria, distributed from the acetabular region to the base of the posterior rosette. Along the dorsal surface and to the left of the uterus runs the vagina, leading to the large receptaculum seminis (*rec. sem.*) located just posterior to the uterus. On each side of the receptaculum seminis lie the follicular ovaries (*ovar.*); immediately in front of it are the vitelline ducts (*vit. d.*) and the first coils of the uterus. The shell-glands (*sh. gl.*) are found around these ducts. It is in this region that the ova are fertilized, unite with the yolk-cells and receive their shell-coating. Behind the receptaculum seminis and the ovaries lies the ventral opening of the rosette canal. This structure may be regarded as consisting of two parts. The first is a flaring "funnel," its opening terminal, its margin frilled and folded till it resembles a carnation, or as the Germans put it, a "Kohlkopf." This funnel passes directly acetabulad; it leads into a narrow canal, which turns at almost a right angle to the course of the funnel, passing to the ventral surface (pl. 34, fig. 15). This ventral opening I have called the "canal opening" (*can. op.*, pl. 46, fig. 76), in distinction from the terminal funnel opening above described. Funnel and canal together are called by German workers the "Trichter"; Spencer speaks of the funnel-margin as the "rosette" and calls the canal opening the "proboscis."

Gyrocotyle fimbriata (pl. 48, figs. 80, 81), while bearing a general resemblance to the described species of the genus, differs markedly in certain external characteristics. The body in expanded condition is about four times as long as wide; the lateral frills never totally disappear in any stage of expansion, but can be distinguished from the median portion of the body under all conditions. They are about one-fourth the total width of the body in depth. In contracted specimens the folds of the two sides are invariably drawn toward each other on the ventral (canal opening) surface. The posterior terminal rosette (*post. ros.*, pl. 34, figs. 10, 12-15), is from one-half to three-quarters the greatest width of the body in transverse diameter. Its depth is

about one-third its width, and its dorso-ventral diameter varies from one to one-half the transverse diameter, or even, in exceptional cases, to twice this diameter. The folds of the rosette are not simple, but are secondarily folded, standing in marked contrast to the lateral folds, which consist of a single series of undulations. The appearance suggests that the outer wall of the funnel is more contractile than the inner, the result being the production of a multitude of small secondary folds on the inner surface of the funnel. The gross appearance of this type of rosette suggests a finely villous surface, such as an intestinal mucosa. The large folds with long axis parallel to the long axis of the body, so prominent in other species, are almost obliterated here, especially in preserved specimens.

The anterior or acetabular extremity (pl. 33, figs. 7-9; pl. 36, figs. 22, 23), is bluntly pointed and bears a lateral "fin" of tissue, to a point about half-way to its tip. The acetabulum (*acet.*) is contractile within itself to a high degree and the structure as a whole can be drawn back into the body by the strong longitudinal muscles. This occurs in the most strongly contracted stage (*acet.*, pl. 34, fig. 10). The body is markedly asymmetrical, owing to the formation of a deep "genital notch" in the left margin (*gen. notch*). The vaginal opening lies at the angle of this notch on the ventral (canal opening) surface, appearing as a narrow slit bounded by a slightly elevated ring; the penis opens dorsally in a pit at the base of a very low and inconspicuous mound, about two-thirds of the distance from the apex of the notch to the median line (*p. op.*, pl. 36, fig. 23). The relation of penis to vagina varies within narrow limits, but in general they may be said to be at practically the same antero-posterior level.

The lateral frills extend anteriorly to about the level of the genital notch, in front of which they are continued as the unfrilled "lateral fin" above mentioned. Posteriorly they extend to the tip of the posterior rosette. The funnel, whose margin is formed by the posterior rosette, narrows rapidly to a small canal, which turns at an angle slightly greater than 90°, and opens by a small aperture on the ventral (vaginal opening) surface (*can. op.*, pl. 46, fig. 76). The margin of the aperture is raised into a ring, and is crenate (*can. op.*, pl. 34, figs. 14, 15).

Specimens taken from decaying fish have very generally shown a marked diminution in both lateral frills and terminal rosette. Comparison of these with behavior of fresh specimens kept in culture media shows that the diminution is due to an actual disintegration of tissue. The lateral frills are cut off along a perfectly definite line, running in a slightly irregular antero-posterior course. The line can be made out some twenty-four hours before autotomy actually occurs. In every case where a specimen appears to have no lateral frills or noticeably reduced ones, examination shows a cut edge, along which the frills have dropped off. It is possible that Diesing's original figure was taken from a specimen in which this autotomy had taken place. The frills of the terminal rosette do not appear to be cut off in this regular fashion, but disintegrate on the margins only; ragged strings of tissue will be found attached to the body of the rosette. Most of the reduction in the size of the rosette in decayed specimens I believe to be due to intense contraction of that region, though undoubtedly accompanied by a certain amount of actual disintegration of tissue. When the parasite is left in the dead fish over twelve hours, at ordinary temperature, this decay begins.

The spines characteristic of this genus are very prominent in *G. fimbriata*. Their arrangement is in a constant pattern, characteristic of this species. This pattern is described in detail later, under the discussion of the cuticula, but its general outline will be given here also for the sake of convenience. In the anterior region, borne on the lateral "fins" above mentioned, are from five to seven rows of very large black spines (pl. 36, figs. 22, 23.) They are borne on very low papillae. There are about twenty-five of these spines; they vary in length, the more anterior and marginal ones being in general the larger. Their form and structure are discussed below, in connection with the description of the cuticula.

In the posterior region of the body, the spines are longer than those above described. They are borne on large rounded papillae. They form a "collar" (pl. 34, figs. 10, 12) around the region of the body between the funnel opening of the rosette and the canal opening. On the dorsal surface, no spines are found in front of this collar, which does not extend quite to the level of the canal

opening. On the ventral surface a line of scattered spines streams off laterally and anteriorly from the tips of this semi-circle to about the level of the receptaculum seminis. No spines are found on the lateral frills. The arrangement of the spines on the ventral surface (pl. 34, fig. 10) is a fairly constant one. It is of interest when considered in connection with Lönnberg's (1891) theory of the formation of the funnel and canal by means of the partial fusion of folds of the ventral body wall.

Gyrocotyle urna (Wagener) var.?

In the material collected by Dr. Kofoid near Monterey, off the California coast in 1904, were found three specimens differing from the rest in certain characters which seem to constitute a basis for specific distinction. Later, in 1907-1908, the writer found several similar specimens. The characters peculiar to this form are as follows:

1. The lateral frills are less voluminous.
2. The folds of the posterior rosette are simple (*i.e.*, not thrown into irregular secondary frills, as in *G. fimbriata*), varying in diameter from one-sixth to one-third of the width of the body.
3. The lateral frills do not extend to the base of the rosette but taper off gradually, disappearing posterior to the receptaculum seminis.
4. Spines are present over the whole of the ventral surface as far forward as the middle of the length of the uterus, and extend thence in two lateral wings forward to a point just back of the level of the opening of the uterus. There is no distinct pattern discernible as in *G. fimbriata*. There are only a few scattered spines on the dorsal surface, except around the "collar," immediately in front of the base of the frill of the posterior rosette.
5. The relative position of the opening of the penis, uterus, and vagina is markedly different from that seen in *G. fimbriata*. (See measurements, p. 381.)

Except in two particulars, *i.e.*, the distribution of the spines and the fact that penis and vagina open at approximately the same antero-posterior level, this form seems to be identical with

Gyrocotyle urna as described by Wagener and Lönnberg. The distribution of spines may vary with age, though it has been found constant in specimens of all sizes of *G. fimbriata*. It is also possible that the non-appearance of the spines may be due to action of reagents on preserved material. The figure given by Wagener (1852) shows a very close approach to the pattern given above as characteristic for *G. fimbriata*. The whole question of distribution of spines cannot be settled until more material is available.

The question whether penis or vagina opens more anteriorly is a difficult one. In specimens killed between glass plates, these relations can be very easily distorted. On the other hand, in specimens not killed thus, it is very difficult to compare the positions of the two openings, as they are on opposite surfaces of a body too thick to be made transparent by clearing agents. The specimens in my possession show the two openings at practically the same level, with a small range of individual variation, depending upon the degree of extrusion of the penis-papilla.

Not having specimens of *G. urna* for comparison, it has been impossible to decide whether this form is really a distinct one, or belongs to Wagener's species. Until comparison can be made, it will be referred to as *G. urna* (var.?).

III. BEHAVIOR OF THE LIVING ANIMAL.

The shape of the body varies greatly in the living animal, and also in preserved specimens. Wagener's figures (pl. 48, figs. 84, 85) are the best in the literature, so far as giving a faithful reproduction of the appearance of the living worm. His figure of the preserved specimen, on the other hand, resembles very slightly any specimen that has come under the writer's notice. The acetabular extremity of the living animal is extended into a long, slender, cylindrical proboscis, along the sides of which the spines above referred to are distributed. This part of the worm is in constant motion. Posterior to the genital openings, in the region of the lateral frills, the body is flattened, slightly convex dorsally. Posterior to the uterus the lateral frills become less deep, and the body less flattened. This "neck" region can be very considerably extended. On the posterior extremity is borne the rosette, of

greater size in *G. fimbriata* than in *G. urna*, and its folds many times as complex, but generally held in a position exactly like that shown in Wagener's second figure, that is, the opening of the funnel, the rosette surface, lying, not at right angles to the surface of the body, but parallel to it.

The stage shown in Wagener's first figure represents the most extreme stage of expansion noted by the writer. No stages corresponding to those figured by Lönnberg (pl. 33, figs. 1-4) were seen, although the specimens observed were in many cases perfectly fresh and very active, contracting and expanding with great freedom, and moving about in the dish. But the shape of the posterior rosette was never materially altered, nor did the lateral folds completely disappear. Further, in the observations by Wagener, by Dr. Kofoid, and by the writer on the worm, an expanded condition always involves expansion of the acetabular extremity as well as the neck of the rosette. None of Lönnberg's figures shows anything suggesting the very characteristic acetabular extremity as first figured by Wagener. In observations of twenty-three living worms the writer has never failed to find the acetabular extremity assuming and maintaining this appearance throughout the period of activity. Lönnberg's observations, as above noted, are corroborated by Olsson (1896), who adds the astonishing statement that the worms preserve this form in alcohol. As the parasite is exceedingly sensitive to chemical stimuli, and invariably reacts to even a very dilute solution (5 per cent.) of alcohol by strong contraction, this seems to indicate that Olsson at least was dealing with some form other than *Gyrocotyle*. The writer found on two occasions, while searching for *Gyrocotyle* in *Chimacra collicei*, a distome strongly suggesting Lönnberg's figure and maintaining its shape in killing fluids, which might have been mistaken for *Gyrocotyle*. But since Lönnberg states explicitly that these transformations in form took place under his eyes, this explanation seems scarcely possible. We are forced to accept a discrepancy in results here, only to be removed by further investigation.

The living worm, in the intestine of a fish that has just been caught, is translucent, of a dull pink color, exactly similar to the intestine on which it lies. The worm in perfectly fresh fish

is firmly attached by the terminal rosette, which is spread over an area of ten to twelve millimeters in diameter. The folds of the rosette fit over the villi of the intestine. The canal opening (on the ventral surface) is closed as long as the rosette remains attached. A series of waves of contraction passes from the margin of the rosette toward the canal opening, during the attachment of the rosette. The lateral frills are present even in the most expanded state of the worm, constituting one-half of the total width of the body. The acetabulum is very active, thrusting itself backward, under, over or to the side of the body. The whole worm contracts and expands frequently without any apparent stimulus. The parasite is not easily affected by mechanical stimuli under these conditions, but will contract if exposed to direct sunlight, and is very sensitive to chemical stimuli. The acetabulum has never been found attached, or in any sense functioning as a sucker. This statement is borne out by all investigators.

Shortly after the death of the fish, the fluid intestinal contents become thick and opaque, and the worm detaches itself and contracts, losing its translucence and becoming creamy-white in color. The region of the mucous membrane to which the rosette has been attached is of a deep purplish red, and appears inflamed after the rosette has detached itself. Many of the worms are found in this opaque condition, and do not again become active. From observations on the behavior of the attached specimens, and from the fact that inactive specimens are found in all parts of the intestinal tract, in the mouth and on the gills, it appears fairly certain that the worm attempts to leave the dead host, and very frequently succeeds in doing so. In one case, the worm was found crawling up the first turn of the valve, when the intestine was opened. The fact that specimens are so often found, either in the first or next to the last turn of the valve, also points to this conclusion. Finally, the finding of a living specimen crawling on the bottom of a jar of sea-water in which a *Chimaera* had been placed, is fairly conclusive evidence that the worm occasionally succeeds in escaping from its host. The parasite is never found attached elsewhere than in the spiral valve. Spencer (1889, p. 138) remarks in this connection: "The specimens

[of *Gyrocotyle rugosa*] obtained by myself—three in number—were taken from the mouth of *Callorhynchus antarcticus*, and their presence in such a position was doubtless associated with the fact that the fish had been dead some twenty-four hours, though the parasites were still living and evidently trying to find their way out of the dead body." Wagener (1852, p. 543) says: "Nur einmal fand es sich an den Kiemen, wobei jedoch bemerkt werden muss, dass die Fisch schon 12 Stunden ausserhalb des Wassers sich befand." Lönnberg (1891) mentions the finding of *G. urna* living free, but supposes the worms to have finished their cycle and to have been cast out with the excrement of the host. He seems to imply in the following statement that the worms leave the dead host (writing of the almost invariable occurrence of the parasite in *Chimaera*): "In zwei anderen, die ich in Upsala untersuchte, die aber von Trondhjem stammten, habe ich ihn nicht gefunden, aber diese Fische waren schon seit mehreren Tagen ausserhalb des Wassers." It may then be regarded as an established fact that the parasite is capable of a very considerable amount of locomotion, and that it can, under favorable conditions, leave its host and live for some days outside the intestinal tract. The most important condition seems to be temperature; a low temperature (about 10°-12° C.) is most favorable. In warm weather the worms remain active for only a very short time, and have never succeeded in getting out of the intestine in any case under my observation. This ability to leave the host, taken in connection with the behavior of the isolated parasite as described below, has an important bearing both on the problem of orientation and on the question of the habitat of the parasite, which will be discussed later.

The worms on being removed from the fish were placed in culture fluids. The worm is very active, if removed soon after the death of the fish and kept at a low temperature. The culture solution quickly becomes contaminated with bacteria, and the worm contracts and grows sluggish. When changed to fresh solution the parasite expands and renews its movements. These consist of the following:

1. Thrusting and exploring movements of the acetabular extremity, accompanied by contraction and expansion of the body.

2. "Righting-up" movements, in which the worm turns from one surface to the other. These take place when the worm is placed on its dorsal surface and also when it is exposed to strong light.

3. This turning over is accomplished in two typical ways, either by turning completely over on one side on the frills as an axis, or by a more elaborate process of tucking under the acetabulum until it emerges posterior to the rosette, when the rosette is elevated and the overturning accomplished after the manner of a somersault.

4. A rotation from side to side of the terminal rosette, accompanied by a wave-motion in the margin of the frills, takes place during the worm's most active period.

5. Locomotion in a definite direction is accomplished by means of a series of expansions and contractions, with some help from the mobile lateral frills. The acetabular extremity is in every case directed anteriorly; the rosette is held in the typical position, raised, with the canal opening ventral and the funnel opening dorsal. The acetabulum is thrust out, and the whole body elongates, the rosette remaining stationary. This expansion leaves the rosette end where it was before, the acetabular end some two centimeters further toward the goal than at start. Then a wave of contraction sets in, bringing the rosette end nearer the acetabular end, which also moves backward a short distance, approaching the rosette. The net result is an advance in the acetabular direction. The acetabulum remains contracted, while the rest of the body expands. In this expansion the rosette must either retreat, or the whole contracted anterior extremity be shoved forward. The latter is what actually occurs, as shown by careful marking of the relative positions of the two ends before and after the wave of expansion. This method of procedure is very effective, resulting in an average gain of about two centimeters for each wave of contraction. A distance of fourteen centimeters was traveled in ten minutes by one specimen; but in this case more than the average gain was made, the whole distance being accomplished in five contractions.

IV. CHARACTERISTICS FOR SEPARATION OF SPECIES.

The characteristic peculiarities of each species have been set forth by its discoverer, but there has been no systematic attempt to assess the worth of these characteristics for the genus as a whole since that of Braun (1894). He was not acquainted with at least one very important set of species characteristics, that proposed by Haswell (1902).

The first species characteristics were proposed by Diesing (1859). He distinguishes *G. rugosa* from *G. urna* by the presence of lateral frills and spines and the greater size of the tail rosette in that species.

Monticelli also recognizes these two species, separating them by the following points:

1. The absence in *G. rugosa* of the frilled lateral margins.
2. The greater length of the uterus in *G. rugosa*, possibly correlated with the following character.
3. The presence of hooks in the embryo within the uterus of *G. rugosa*.

Braun (1894) recognized *G. urna* and *G. rugosa*, but only as doubtfully distinct. The basis for separation he finds in the position of the opening of the vagina and penis; the former being the more anterior in *G. urna*, the latter in *G. rugosa*.

Haswell (1902) recognized *G. urna* and *G. rugosa* and tentatively proposed a new species, *G. nigrosetosa*. He distinguished *G. rugosa* from *G. urna* on the following grounds:

1. Relative position of the apertures of penis and vagina.
2. Presence of an eversible cirrus adapted to self-impregnation in *G. rugosa*.
3. Spinules lining the ejaculatory duct in *G. urna*.
4. Presence of hexacanth embryo in the uterine egg of *G. rugosa*.
5. Shape of spines.

G. nigrosetosa he distinguishes on the following grounds:

1. Size of eggs, 0.08 mm., as distinct from eggs of *G. rugosa*, 0.1 mm.
2. Presence of operculum, distinct from *G. rugosa* and *G. urna*.

3. Absence of hooked embryos.

After careful comparison of the available figures and descriptions and a study of about forty specimens, ranging in state of preservation from those perfectly fresh, attached to the intestine of the host, down to badly disintegrated specimens from various regions of the alimentary tract of decomposing hosts, the writer has found certain of these proposed criteria to be useful and valid. Certain others seem untrustworthy. These specific characters may be listed and criticized as follows:

1. *Presence of lateral frills*.—It seems fairly certain that lateral frills are present in all species of the genus, when the specimen is in a good state of preservation. Presence of the frills is therefore not a basis for specific distinctions. The amplitude of the frills, and their relative width (in terms of total body width) for any given state of contraction or expansion, is however a characteristic of real value in the recognition of species. *G. rugosa* (pl. 38, fig. 36) has comparatively scanty and narrow frills; in *G. nigrosetosa* the frills are deeper and more voluminous; in *G. urna* (pl. 47, figs. 84, 85) they are twice the depth of those in *G. nigrosetosa* and many times as voluminous. In *G. fimbriata* (pl. 34, fig. 10) they are still more ample and about the same depth as in *G. urna*. While these differences can be easily seen, the extreme contractility of the animal makes it impracticable to attempt to use this characteristic as a basis for separation of species. It is a concomitant, rather than a critical characteristic, not available for exact description.

Diesing's specimen without frills was taken, it will be recalled, from *Maetra*. According to the best of our knowledge the only host of the adult parasite is some member of the family *Chimaeridae*; this specimen, having been set free from its host in some fashion, probably entered the shell of the mollusk by accident. Certainly not adapted to life as an ectoparasite, processes of disintegration would undoubtedly speedily set in, and my own experiments with *Gyrocotyle* in culture media show that deterioration invariably begins by cutting off of the lateral frills in increasingly deeper layers.

2. *Presence of spines*.—This is critical only when applied to living specimens and to those which have been preserved in such

a manner as not to injure the spines. In addition to the effect of reagents, disintegration results in the early loosening and disappearance of the spines. In no case where the living worm has been examined have the spines been absent.

The distribution of the spines affords a useful basis of distinction. In *G. rugosa* (Spencer, 1889), "spines are scattered over the whole surface of the body"; in *G. nigrosetosa* (Haswell, 1902) "they are mainly confined to the dorsal surface, except at the anterior end. Over the rest of the ventral surface are scattered a very few, much smaller than those on the dorsal surface." In *G. urna* (Lönnberg, 1891), the distribution is confined to the extremities and the lateral margins of the body, leaving the middle of the body, from just in front of the canal opening to the level of the acetabulum, free from spines. In *G. fimbriata* the condition is as described by Lönnberg for *G. urna*, except that spines are absent from the greater part of the lateral margin of the body, and do not occur on the lateral frills. Possible variation with age and the ease with which spines may be lost by slight disintegration or action of reagents, makes any distinction resting on them somewhat impracticable. Here again we have differences coördinated with, but scarcely useful as, specific distinctions.

3. *Size of tail rosette.*—This character appears to depend less on the state of contraction than do the width and amplitude of the lateral folds, and if reduced to a definite statement in terms of some other dimension of the animal, would probably be found to vary about a mean characteristic for each species. The astonishing illustrations given by Lönnberg (pl. 33, figs. 1-4) would, if corroborated, not necessarily invalidate the worth of this characteristic, provided comparisons were made between specimens in a similar state of contraction. *G. rugosa* (pl. 33, figs. 5, 6) in a contracted state has a rosette about one-fourth its greatest body-width in diameter. In *G. nigrosetosa*, the rosette is about five-sixths the body-width; in *G. urna* about one-half; while in *G. fimbriata* it varies from two-thirds to three-fourths or even more.

4. *Length of uterus.*—This is a character which it is exceedingly difficult to apply. The length of the much-contorted

uterus is hard to estimate, the number of turns may vary with the state of contraction, and certainly varies with age. I have been unable to reduce this to definite measurements. From Spencer's diagram it seems probable that the uterus occupies more space in *G. rugosa* than it does in *G. fimbriata*, or, according to Haswell, in *G. nigrosetosa*.

5. *Presence of hooked embryos in uterine eggs*.—This is a character easily applied and apparently thoroughly critical. It serves to set off *G. rugosa* from the rest of the genus.

6. *The relative positions of the openings of the penis and vagina*.—This character is perfectly definite and, applied to material not flattened under pressure when killed, seems trustworthy. There is one possible source of confusion, in the fact that the penis opening is on the summit of a papilla, very mobile and capable of considerable extension. The vagina is fixed in position. In case this papilla should be fully extended, the penis opening might lie in front of the vagina; while if withdrawn it would lie well behind it. The same criticism might hold for medio-lateral relations. The fact that *G. rugosa*, the only form in which the penis papilla has been observed greatly extruded, is also the only one in which the opening is definitely in front of the vaginal opening, suggested this possible source of error. Spencer's figure seems to point in this direction.

7. *Presence of an eversible cirrus, adapted to self-impregnation*.—This arrangement has been reported only by Haswell for *G. nigrosetosa*. It does not seem probable that only one species of the genus possesses a type of cirrus adapted to self-impregnation, especially when it is reflected that single individuals of all reported species have been found repeatedly in their hosts. It is strange that no eversion of the cirrus has ever been noted in any except the one specimen of *G. rugosa* studied by Haswell, and possibly in the one figured by Spencer.

8.—*Spinules lining ejaculatory duct*.—This character is of service in setting off *G. rugosa* from the rest of the genus; spinules (interpreted by Lönnberg as cilia) have been observed in the ejaculatory duct of *G. nigrosetosa* by Haswell, of *G. urna* by Lönnberg, and in *G. fimbriata* by the writer.

9. *Shape of spines*.—The data on this point need revision.

The shape of the spines may vary somewhat in different regions of the same animal. Furthermore, all the spines thus far described correspond exactly to those figured by Lönnberg, with the exception of Spencer's figure of the spines of *G. rugosa*. Possibly a study of more individuals of the latter species may show closer similarity to the type of the genus.

10. *Size of eggs.*—This character must be regarded with some distrust, in view of the fact that one individual may yield ripe eggs varying in size from 0.075 mm. to 0.115 mm.

11. *Presence of an operculum in the egg-shell.*—Haswell (1902) figures an egg of *G. nigrosetosa*, having a thick shell, with a thin plate at one pole, in diameter less than one-third the greatest transverse diameter of the egg (see my plate 47, figure 81.) "A circular area of the shell at one pole is much thinner than the rest, and is probably differentiated as an operculum." The same observer studied eggs of *G. rugosa*, and states that in them the shell does not appear to be provided with an operculum. The eggs of *G. fimbriata* show when discharged no such thin plate; but eggs taken from poorly preserved specimens show an operculum, its diameter a little more than half the greatest transverse diameter of the egg, in which the shell is slightly thinner than elsewhere. Its margin is serrated. This cap differs in size, thickness, and character of margin from the operculum of Haswell, but seems to be an homologous structure. The significant point is that there is no trace of it in the freshly discharged ova, and that it does appear very clearly later. Probably the ova of *G. urna* and *G. rugosa* would also show a similar structure, at a similar stage. The problem is whether Haswell's operculum is present in a freshly discharged or intra-uterine egg, or whether it is merely an early stage of the formation of this cap. Only in the former case does the operculum become a good specific character. Haswell explicitly observes that "the specimens were not in good condition for minute investigation." His figure (see my plate 47, figure 80) shows the neck of the rosette as swollen, recalling an appearance characteristic of worms kept too long in culture media. But in the absence of any definite statement as to the condition of the two specimens of *G. nigro-*

sctosa, the presence of an operculum in uterine eggs must be adopted as a specific characteristic of *G. nigrosctosa*.

In addition to these characters which have been proposed and found trustworthy, the writer suggests the following:

1. *The character of the folds of the terminal rosette, whether simple or complex.* This is correlated with the greater relative size of the rosette; but the fact that the size varies greatly and is difficult to express in a ratio that could be applied to any specimen to be determined, makes the character of the folds themselves seem a more easily applicable test. The writer is convinced that this character is constant in all stages of contraction, at all ages, and after treatment with all the ordinary reagents. It becomes unrecognizable only after decay has proceeded very far indeed.

2. *The ratio between the distance from the opening of the uterus to the tip of the acetabulum, and the distance from the opening of the uterus to the level of the opening of the penis.* While these absolute distances vary enormously with the state of contraction, a series of measurements shows that the ratio is fairly constant about a mean characteristic of the species.

TABLE I.

Ratios of Measurements of Position of Genital Pores in *Gyrocotyle*.

<i>G. fimbriata</i>	<i>G. urna</i>	<i>G. rugosa</i>	<i>G. urna</i> (Wag.)	<i>G. nigrosctosa</i>
.4615	.266	.515	.333	.490
.4500	.222	.582		
.4444	.200	.592		
.4444	.200			
.4375				
.4375				
.4295				
.4295				
.4295				
.4290				
.4000				
.4000				
.3809				
.3333				
.3333				
.3333				

V. KEY TO SPECIES OF *GYROCOTYLE*.

On the basis of the above discussion, the following classification is proposed:

A. Frills of posterior rosette simple.

- I. Uterine eggs containing hooked embryos. Opening of penis laterad of, and anterior to, vaginal opening.

G. rugosa.

Host: *Maetra edulis*. Diesing (1850, p. 408) Brazil. Monticelli (1889b, p. 228).

Callorhynchus antarcticus. Monticelli (1889c, p. 327), Dunedin, N. Z. Spencer (1889, p. 138), Australia.

- II. Uterine eggs not containing hooked embryos. Opening of penis mediad to vaginal opening.

- (1) Opening of penis posterior to vaginal opening.

(a) Eggs without operculum.

G. urna.

Host: *Chimaera monstrosa*. Wagener (1852, p. 545). Nice. Kröyer, *Dänmark's Fiske*, v. 3, p. 813. Van Beneden and Hesse (1864, p. 54). Olsson (1868, p. 58; 1896, p. 508). Lönnberg (1891, p. 14). Bergen, Christiania. Monticelli (1889b, p. 229; 1889b, p. 327). Mediterranean. Hansson. Free-living off the west coast of Sweden. (Lönnberg, 1891, p. 14).

(b) Eggs with operculum.

G. nigrosetosa.

Host: *Chimaera ogilbyi*, Haswell (1902, p. 48). Australia.

- (2) Opening of penis at the same level as vaginal opening.

G. urna (var?)

Host: *Chimaera colliciei*, from the California coast. Has been found attached by terminal rosette to mucosa of spiral valve.

- B. Frills of posterior rosette complex. Opening of penis mediad to vaginal opening, at same level.

G. fimbriata.

Host: *Chimaera colliciei*; off the California coast. Has been found attached as above, free in intestine, and in mouth and on gills of host.

D. GENERAL MORPHOLOGY AND HISTOLOGY OF GYROCOTYLE.

I. MATERIAL AND METHODS.

The structure of the worm has been studied in living specimens, in whole mounts stained and cleared, and in serial sections. The following killing fluids were used: Gilson's fluid, aceto-sublimite, Zenker's fluid and Vom Rath's mixture. The greatest difficulty is found in preventing extreme contraction of the specimens. Stupefaction with chloretone resulted in contraction as intense as that produced by the killing fluid: the use of hot reagents was of some small advantage. Flattening between plates of glass gave the least contraction, but had the disadvantage of producing some distortion. The best results were obtained from specimens killed in Zenker's fluid; the poorest from those killed in Gilson's fluid. It is difficult to obtain good infiltration with paraffine, especially in the normal (not flattened) specimens. The modification of Apathy's method given by Lee was very successful, leaving the tissues in good condition. High temperatures (over 50° C.) are rapidly fatal to the integrity of the tissues. The shortest possible time in paraffine of the lowest melting point that can be used gives the most satisfactory result.

The worm is very difficult to section because of the great mass of eggs it contains. Various macerating agents were tried, but none was of any great service. Sections were cut as thin as 4 μ ; most of the series ranged from 8 μ to 16 μ , the latter in collodion.

The stains used were: Heidenhain's iron haematoxylin, Benda's iron haematoxylin, Mayer's acid haemalum, Mallory's connective tissue stain, Delafield's haematoxylin, Ehrlich's haematoxylin, Lönnberg's borax carmine-Lyons blue, toluidin blue. Iron haematoxylin preparations are excellent for the study of cuticula, musculature and sex-cells; they are worthless for the study of the nervous system and unreliable in many details. No statements are based on results given by this stain alone.

Mallory's connective tissue stain colored nervous tissue, with the exception of the nuclei, bright blue. Its action was too

uneven to be of special value. Mayer's acid haemalum, Delafield's haematoxylin and Ehrlich's haematoxylin gave satisfactory results for general morphology. Lönnberg's borax carmine-Lyon's blue method gave the best result for the study of the nervous system. This in general is the method used by Lönnberg in his work on *Gyrocotyle*. A brief description of the process is given by him (Lönnberg, 1891). The material is stained *in toto* in Grenacher's alcoholic borax carmine, 60% alcohol, decolorized in acid alcohol (5 drops conc. HCl to 100 cc.); after sectioning and mounting the sections are run very quickly through absolute and 90% alcohol to a saturated solution of Lyon's blue in 60% alcohol, plus three drops n/10 HCl to 35 cc. of stain, where they remain fifteen minutes. The sections are decolorized in ammoniacal 85% alcohol made up of one part 85% just basic to litmus to 4 parts neutral 85%. Decolorization requires from two to three minutes and must be stopped when the sections appear violet in color. On washing in neutral 90% the differentiation takes place. The sections must not be left in 90% or absolute longer than one or two seconds, else the stain is blurred. This method gives beautiful preparations in so far as differentiation of tissues is concerned, but is rather poor for cytological differentiation, especially in cell-boundaries.

The nervous system stains uniformly a light blue, easily distinguished from all other tissues except condensed connective tissue. The blue is clearer in the nerves than in the connective tissue; the nervous tissue can easily be recognized with a fair degree of certainty by this fact, coupled with its distinctive histological structure.

The statement generally made that Lyon's blue should be used in very dilute solution for corrosive sublimate material is not applicable in this case. Weak solutions give no result, for all the color drops out at once, leaving no differentiation.

II. BODY-COVERING AND SPINES.

The body is covered by a thin membrane, composed of finely felted fibres imbedded in a homogeneous matrix (*cut.*, pl. 42, figs. 55, 58). These fibres are exceedingly delicate, tangled in an irregular fashion, but in general parallel to the surface of the

body. The outer surface of the membrane is bounded by a fine, deeply stained layer of ragged fibres (*ext. cut. l.*). This is seen only in perfectly preserved specimens. Vesicles occur frequently in the membrane. There are also breaks in the margin, resembling sections of the "pore-canals" figured by Blochmann (1896). The thickness of this membrane varies in different regions, being slightly less on the lateral folds and on the surface of the acetabulum. The average thickness on the surface of the body proper is about 3.8μ ; on the lateral folds, etc., about 2μ . This membrane will be referred to as a "cuticula," following the common usage among writers on the subject; but the word is not used in its strict sense, as denoting a body-covering derived from an underlying epidermis. The cuticula of *Gyrocotyle* may or may not be derived from the "subcuticular" layer referred to below; structural relations indicate that it is, but in the opinion of the writer the question can only be settled by embryological data which are not available.

Lönnerberg (1891) describes a two-layered cuticula, agreeing in general with the appearance of that of *G. fimbriata*; but he describes the fibres seen in the "Hauptschichte" or principal layer, as running perpendicular to the surface. He finds this only in sections in which the cuticula is torn or affected by reagents; from appearances presented in similar sections, the writer thinks he was probably dealing, not with the cuticular layer, but with a layer of perpendicular fibres lying beneath the cuticular muscles, to be described later.

Immediately beneath the cuticula (*cut. trans.*, pl. 42, fig. 55) is a layer of cuticular muscle-fibres running round the body at right angles to its long axis (*cut. trans.*, pl. 42, fig. 58). Close beneath this layer lies a set of longitudinally arranged muscle-fibres (*cut. long.*); these are heavier than the transverse fibres. These layers of muscles are distinguished as the cuticular musculature. Some distance below these muscle fibres is an irregular layer of large nuclei, about twice the size of the ordinary parenchyma nucleus, resting on and often imbedded in the outer transverse layer of body musculature (*sub. cut.*). This layer may be one or two nuclei deep, or it may be from five to eight deep. In the neighborhood of a spine the layer becomes three

to five times its ordinary depth. These nuclei, the "Matrixzellen" of Lönnberg, are richly supplied with chromatin. Definite cell-boundaries can sometimes be seen; the cytoplasm stains deeply and shows a granular structure. The writer was unable to establish any processes running from these cells out to the cuticula through the cuticular muscle-fibres, or to make out any structural connection existing between cuticula and subcuticula. The space between the subcuticular layer and the longitudinal cuticular muscles is filled with very delicate muscle-fibres (*sag. fib.*) and thread-like processes of the subcuticular cells, taking in general a direction perpendicular to the surface. There are also many fibres running parallel to the surface, as shown in transverse section by their cut ends, but these are not so conspicuous as the perpendicular threads. It was probably this layer which Lönnberg mistook for the principal layer of the cuticula in his sections. The writer has found similar appearances, due to the fact that the cuticula is very easily affected by reagents. In a specimen preserved in early stages of decomposition or imperfectly fixed by the killing fluid, the cuticula is almost invariably found to be sloughing off in thin strips, broken, notched and ragged. It presents both horizontal and perpendicular planes of cleavage, but shows a marked tendency to split in layers parallel to the body-surface. This is the only indication of lamination noticed; it is more justly interpreted as a splitting in the direction taken by the greater portion of the fibres of which it is composed.

The cuticula in the region of the rosette shows marked changes. That lining the funnel is noticeably thinner, the cuticular muscular layers are much reduced, and the subcuticular cells are very few. As the much-folded margin of the funnel is approached, the subcuticular cells of the outer wall also become much reduced, sink deeper and cease to be a distinct layer; lying within them large gland cells can be seen. In the writer's opinion these are not related to the subcuticular cells but belong to the central part of the body just as do the shell-glands and the prostate glands, arising in the neighborhood of the inner longitudinal muscular layer.

The most prominent feature of the body-covering is the

spines, frequently referred to in the preceding discussion of the literature of the subject. In *G. fimbriata*, the spines are arranged in a definite pattern, from which there is no great amount of individual variation, though the number of spines varies considerably. At the anterior extremity, on the lateral fin on each side of the acetabulum are two groups of large spines (pl. 36, figs. 22, 23). They are arranged in five rows, two each on the dorsal and ventral surfaces and one row on the margin. There are from five to seven spines in a row, from 20 to 30 in each group. Here, as elsewhere, the spines are borne on rounded papillae, which are in this region of greater size than elsewhere on the body, except around the "neck" of the rosette. The papillae extend back along the lateral fin to the beginning of the lateral folds, but bear spines only at the region shown in the figure, at the level of the posterior half of the acetabulum. In addition to these large spines, of the shape shown in fig. 28, there are a number of very much smaller, less definitely shaped spines (pl. 37, fig. 32), in among the larger ones.

There are no spines on either surface, throughout the length of the body, back to the posterior border of the receptaculum seminis. Here on the ventral surface two groups of spines appear, near the base of the lateral folds, extending backward in converging lines toward the canal opening. They flank this opening, increasing in number and size, and spread out posteriorly on the surface of the neck of the rosette in its median half. At the posterior border of the neck they extend laterally, passing around to the dorsal surface. On the extreme lateral margins of the ventral surface appear two groups of spines, which pass over on the dorsal surface, forming with the ring above described a belt of spines on the dorsal surface of the neck. The number and direction of these spines is shown in the figures (pl. 34, figs. 10, 12).

In *G. urna* (var.?) the distribution of spines (pl. 36, fig. 24; pl. 34, figs. 11, 13) is markedly different. The ventral surface, to the level of the uterus opening, is thickly set with large spines; there is no special pattern in the arrangement about the neck, there being six or seven irregular rows of spines, encircling the base of the rosette. On the dorsal surface the spines are

fewer and scattered irregularly over the whole surface. It should be noted that the two marginal clumps of spines at the level of the acetabulum occur as they do in *G. fimbriata*.

The distribution of spines was worked out in living as well as preserved material, that no error due to loss of spines by deterioration or action of reagents might enter. The distribution found resembles that given by Lönnberg for *G. urna*, except that he describes spines as present along the whole length of the lateral margins of the body, and along the lateral folds. The distribution as given by Spencer (1889, p. 140) for *G. rugosa* is substantially that found in *G. urna* (var.?):

“They are distributed generally over the body surface, but are most numerous along the side folds, and more especially at the anterior end, both on the dorsal and ventral surfaces, and again at the posterior end, beyond the region of the side folds. They are sparsely distributed over the central part of the body, both dorsally and ventrally.”

Haswell's figures (see my plate 47, figure 80) show spines of great size distributed over the whole of the surface of the animal. Wagener's (1852) figures show the acetabular clumps, and a distribution of the spines in the posterior region similar to that described by Lönnberg and given above for *G. fimbriata*.

The small spines, irregularly distributed, vary in size from 40μ to 60μ by 15μ to 25μ , and in shape from simple rounded spinules to a blunt-tipped, swollen-based form. Broad, triangular, sharply pointed forms also occur, but less frequently (pl. 37, fig. 32). These spinules are not borne on papillae; they rarely contain more than three concentric layers.

The spines proper, from the extremities of the body, are of fairly constant shape and size. In the acetabular region (pl. 37, figs. 28, 29) they are bluntly rounded at the tip, swollen in the middle third of their length to nearly three times the diameter of the tip, narrowing again at the bluntly rounded base. They are about 130μ by 36μ in size. In the rosette region, the spines are of the same general shape (pl. 37, figs. 30, 35), but are of considerably greater size, ranging from 185μ by 45μ to 220μ by 55μ .

The spines are composed of concentric layers of uniform thickness, and are hollow. In macerated specimens the layers

are seen to be composed of a finely felted mass of fibres, circular in general direction, embedded in a homogeneous interstitial substance which is acted on by the macerating agent (which also removes the cuticula from the body) (pl. 37, fig. 33). Each spine is set in a pit lined with a very thin cuticula of felted fibres (*par. felt*, pl. 37, fig. 34) which passes indistinguishably into the fibres of the surrounding parenchyma. The spine is surrounded by muscle-bundles, which serve to protrude and retract the spine. The retractors are muscle-bundles from the outer transverse layer of the body musculature; they insert at the base of the spine (pl. 37, fig. 30). The protractors are bundles of fibres inserted at the base and for some distance on the sides of the spine; they originate or are attached to the cuticular musculature, principally to its transverse layer.

The direction of the spines is shown in the figures (pl. 34, figs. 10-13). In general they may be said to be directed anteriorly and laterally. This is the most advantageous arrangement possible for maintaining the attachment of the parasite to its host; the position of the greatest number of spines on the ventral surface and around the rosette also further this end. For locomotion, the spines seem to be arranged to hinder rather than help; but they are probably so completely retracted that their rounded ends offer no special resistance to the forward movements of the worm. At all events, however theoretically difficult their arrangement and direction render locomotion, the worm does move, and with considerable rapidity, in spite of them. Naturally, ease of locomotion is a secondary and firmness of attachment a primary consideration in the economy of this creature.

III. MUSCULATURE.

The musculature of *Gyrocotyle* is exceedingly well developed, and composed of powerful, neatly balanced sets of muscles. It constitutes the great bulk of the body. This is not surprising, when the extreme contractility and general activity of the worm is considered.

In general, muscles are grouped in pairs running at right angles to each other. There is throughout the body, but especially prominent in the region between the acetabulum and the

canal opening, a set of sagittal fibres, very delicate, not organized into bundles, running from the outer cuticular muscle layer of the dorsal surface to that of the ventral surface. The fibres insert directly in the cuticula, as do those of the protractors of the spines.

In addition to these sagittal fibres, six distinct coats of muscle fibres can be distinguished, in the body proper. These may be grouped according to their action, which gives us three sets of opposing muscles, each set a longitudinal opposed to a transverse; or they may be grouped according to their position with respect to the other tissues of the body. Such a division gives us two groups, one of which may be again subdivided into two.

1. *Peripheral*, including all muscles lying without the vitellaria. May be divided into:

(a). *Cuticular*, including all muscles lying without the subcuticula or "Matrix-zellen."

(b) *Intermediate*, including all muscles lying between the subcuticula and the vitellaria.

2. *Central*, muscles lying within the vitellaria.

The cuticular muscles have been described in connection with the cuticula (p. 385). Immediately beneath the subcuticular cells, frequently invading their territory, is a layer of muscle-bundles directed around the body, at an angle of about 60° to its main axis. Thus in a cross-section we get only broken segments of this layer, not a continuous sheet, as in the deeper-lying transverse muscle layer. These fibres run in two interlacing sets whose directions are at an angle of 60° to each other. These bundles all break through the subcuticula to insert by fine threads on the cuticula (pl. 42, fig. 55).

Immediately beneath the outer transverse layer above described are found the bundles of fibres running parallel to the longitudinal axis of the body. These are heavier and grouped into more definite bundles than any previously described. The layer is one or two bundles thick and occurs over the whole body, but becomes very thin in the region of the lateral folds. These fibres insert on the cuticular musculature, and with the outer transverse just described produce the transverse ridges so characteristic of the worm in its contracted state. Within this layer

lie the inner transverse muscles, a very heavy sheet of fibres running at right angles to the longitudinal axis, around the body. These fibres also are continued for some distance into the region of the lateral folds, but are considerably reduced. These muscle layers constitute the peripheral musculature and are found throughout the whole body, though less and less strongly developed the further laterad they pass.

Within the inner transverse muscles lie the vitellaria, the large excretory canals, the central nervous system, the glands of the reproductive system, and the strongest muscles of the body, the inner longitudinal. In the region of the body anterior to the testes and posterior to the ovaries, these muscle-bundles occupy the whole of the space inside the vitellaria. In the intermediate region, especially in the region of the uterus, the layer is considerably reduced, and pushed to one side. It is quite thick ventrally, but there are very few fibres dorsal to the uterus. These longitudinal fibres insert on the acetabulum, and around the neck of the rosette and on the walls of the canal. It is by the contraction of these powerful muscles that the worm moves about, thrusts forth and around and withdraws the proboscis-like acetabulum, and firmly attaches the posterior rosette. Furthermore, as Lönnberg pointed out, this muscle layer being absent in the lateral frills, and the outer longitudinal fibres being very weakly developed there, on contraction of the longitudinal muscles the lateral folds are increased in amplitude. Lönnberg regards the frills as due wholly to contraction of the body musculature; the writer, in agreement with Wagener, regards them as independent structures, existing in all states of expansion of the animal.

The musculature of the acetabular region (pl. 40, fig. 43) shows plainly the origin of the acetabulum as an invagination of the anterior extremity of the body. There is a doubling of the layers, giving twelve instead of six. By inverting the anterior extremity we get a mass of predominantly longitudinal muscles, corresponding to the inner longitudinal body-layer, on the outside of the acetabulum. These fibres are meridional with reference to the acetabulum as a whole and constitute more than half its bulk. Inserting along the surface of this mass are the inner

longitudinal muscles of the body, most numerous toward the anterior extremity and in large masses around the margin of invagination; on contraction of the inner longitudinal muscles, the whole mass of the acetabulum is drawn back (pl. 40, fig. 43). This is the state invariably found in killed specimens. In the living animal in the expanded state the mouth of the acetabulum is at the anterior extremity (pl. 33, figs. 7, 9); further evagination is impossible. The great lengthening of this region observed in active specimens must be due to expansion of the acetabulum itself.

The fibres of the outermost layer (*out. mer.*), constituting the bulk of the acetabulum, are derived from the inner longitudinal layer of the body and are meridional in direction, presenting in section a margin of cut edges surrounding the acetabulum. This layer is densely supplied with finer radial fibres (*rad. fib.*), at right angles to the long axis of the acetabulum, passing from dorsal to ventral surface. These are the homologues of the sagittal fibres of the body musculature, greatly increased in size.

Immediately within this outer heavy layer lies a set of fibres predominantly transverse (*out. circ.*), passing from left to right of the acetabulum, the homologue of the inner transverse layer of the body. This layer is even more abundantly supplied with radial fibres than is the outermost one. These pass from dorsal to ventral, at right angles to the radial fibres of the outer layer. Within this layer is a second set of meridional fibres (*in. mer.*); the homologues of the outer longitudinal muscles of the body, followed by a thin layer of fibres passing circularly around the opening of the acetabulum, corresponding to the outer transverse muscles of the body. Lying next to the cuticula are thin longitudinal and transverse layers, the homologues of the cuticular musculature elsewhere. At the mouth of the acetabulum a special sphincter muscle has been developed, composed of fibres from the inner transverse, the inner longitudinal and the circular muscle layers of the acetabulum (*acet. sphinc.*). Most of the fibres are circular in direction; they are grouped in heavy bundles and form a large ring-muscle about the acetabular opening.

The musculature of the funnel-region has been worked out

by Lönnberg (1891). There is here a doubling of layers, due to folding on the ventral surface, and an increase in the inner transverse layer to produce two "wing-muscles." Lönnberg's tabulation of the funnel muscles and their homologues in *Gyrocotyle urna* the writer finds substantially correct for *G. fimbriata*. Here as in the acetabulum the development has been mainly in the inner transverse layer, and in the sagittal fibres. By means of these a very effective sphincter is produced at the base of the rosette. Posterior to the collar or "neck" (the region occupied by this sphincter) and anterior to it near the canal opening, the development of the transverse muscle layer is much reduced, though still greater than in the body in general.

Lönnberg concludes from the above described arrangement of muscle layers that the rosette and canal were formed by a folding from the posterior extremity forward in the ventral surface. This was first a furrow or trough, which functioned as a sucker, a condition common among the lower cestodes; later the ventral walls fused to form a tube, and finally only the most posterior part of the tube functioned as an organ of attachment, its anterior extremity remaining open as the present ventral opening of the canal. Lönnberg hazards no opinion as to the significance of this anterior canal opening. Observations on the attached worm show that the mouth of the opening is always closed while the rosette is attached to the mucosa. When the canal mouth opens, flaring out as in Spencer's figure 2, the hold of the rosette loosens and the worm drops from the mucosa. During attachment there is a series of waves of contraction, running from the margin of the rosette forward to the canal opening. The whole posterior extremity thus forms a suction-cup of high efficiency. The musculature of the ventral canal-opening, developed from the peripheral muscles, is shown in plate 40, figure 44.

The finer structure of the muscles in *Gyrocotyle* is very simple. The sagittal fibres (radial fibres of acetabulum and rosette collar) are not aggregated into bundles but are simple strands running through the body, distinguished from parenchymal fibres by their size and also by the position of the nucleus (pl. 42, fig. 57). This lies to one side of the fibre, forming a

bulging prominence. These nuclei are larger and more easily seen than those of the other muscle fibres; this is in harmony with the generally primitive and undifferentiated character of this set of muscle fibres. In the outer transverse muscle layer the fibres are longer, very slightly swollen in the middle of their length, where the nucleus lies very closely applied to one side of the fibre. The nucleus also is elongated, rather than round as in the dorso-ventral fibre (pl. 42, fig. 57). In the two inner layers, the inner circular and the inner longitudinal, the nucleus is very hard to distinguish (pl. 42, fig. 56). The fibres are heavy, elongated, tapering gradually toward their extremities. The nucleus is exceedingly slender, flattened against the surface at one side of the fibre, but still within the fibre. In cross-sections of fibres the nucleus is difficult to distinguish, appearing merely as a thickening of the cell-wall; in longitudinal sections it can be made out more easily. Had not the nucleus appeared so unmistakably in the outer and sagittal muscles, it probably would have been overlooked in these inner fibres.

In the cuticular muscle fibres there is no trace of a nucleus. The fibres are slender, long, of even diameter. Those of the transverse layer are exceedingly fine, while the longitudinal ones are of ordinary diameter. The great number of processes running from the subcuticular cells, apparently to insert in the cuticular musculature, suggests most strongly that some of these cells, at least, are the myoblasts of the cuticular musculature. The fact that elsewhere in the body the nucleus lies in the fibre makes this seem improbable, yet the writer is at a loss to explain the processes and their connection with the musculature in any other way.

All the fibre bundles are penetrated throughout and enveloped by parenchymal threads, with their accompanying nuclei. The latter can always be distinguished from muscle-nuclei by their shape and size, as well as by position.

It is of interest to note that Salensky (1874) found in *Amphiliina foliacea* smooth muscle fibres with laterally attached myoblast, this being one of the earliest cases in which a nucleus for a muscle fibre was discovered. Furthermore, the description above given of laterally attached nucleus in the dorso-ventral,

transverse and longitudinal muscles and of nucleus some distance removed from the fibre in the subcuticular muscles, corresponds to the classification given by Braun (1901, p. 1351). The only difference is that the laterally attached nucleus in *Gyrocotyle* is inside the fibre, not in an adjacent myoblast. The occurrence of nuclei within muscle fibres is reported, according to Braun (1894, p. 1351) in the scolex of the Tetrarhyncha, and in the longitudinal muscles of the proglottides of *Taenia dendritica*. That a form as primitive as *Gyrocotyle* should exhibit a muscle fibre relatively simple and undifferentiated as compared with that of the merozoic cestodes, is exactly what other facts in its structure would lead one to expect.

The staining reactions of the muscle-fibres are of some interest. With iron hematoxylin and toluidin blue the whole fibre stains very intensely. Preparations by these methods are excellent morphologically, mapping out the muscles most sharply; but are quite worthless histologically. With Mallory's connective tissue stain, muscle fibres stain a bright red. As nuclei also stain red, this method is not useful for a study of muscle-nuclei. The same holds true for borax carmine-Lyon's blue preparations. The best results are given by Delafield's hematoxylin, hematoxylin-eosin, or Mayer's acid haemalum, and counter-stains. With these the muscle-fibre stains a dull blue-gray, while the nucleus comes out sharply in blue-black.

IV. REPRODUCTIVE ORGANS.

The organs of *Gyrocotyle* include the following:

1. Female. Ovaries, receptaculum ovarum, vitellaria, shell-glands, uterus, vagina, and receptaculum seminis.
2. Male. Testes, vasa efferentia, vesicula seminalis, vas deferens, penis, and prostate glands.

All of these organs, with the exception of the vitellaria, lie within the inner longitudinal muscles. The female organs are in the second and third quarters of the length of the body; the male organs in the first quarter.

The ovaries (*ovar.*, pl. 39, fig. 42) lie laterad of the uterus, at its posterior border. They are roughly triangular in shape, the lateral lobes united in the median line just posterior to the

receptaculum seminis by a small median portion. They are composed of numerous rounded follicles, from which run collecting tubules to empty into five main oviducts, one posterior, two lateral and two anterior ducts. These lead into the receptaculum ovorum, which is embedded in a mass of loose tissue in a depression on the anterior dorsal surface of the receptaculum seminis. The receptaculum ovorum (*rec. ov.*, pl. 45, figs. 73, 75), is about 3 mm. in its antero-posterior and its dorso-ventral diameter and about 6 mm. in transdiameter. These measurements are the average for several sexually mature worms.

The *vitellaria* are composed of loosely-grouped follicles, each containing ten or fifteen cells, lying just within the inner transverse musculature and outside the inner longitudinal. The follicles are present throughout the body with the following exceptions: (1) dorsal and ventral to the uterus, that is, in the median third of the body in the two middle quarters or more of its length; (2) anterior to the posterior border of the acetabulum; (3) posterior to the level of the ventral canal opening.

The lateral folds are densely supplied with vitellarian follicles, these forming the greater part of the folds. The ducts of these yolk glands unite into four main lateral ducts, which empty into a yolk reservoir, or "Endstück," which lies in the dorsal depression of the receptaculum seminis above mentioned, just posterior to the receptaculum ovorum. It gives off a single efferent vitellary duct, which enters the afferent oviduct, as described below, a short distance back of the entrance of the duct connecting the efferent oviduct with the receptaculum seminis.

The *efferent yolk-ducts* (pl. 39, fig. 42, *vit. d.*), appear in stained and cleared preparations as a dark brown anastomosing network of delicate threads, spread over the receptaculum seminis and the first three or four coils of the uterus, and converging to the yolk-reservoir in the concavity of the receptaculum.

From the ventral surface of the receptaculum ovorum is given off in the median line a single *efferent duct* (*cf. ovd.*) which receives first a short thick-walled duct from the receptaculum seminis (*duct. sem.*); and then an efferent duct from the yolk reservoir (*cf. vit. d.*, pl. 45, figs. 71-74). This duct

(oot.) then becomes the uterus, passing to the left of the receptaculum seminis and around it to the ventral surface, across the ventral surface and forward, at once increasing in size. The first two or three coils of the uterus, as above described, may be regarded as an oötype. They are surrounded by shell-glands, and within them the compound eggs are formed. In the dorsal (proximal) part of the first coil, and to the left of the receptaculum seminis, the yolk-cells are seen to be aggregating about a single ovum and the uterus is full of droplets of a yellow homogeneous material, which form a coating around the combined ovum and yolk-cells. The uterus contains fully formed eggs in the convolutions anterior to the receptaculum seminis. It winds back and forth across the median third of the body through from fifteen to twenty convolutions, the duct increasing steadily in size, ending finally in a greatly dilated pouch which opens to the exterior by a large aperture on the dorsal surface in the median line posterior to the opening of penis and vagina.

The uterus is lined at its inception and throughout its course by a thin fibrillated layer, increasing in thickness from the posterior coils forward. This layer is covered with fine cilia, in the first five or six coils of the uterus. These cilia are connected with scattered nuclei beneath the cuticula, by means of delicate fibrils strongly suggesting those figured by Lönnberg (1891) for the cilia lining the excretory canals. Their direction is in general at right angles to the course of the uterus. These fibres lie in a nucleated meshwork of parenchymal fibres, which pass indistinguishably into the cuticular lining of the duct. Further forward, the nucleated circular muscle fibres disappear, and a typical subcuticular layer of cells appears coincidentally with the appearance of a typical cuticular musculature, suggesting very strongly a structural connection between subcuticular and cuticular musculature.

The *shell-glands* (*sh. gl.*, pl. 39, fig. 42) are an aggregation of large cells, with characteristic nuclei, lying close to the receptaculum seminis on its dorsal, ventral, and posterior surfaces. This relation to the receptaculum seminis is of course due to the fact that the earliest convolutions of the uterus lie on these surfaces of the receptaculum. The greatest mass of cells lies to the

right and left; the posterior median mass is very thin. The lateral masses extend dorsally and ventrally well into the main longitudinal muscle mass, and in general the dorsal mass is greater than the ventral. The efferent oviducts and yolk-ducts pass through this mass of gland cells, but no shell-material is seen except in the first coils of the uterus. The cells of the gland are large, swollen at the base, with slender "necks," leading into intracellular ducts (pl. 44, fig. 68). These ducts appear to open independently in the anterior wall. The cytoplasm of the gland cells is dense, granular, and stains very intensely. The cell wall is sharply defined. The nucleus is large, cloudy, with deeply staining border and faint nucleolus. The nucleus lies in the dilated base of the cell. The ducts have a sharply defined lumen, and are of considerable size.

The *receptaculum seminis*, originally described by Wagener (1852) as the testis, is a large chamber, convex posteriorly, slightly concave dorso-anteriorly, filled with a dense mass of semen (*rec. sem.*, pl. 39, fig. 42). It might be regarded as the dilated blind end of the vagina, which enters its dorsal surface near the anterior border. The receptaculum seminis measures about 1.5 mm. by 1 mm. by 1 mm. It is surrounded, as above noted, by the first coils of the uterus and their accompanying shell-glands; on its dorsal surface lie the yolk reservoirs, the receptaculum ovarum, and their efferent and afferent ducts. From the dorsal surface of the receptaculum is given off a short, thick-walled duct, the ductus seminalis, to the efferent oviduct.

The wall of the receptaculum seminis (pl. 42, fig. 59) is composed of a mass of finely felted fibres, elongated cells with large nuclei and granular, non-fibrillated cytoplasm. Outside this layer are found scattered cells of the shell-glands. This differs markedly from Lönnberg's description (1891, p. 41) of the histology of the wall of the receptaculum. "Das Receptaculum ist von einem dünnen Pflasterepithel ausgekleidet, aber es besitzt eine dicke fibröse Wand, die reich an eingeschalteten Kernen ist." The writer cannot distinguish cell walls in the lining of the receptaculum, but finds scattered nuclei, embedded in a mass of delicate interlacing fibres.

The receptaculum seminis contains, embedded in the mass of

spermatozoa, occasional deeply staining cells, large, and with very large nuclei. These were noted and figured by Spencer (1889, p. 146): he suggests that they "may be simply the spermblastophores from which the ripe sperm have separated, but there is no proof of this." The writer is convinced that they are ova, which have entered the receptaculum seminis through the duct which leads from this structure to the oviduct, the ductus seminalis. The finding of these cells at the entrance of this duct into the receptaculum and their resemblance to the ova, renders this certain.

The passage to the oviduct, the ductus seminalis, has a very thick muscular wall lined with cilia and an exceedingly small lumen, often completely obliterated in sections. For this reason, Spencer was unable to demonstrate it to his own satisfaction, though convinced that it must exist.

The *vagina* passes forward, in the early part of its course much convoluted and lying close to the receptaculum seminis. Further forward it lies in the parenchyma close to the dorsal wall of the uterus; it turns ventrally near the middle of its course and passes gradually to the ventral surface, where it finally opens, laterally and posteriorly to the penis, near the right margin of the body. The lumen of the vagina is lined with a layer similar to that described for the receptaculum seminis, not ciliated. It is not epithelial, as described by Lönnberg. Its wall is composed of a thin layer of longitudinal muscle fibres; it is embedded in parenchyma and lies within the main mass of longitudinal muscles, close to the wall of the uterus. As the vagina nears the anterior margin of the uterus its lumen increases in diameter. During its course past the convolutions of the vas deferens this increase continues, and its wall is also increased in thickness. The lining of the tube becomes much convoluted in its course toward the left margin, and increases suddenly in diameter in the latter half of its transverse course, opening finally by a large aperture with much-folded margins and heavy muscular wall. This region is plainly adapted to copulation.

The *testes* are arranged in two groups not connected and not symmetrical (pl. 39, fig. 42). The left testis extends from the posterior border of the anterior third of the body, forward to

the opening of the penis. The right testis is composed of two lobes, the right and larger of which extends from the posterior level of the left testis forward to the anterior extremity of the body. The left lobe, attached by a narrow bridge posterior to the base of the acetabulum, lies to the left of the acetabulum and in front of the vaginal opening. The testes lie within the longitudinal muscle mass, in a position identical with that occupied by the ovaries in the posterior portion of the body. They are considerably larger than the ovaries, as is shown in plate 39, figure 42, and are composed of loosely-aggregated follicles. Each follicle is covered with a fibrous nucleated layer, the "tunica propria" of Lönnberg, continuous with the walls of the tubules into which the follicle opens. These unite into two main vasa efferentia and empty into a large median vesicula seminalis situated immediately in front of the uterus, nearest the ventral surface. This structure is perhaps more accurately described as a vas deferens, more or less uniformly dilated by the masses of spermatozoa. It coils from left to right and from dorsal to ventral, in three large convolutions (pl. 41, fig. 46), dilating near its anterior extremity to form a bulb, and opening through a muscular papilla into a thick-walled tube, the cirrus-pouch or ejaculatory duct. The wall of this pouch is thick and well supplied with muscles. Its inner lining is greatly folded and covered with delicate spinules. This duct passes almost straight dorsad, turning a little to the left, opening on a rounded papilla on the dorsal surface, a little to the left of the median line and anterior to the mouth of the vagina on the ventral surface. The wall of the duct grows much thinner toward its distal end and its lumen increases somewhat. Heavy bundles of muscle fibres running at right angles to the course of the ejaculatory duct are attached to its wall throughout the whole of its course (*rad. musc. f.*, pl. 43, fig. 65). Outside these lies a large mass of gland-cells extending the whole length of the ejaculatory duct. They are very large granular cells, with definite cell-walls forming intracellular canals (*prost. gl.*, pl. 43, fig. 64). These empty into numerous delicate ducts opening on the surface of the ejaculatory duct and probably constitute a prostate gland. Outside this gland lie heavy longitudinal muscle bundles, a part of the body muscula-

ture. The cells of the gland are embedded in the innermost of these muscle-bundles. The lumen of the ejaculatory duct is lined with a thin cuticula, beneath which are found cuticular muscle fibres and subcuticular cells. Outside this layer is a thick mass of circular muscle fibres, and outside these a heavy longitudinal layer of fibres. To this coat are attached the radially arranged muscle fibres above described, inserting in general at the angle shown in figure 65, plate 43.

Spermatogenesis.—The follicles of the testes are lined by a syncytium in which are embedded rather small rounded nuclei of the spermatogonia. The middle of the follicle is filled with dividing cells and developing spermatozoa. No attempt has been made to work out the details of the process of spermatogenesis. It may be mentioned that in none of the preparations observed by the writer were there any indications of amitosis, but several mitotic figures were observed. The mature spermatozoon is a slender thread tapering at the posterior end, with a well-marked head, several times the diameter of the body and staining intensely (pl. 41, fig. 50).

The Ovary and Oögenesis.—Unfortunately the writer has seen no young specimens of *Gyrocotyle*. While there has been great variation in size, in all individuals the uterus has been full of developing embryos which mark the specimens as sexually mature. Lönnberg, the only investigator who has had the good fortune to work with the immature form, described the ovaries in the young individuals as follows:

“Das Ovarium hat bei jüngeren Individuen eine nicht gewöhnliche Gestalt, indem es viel mehr traubig gelappt als bei anderen Cestoden ist. Es besteht also in diesem Stadium aus kleinen rundlichen Follikeln, die durch weite Ausführungsgänge zu Trauben vereinigt werden, und diese Trauben erster Ordnung werden durch ihre Ausführungsgänge zu Trauben zweiter Ordnung verbunden. Alle Trauben vereinigen sich zu je einer Sammlung aufschmelzen aber allmählig die Trauben zu unregelmässigen Lappen zusammen und es scheint daher nicht treffend, wenn Spencer auf seiner schematischen Figur ein so distinkt traubenförmiges Ovarium bei einem Tiere mit von Eiern prall gefüllten Uterus zeichnet.”

Spencer (1889, p. 144) dealt with sexually mature forms, but found two stages of reproductive activity:

“In the first-mentioned the ova were evidently passing down into the uterus, in which they were but very slightly developed. The ovaries

consequently were full of fully formed ova, having the nature of distinct cells with clearly defined nuclei. In the second the uterus was full of much more highly developed embryos, and no ova, apparently, were passing into it. In this case the ovaries were evidently in the act of developing a fresh supply of ova. Each consisted of a mass of protoplasm containing nuclei, evidently dividing rapidly, whilst the outlines of the cells could only here and there be seen with anything approaching to clearness. Each little ovary has thus, when the ova are not fully formed, the structure of a polynuclear mass of protoplasm, which only subsequently becomes divided up into a number of distinct cells.¹

In all the preparations studied by the writer, the ovaries contained at the same time both fully formed and developing ova; the uterus contained young embryos in its most posterior coils, and older ones towards its anterior opening. It seems that in *G. fimbriata* the process of egg formation goes on uninterruptedly the year round, rather than in a rhythmical fashion, as indicated for *G. rugosa* by Spencer's observations. This may be correlated with the fact that apparently the period of intra-uterine life is longer in *G. rugosa* than in any other species, this being the only form in which the uterus contains hooked embryos.

Each follicle of the ovary is surrounded by a fibrous layer, called by Lönnberg the "tunica propria," continuous with the walls of the oviducts into which the ova are discharged. Plate 41, figure 52 represents a typical follicle with ova in early stages of development. There is a syncytium containing small, round nuclei with reticular chromatin and either a very small nucleolus or none whatever. The other half of the same follicle is cut up into cells with definite walls, denser cytoplasm, clear nuclei nearly double the size of those in the syncytium, with dense marginal chromatin reticulum and very large excentric nucleolus. Plate 41, figure 53 represents stages intermediate between these two, showing the growth of the nuclei and particularly the appearance of a large extra-nuclear body, staining

¹ Dr. M. Hungerbühler's "Studien an *Gyrocotyle* und Cestoden" (1910) was received too late for its results to be incorporated in the body of this paper. He makes the suggestion, based on the facts above quoted mentioned, that Spencer was dealing with two different species of *Gyrocotyle*, that is, with *G. urna* and *G. rugosa*. While this explains numerous discrepancies in Spencer's account, and while my own results show the presence of two species of *Gyrocotyle* in one species of *Chimaera*, yet the forms described by Spencer differ widely in several essentials from *G. urna*, and Hungerbühler's grounds for concluding that one of Spencer's forms was *G. urna* do not seem adequately to account for these differences.

by most methods as deeply as does the nucleus but easily distinguishable from it in strongly decolorized haematoxylin preparations, and also in borax carmine-Lyon's blue preparations. Plate 41, figure 54 shows the origin of this body as an extruded nucleolus, distinguishable even when within the nuclear membrane from the chromatin nucleolus proper. Probably only one such body, or "yolk-nucleolus," is formed during the development of the ovum. In fully formed ova this yolk-nucleolus has greatly decreased in staining intensity, appearing as a mere shadowy ring with a dark center (pl. 41, fig. 51).

The ripe ovum passes from the follicle into the oviduct where it takes on an irregular elongated form, strongly suggesting amoeboid movements. This form has also been noted by Lönnberg (1891, p. 40). These ova are the largest cells in the body, measuring about 26μ by 15μ . Their cytoplasm is very dense, full of shapeless masses of material. The nuclei are about 12μ in diameter, clear, with heavy deeply staining chromatin reticulum and large round nucleus, from 5μ to 6μ in diameter. The nucleolus is larger than any other nucleus in the body, except those of the ganglion cells of the first order and possibly the nuclei of yolk cells. The large, clear bright nucleus with its dense deep-staining nucleolus makes the ovum easily recognizable even under low magnification.

The processes of maturation, which have not been observed, probably occur after the ova reach the receptaculum ovarum. Division of oögonia in the follicles of the ovary appears to take place by true mitotic division. Equatorial plates and anaphases have been observed, but no attempt has been made to work out the phases of mitosis. There are no indications of amitosis, either here or in the follicles of the testes. It seems probable from the evidence in *Gyrocotyle*, that Child's (1907) amitotic figures are the result of confusing the "yolk-nucleolus" with the nucleus proper. Such figures as are shown in plate 41, figures 52, 53, 54, could easily be taken for unequal mitotic divisions of the nucleus, were it not for the differential staining.

The vitellaria are follicular, each follicle being surrounded by a fibrous tunica propria as in ovary and testes. The early stages of yolk-cells resemble those of the young ova. A single

follicle frequently contains a great variety of stages. Near one margin are found scattered nuclei in a syneytium; the rest of the follicle is filled with cells with well-defined walls and full of yolk-spheres (pl. 41, fig. 49). The cells are large, about 20μ , with round clear nuclei, dense marginal chromatin and a round central nucleolus. The cytoplasm is reduced to a thin marginal layer in which the nucleus is embedded. The body of the cell is packed with yolk-platelets, from $\frac{1}{2}\mu$ to 2μ in diameter, granular in composition, and staining rather faintly except with Lyon's blue and toluidin blue, with both of which the platelets stain very intensely. The whole cell breaks out of the follicle and enters the system of yolk-ducts, through which it makes its way to the yolk-reservoir and thence to the uterus. The yolk-plates have been observed by me only within a nucleated cell. The cell as a unit becomes one of the components of the compound egg formed in the uterus.

This statement is not in agreement with Lönnberg's description of conditions in *G. urna*. He says: "Die Dotterzellen zerfallen schliesslich, so dass nur die Körnchen durch die Gänge zu den Eizellen gelangen." That is, only the yolk-platelets, not the yolk-cells themselves, enter into the composition of the uterine egg. Aside from the fact that yolk-ducts, reservoir, and the beginning of the uterus are all full of typical nucleated yolk-cells, the most cursory examination of the early coils of the uterus shows that the eggs, even before the shell is completely formed, are multicellular. Lönnberg saw this, but interpreted it as evidence of a very early cleavage of the ovum. "Die Eifurchung tritt sehr frühzeitig ein, so dass man Eier findet, deren Schalen noch nicht fertig gebildet sind, aber wo das Embryo schon gebildet ist." But a careful examination of such an early uterine egg shows that it contains cells of two kinds, one having the characteristic size, staining reactions and nuclear structure of the ovarian ovum (*ov.*), and the others typical vitellarian cells (*yk. c.*, pl. 9, fig. 47). Cleavage of the ovum does not begin for some time after the shell is completely formed. Spencer's (1889, p. 145) observations concerning the yolk-gland and his figures of yolk-follicles are very puzzling. His statements are as follows:

"A difference of structure has been noted above in the case of the

ovaries of the two examples examined, containing embryos at different stages of development in the uterus, and a curious difference obtains also in the yolk-glands of the two forms. In the one containing highly developed embryos the yolk-glands, like the ovaries, are evidently providing a fresh supply of material in prospect of the next period of reproductive activity. Each consists of a mass of cells, the outlines of which are somewhat more clearly marked than in the case of ovaries, with large nuclei evidently undergoing division. The cells are remarkably similar to ova, but the relative size of the yolk masses and their definite superficial position renders them distinct from the ovaries. In the case of the form containing the ova passing down into the uterus, the yolk-glands are in a much more advanced stage. Each is filled with a mass composed partly of distinct yellow globular bodies, and partly of nucleated cells. So far as can be seen there are no definite "shell-glands" present; all the other structures connected with the reproductive organs could be distinctly made out by means of sections, and presumably shell-glands would have been able to be recognized if they were present as distinct and separate structures. In plate 13, figure 2, is represented a portion of the first part of the uterus, in which evidently the shells are being formed around the ova. In addition to nucleated cells, the uterus contains very numerous little drop-like yellow structures, which resemble exactly those which have been previously described as present in the yolk-glands. It appears as if these, as it were, "ran together," and formed a case enclosing certain of the nucleated cells, some of which are ova, and some probably cells from the yolk-glands which will serve as food for the developing ova. This appears to be the only construction which can be placed upon the appearances."

Failing to find any shell-glands in *G. rugosa*, Spencer's hypothesis (though not definitely stated to be such) seems to be that both shell-material and yolk-platelets are formed in the yolk-glands, as indicated in his plate 13. Nothing resembling this type of follicle, or indicating such a function of the vitellaria, has been seen in *G. fimbriata*. It is hard to believe that Spencer could have observed so delicate and obscure a structure as the network of yolk-ducts in the region of the receptaculum seminis, and overlooked the large and unmistakable masses of the shell-glands, had they been present in *G. rugosa*. Lönnberg (1891), who observed the shell-glands in *G. urna*, suggests that Spencer mistook the central mass of the shell-glands for the central part of the ovary. This suggestion is rendered less plausible by the fact that the main mass of the shell-glands lies, not in the median line, but laterad of the receptaculum seminis, and is simply marked off from the mass of the ovaries. A revision of Spencer's material seems to be the only way in which the discrepancy in observations can be explained.

V. FORMATION OF THE COMPOUND EGG AND CLEAVAGE
OF THE OVUM.

The formation of the compound egg of *Gyrocotyle* in the first coils of the uterus has been described above. The completed egg presents the appearance shown in plate 41, figure 47, taken from the fifth coil of the uterus. Cleavage begins very shortly; at the same time the walls of the yolk cells become less definite and their nuclei fainter. There is no indication of cleavage of the yolk-cells. The mass of cells resulting from cleavage of the ovum appears to be a syncytium (pl. 41, fig. 48); this mass increases in size with the diminution of the yolk cells. It is impossible to make out cell walls or to discover any orderly arrangement of the nuclei, in the preparations available. The eggs cannot be made sufficiently transparent for study *in toto*; and the shells are so resistant that no successful infiltration with paraffine was obtained. The best preparations, and the ones on which these statements and figures are based, were celloidin sections stained with Delafield's hematoxylin. The egg-shells show no opercula, and no trace of hooks on the embryo could be discerned. *G. rugosa* seems to be the only member of the genus which possesses hooked embryos in uterine eggs.

The eggs when extruded are surrounded by a gelatinous substance which forms a jelly on contact with sea-water. They are discharged with considerable force. The discharge has been observed repeatedly when the intestine of the host was first slit open, and also when the animal was changed from one solution to another. Eggs are always found in the intestinal contents of *Chimacra* infected with *Gyrocotyle*. The eggs when first discharged are white and glistening, resembling finely cut sand-grains. They are about .095 mm. by .065 mm. and ellipsoidal in shape. The size varies widely in eggs from the same individual, discharged at the same time, ranging from .075 mm. to .112 mm., in longest dimension.

The newly discharged eggs do not possess opercula (pl. 38, fig. 41). There is a faint differentiation occasionally seen at one pole of the egg, but nothing which could be definitely identified as an operculum has ever been found in fresh eggs. In speci-

mens which had begun to decay in the intestines, and in preparations made by Von Rath's method, a perfectly definite and clearly marked operculum was found (*operc.*, pl. 38, figs. 38, 39, 40). This does not appear to be comparable to the operculum figured by Haswell (see my plate 47, figure 81). Its margins are finely toothed, and the shell is somewhat thinner in the opercular cap than elsewhere.

VI. EXCRETORY SYSTEM.

The network of excretory canals, so richly developed in *Gyrocotyle*, is one of the first features to strike the eye in observation of the living animal. Wagener (1851) saw and described it, and noted particularly its wonderfully elaborate development. The excretory system consists of the following parts: (1) "flame-cells," (2) capillaries, (3) excretory canals distributed outside the inner longitudinal muscle layer, (4) excretory canals lying within and among the fibres of the inner longitudinal muscles.

The "flame-cells" (pl. 43, figs. 62, 63) are large, with swollen base in which lies an oval nucleus with rich, deeply-staining chromatin reticulum. The surrounding cytoplasm is granular, occasionally vacuolated, and stains as heavily as does that of the gland-cells. Running apparently from the apex of the nucleus is a fine thread, extending for some distance through the hollowed-out body of the cell. Each flame-cell thus forms an intracellular canal, which leads into a capillary. These flame-cells are found only in the outer layers of the body in what has been described as the "intermediate" region, within the subcuticular layers and outside the inner longitudinal muscle mass. Neither Spencer (1889) nor Wagener (1852) found any such structures; Lönnberg (1891) found them, but tells us nothing about them, except that they lie in the "Rinden-schicht."

The *capillaries* are the fine tubules into which the intracellular ducts of the flame-cells lead. They have very thin walls, and differ from the excretory canals in not having a cuticular lining or a muscle layer. They are found throughout the body wherever flame-cells appear.

The *excretory canals* lying outside the inner longitudinal muscle mass differ from those lying within this layer chiefly in

size. They are lined with a cuticula resembling that covering the body, and are surrounded by a well-developed band of circular muscle fibres (*circ. musc. l.*, pl. 11, fig. 60) resembling in size and shape the cuticular longitudinal fibres of the body. Outside of this circular muscle layer is a mass of parenchyma fibres passing in the same direction. Nuclei are scattered about irregularly in the neighborhood of this layer, but often at some little distance from it.

In the larger of these canals, a large tuft of cilia projects into the lumen, through a break in the cuticular lining, running the whole length of the canal. These ciliated canals receive the smaller non-ciliated ones. The non-ciliated canals are plainly to be seen in the living animal in the lateral frills, in close relation to the follicles of the vitellaria, emptying on the one side (lateral) into a small non-ciliated "sinus terminalis" (Wagner) and on the other side (medial) into a ciliated canal of about twice their own diameter (pl. 35, fig. 20). Still further mediad, near the base of the lateral folds, is a second ciliated canal, of the same size and appearance as the first. In it, however, the waves of motion traverse the cilia in the opposite direction from that taken in the more lateral canal. Thus, if in the outer one waves pass from anterior to posterior, in the inner one they run from posterior to anterior. The motion is almost incredibly swift and very regular.

The largest excretory canals lie within the central core of the body, among the inner longitudinal muscles, the ovaries and testes. Running the length of the body, on either side of the uterus, is a very large ciliated canal, the largest in the body. The structure of these canals is like that of the smaller peripheral canal described above, except that the lining is thicker, the muscular layer better developed and nuclei more numerous in the neighborhood of the wall of the canal. In no case has it been possible to recognize any connection between the cilia of the canals and the neighboring nuclei, such as was figured by Lönnberg (1891, Taf. 3, figs. 39, 40).

Around the anterior margin of the acetabulum there is a fairly well-defined ring-canal, receiving many small anastomosing longitudinal branches. Its diameter and relations shown

by sections do not indicate that it is connected with the central canal-system, but rather with the peripheral non-ciliated system of the lateral folds. The same is true for the dense network of non-ciliated canals found in the posterior rosette. This rosette region is riddled through and through with small canals, much like capillaries in size and structure of wall. No flame-cells appear in this region. A ring-canal appears in the "neck," at the level of the canal opening. Like the acetabular ring, this appears to be immediately connected with the peripherally situated canals, and through them with the deeper-lying larger vessels (*ant. ex. r.*, pl. 36, fig. 26.)

In several specimens a dilation of one of the large longitudinal canals has been found in the region of the vaginal opening, usually posterior to it. These dilations take the form of a thin-walled sphere, into which the large canal empties, containing droplets of a structureless yellow material. It is certain that this "bladder" is not a constantly occurring structure. No external openings have ever been found, except by Spencer (1889) on *G. rugosa*: "Wagener was unable to find any external opening of the excretory system, but, after long searching, I have been able to find two unmistakable openings on the ventral surface, one on either side of the body, slightly in front of the opening of the uterus to the external surface." Lömberg (1891) was unable to find these openings; the writer has never seen them. But it seems highly probable that these temporary "bladders" may burst through the wall of the body to form a temporary external opening, closing up after the collapse of the "bladder," due to the discharge of its contents.

VII. NERVOUS SYSTEM.

The nervous system of *Gyrocotyle* is of great interest with reference to the problem of orientation, both in the genus itself and in merozoic cestodes. It may be divided into central and peripheral parts, according to the muscle layers with which the nerve stems are related. The sense in which the phrase "central nervous system" is used is of course quite distinct from the meaning usually attached to it when applied elsewhere, as for example to vertebrates. Neither should this use of the term be

confused with that advocated by Cohn (1898) for merozoic cestodes. He believes that all of the longitudinal nerves, together with their transverse connections in scolex and proglottides, constitute the central nervous system. The branches from these to the various organs and to the surface of the animal he regards as the peripheral system. While all the evidence indicates that such a division would be justifiable in *Gyrocotyle*, it is not in this sense that the terms are here used, but purely with reference to position, not at all with reference to structure or function.

The *peripheral nervous system* consists of eight longitudinal stems, lying in the intermediate muscle layers, just outside the outer longitudinal set of fibres, and communicating with the central system by means of the anterior nerve ring around the margin of the acetabulum. There are no ganglion cells in these strands; they are very small and exceedingly difficult to trace. With borax carmin and Lyon's blue they stain a very clear light blue, and can be recognized with some ease in the neighborhood of the acetabulum, especially near their junction with the anterior ring. These strands have not been previously described. They innervate the intermediate muscle layers (outer transverse and outer longitudinal), wherever these occur in the body proper, in the inner layers of the acetabulum, and in the inner layers of the funnel.

In dealing with the central system it is important to remember and recognize the existence of these extra-central nerves, for it is only when the central system is clearly distinguished from the others that the relations of its parts become intelligible. It is perhaps because of their failure to take account of this division that the results of investigators of the nervous system of *Gyrocotyle* have shown so little agreement in details.

It is hardly necessary to say that the study of the nervous system by means of serial sections, already made difficult by the great contractility of the body, is rendered a much more serious problem by the necessity of dealing not with two stems, their branches and connectives, but with six or perhaps ten such stems. To determine whether a complete ring is present in any part of the body becomes a task of serious difficulty, and indeed one impossible without the assistance of the relations of the different

sets of nerves to the muscle layers, which can always be distinguished from one another.

The *central nervous system* lies within (mediad to) and among the inner longitudinal muscle-fibres, and within (mediad to) the large longitudinal excretory canals. It consists of the following parts:

1. Two lateral longitudinal stems.
2. An anterior bridge commissure and an anterior ring commissure, in the acetabular region.
3. A posterior bridge and two ring commissures, joined by eight longitudinal connectives.

The nervous system was first recognized by Wagener (1852), who saw only the anterior commissure. Monticelli (1889a) and Spencer (1889) recognized the posterior commissure. According to Spencer, this commissure is continuous around the canal, forming a complete ring surrounding the canal; the dorsal half of the commissure extending farther posterior than the ventral half. According to Monticelli this is not the case. He found that on the ventral surface the two parts did not unite, but merely ran alongside each other, then separating passed posteriorly, each ending independently in the margin of the "Trichter." Both these investigators agree in placing the anterior, heavy and indubitable part of the commissure on the same surface as the canal opening, *i.e.*, the ventral face (dorsal of Spencer and Monticelli). This puts the anterior (acetabular) commissure on the opposite surface from the posterior (sclex) commissure.

Lönberg (1891) described both commissures as lying on the ventral surface. He found the posterior commissure to be a bridge, not a complete ring, posterior to which the longitudinal stems are continuous to the margin of the funnel, where each breaks up into many branches, which probably form by their anastomoses a ring about the margin of the funnel opening. Thus his account differs from Monticelli's in (1) the presence of a marginal ring at the posterior extremity, and (2) the absence of any statement of the near approximation of the posterior nerve stems to each other posterior to the commissure. It differs from Spencer in the first point, and also in the absence of any indication of the completion of the posterior commissure to form

a ring surrounding the canal. Lönnberg also differs from Spencer and Monticelli in placing the posterior commissure "ventrally." The apparent contradiction in these results is due to incomplete rather than erroneous observation.

The longitudinal nerve stems or lateral connectives (*long. n. st.*, pl. 39, fig. 42) lying in the dorsal half of the central region of the body, run from the anterior to the posterior commissure. They are separated from each other by one-third of the width of the body in the anterior quarter of the body, but spread further apart at the level of the birth pore, lying near the lateral margins of the uterus. In the region of the ovaries they approach the median line again. Each stem gives off two sets of branches, one in the sagittal and the other in the horizontal plane. These branches are heaviest and most profuse in the regions of the ovaries and the testes.

The *acetabular nervous system* consists, as elsewhere in the body, of a central and peripheral portion. The peripheral system comprises eight longitudinal strands with many anastomosing branches. These strands innervate the peripheral muscle layers of the body, and the homologous muscle layers of the acetabulum. They come into relation with the central nervous system by means of the anterior ring in the margin of the acetabular opening (*acet.*, pl. 39, fig. 42.)

The *central system* includes an anterior bridge commissure, lying just in front of the posterior margin of the acetabulum on its dorsal surface; a pair of anterior lateral stems with branches; and an anterior nerve ring (pl. 39, fig. 42). The commissure forms a bridge between the two longitudinal nerve stems. There is a ganglionic enlargement of the lateral stem at a point where it is joined by the bridge commissure. The commissure is in the shape of an arch, enlarged at the ends and smaller in the middle of its course. Its mass with respect to the rest of the body varies widely, perhaps with the state of contraction of the animal; it is fairly constant with respect to the nervous system as a whole. No branches are given off from the commissure itself. The marginal ganglionic knots are about double the diameter of the lateral stem (*ant. br. comm.*, pl. 39, fig. 42). They are enlargements of the lateral stems, beginning at the point where the

anterior bridge commissure is given off and reaching their greatest size in that region. Anteriorly they pass into the anterior longitudinal stems, extending fully a third of the total distance from the commissure to the anterior ring. From each ganglion the following branches are given off (pl. 36, fig. 27).

1. An anterior lateral nerve stem, a prolongation of the anterior nerve stem in front of the anterior bridge commissure, runs forward along the dorso-lateral margins of the acetabulum. From these stems there are given off dorsal, ventral and lateral branches to the body musculature, and median branches to the outer coat of the acetabular muscles. Certain branches from the dorsal surface run forward, to the dorsal sensory ridges later described, and from the ventral surface of each stem near its anterior extremity a large nerve runs forward ventro-laterally to the sensory pits on the ventral surface. At the anterior extremity of the worm near the acetabular opening, each lateral nerve stem divides into two branches which pass, one ventrad, the other dorsad, at right angles to the longitudinal stem. These nerves break up in the median line to form the anterior nerve ring.

2. Four nerves are given off from the ventral surface of the knot, two of which are directed posteriorly and two anteriorly. The posteriorly directed pair of branches are distributed to the follicles of the testes (*test. n.*, pl. 36, fig. 27). The anteriorly directed pair pass around the posterior margin of the acetabulum on its ventral surface and send out branches on this surface.

3. Four nerves arise from the dorsal surface, running forward and laterally into the inner longitudinal muscles.

4. Two nerves arise from the lateral surface of the ganglion, one running forward and ventrally, the other towards the dorsal surface, into the central musculature of the body and the vitellaria.

5. Several nerves are given off from the anterior face of the ganglion and run forward along the surface of the acetabulum to innervate the outer meridional acetabular muscle coat (the homologue of the inner longitudinal coat of the body musculature).

The Anterior Ring Commissure.—The anterior end of the worm is pierced by a round opening into the cavity of the

acetabulum. The circular margin of this opening is rounded and thick, due to the presence of a heavy sphincter. Surrounding this opening, within the sphincter of the margin, is the anterior excretory ring and the anterior nerve ring. This is formed as described by dorsal and ventral terminal branches of the anterior lateral stems, united in the median line by a dorsal and ventral anastomosis. This ring is thus composed laterally of a single large nerve, but in the median line of many small anastomosing threads (pl. 39, fig. 42). In its lateral portions at the points of junction with the lateral nerve stem, there is a slight enlargement in which typical ganglion cells are present. From the ring are given off nerves ramifying in the margin of the acetabular opening, and in the outer layer of the acetabular muscle coat. The ring also receives the peripheral stems mentioned above.

The Central Nervous System of the Rosette and Canal.—The posterior rosette may be considered as composed of two parts,—a funnel and a canal. The wide-mouthed funnel with glandular, much folded walls is circular in cross-section, and roughly V-shaped in sagittal section, the point of the V being directed anteriorly. That is to say, the course of the funnel tube is almost straight forward through the center of the body (pl. 46, fig. 76). Its posterior margin is bordered by the frills which make up the posterior rosette. At the base of these frills there is a thickening of the walls of the funnel commonly referred to as the neck of the rosette, due to the formation of a sphincter by the inner transverse muscle. This funnel leads into the canal, a narrow, non-glandular region, passing a little anteriorly and almost directly ventrad to open on the ventral surface of the valve-like canal opening. The region where the canal joins the funnel, the apex of the V, will be called the *tope*, from the corresponding region of an ordinary funnel. The walls of the canal itself show no central innervation. There are apparent fine fibres of the intermediate and cuticular nerves but no branches of the central system. From the *tope* of the funnel posteriorly the walls of the passage are weakly innervated by a complicated set of commissures, stems, and branches, all belonging to the central system, consisting of the following parts:

1. A posterior bridge commissure connecting laterally situated ganglionic knots.

2. A proximal ring commissure directly connected with the posterior margin of the ganglionic knots.
3. A distal ring commissure, connected with the proximal ring by eight connectives.
4. Anastomoses between these connectives in the lateral walls of the funnel.
5. Eight branches running posteriorly from the distal ring commissure into the folds of the terminal rosette.

The main longitudinal stems lie as above noted in the dorsal half of the central region. At a point just posterior to the tope, close to the wall of the funnel, each stem enlarges to form a ganglionic knot (pl. 35, fig. 17). These knots are connected dorsally by a transverse bridge which is fairly large laterally, but narrows to the merest thread in the median region, not distinguishable with a magnification of less than 300 diameters. The ganglionic knots at the ends of this bridge commissure pass diagonally across the lateral walls of the cavity. This forms the "bow-commissure" of Spencer. Each ganglionic knot divides into two main branches, a dorsal and a ventral, which pass toward the median line to join similar branches from the opposite side, thus forming the proximal ring commissure, lying about half-way between the neck or sphincter region and the tope of the funnel. It was probably the ventral half of this ring which Spencer regarded as forming the "dorsal" region of his bow-commissure, embracing the funnel. Lönnberg's "ventral" commissure was probably the dorsal half of this same ring, plus the lateral ganglionic knots of the posterior commissure, the half-ring and knots being connected by one of the primary lateral connectives to be described later. The middle third of the dorsal posterior bridge commissure is so delicate that it is easily overlooked. However, the continuity and independence of both the dorsal commissure and the dorsal half of the ring can be easily demonstrated in serial sections with a magnification of about 300 diameters.

In the neck or sphincter region there is formed a second ring which completely encircles the posterior margin of the funnel at the base of the frills. This posterior ring is connected with the proximal ring by eight connectives (*lat. long. conn.*, pl. 35, fig.

17). Of these, the two lateral pairs are derived from the primary longitudinal stems, each divided into two and continued posteriorly from the ganglionic knots. The two lateral connectives of each side are interconnected by anastomosing branches, lateral and irregular, nearly parallel to the proximal ring, and frequently quite as heavy. The dorsal and ventral median pairs, lying in the median third of the funnel wall, extend only from the proximal ring to the distal ring. From the distal ring branches run out into the frills at the points where the longitudinal connectives enter the ring.

Distribution of Ganglion Cells.—No attempt has been made to deal with the histology of the nervous system, further than is necessary for understanding the significance of the structure of the ganglionic knots at the lateral margins of the anterior and posterior commissures. The nerve stems, both longitudinal and peripheral, are composed of exceedingly delicate fibrils, woven together in a dense meshwork (pl. 34, fig. 16). Around the stem is a covering of nucleated parenchyma fibres, or sheath cells. There are no nuclei within the meshwork. At intervals along the two main lateral stems, where branches are given off, there appear just inside these "sheath cells" a cluster of cells having homogeneous cytoplasm and oval, clear nuclei, with a few chromatin nucleoli (*gang. 1st.*, pl. 44, fig. 67). These correspond to the "first type" of ganglion cells described by Pintner (1880) and by Niemiec (1886). They occur only at the margins of the main lateral nerve stems and in the nerve rings: the anterior ring, the proximal and distal ring commissures. In the ganglion knots there occur very large cells, with coarsely granular, intensely staining cytoplasm, and a large, clear nucleus containing one large and several small chromatin nucleoli (pl. 44, fig. 66). With Lyon's blue these cells stain a dark violet blue quite distinct from the clear "Himmelblau" as Lönnberg calls it, of the fibrous tissue. These occur only in the ganglion knots of the anterior and posterior bridge commissures, not at all in the median sections of the commissures, in the rings, or lateral stems. They are not numerous, their total number not exceeding seventy or eighty. They correspond to the second type of cells described by Pintner and by Niemiec, commonly referred to as giant cells.

VIII. SENSE ORGANS.

The presence of sensory end-organs in cestodes has been several times suggested, but never established to the satisfaction of investigators in general. Lang (1891) says "The cestodes no longer possess any specific sensory organs." Braun (1894) in Bronn's *Thierreich* (p. 1300) quotes Blumberg (1877) as observing nerve endings in the limiting membrane or cuticle of the *Taenia* of horses. These endings are in the form of delicate threads terminating in a swollen knob. Braun thinks that, considering Zernecké's observations, it seems probable that Blumberg saw actual nervous end-organs. Linton (1891) briefly describes an organ of hearing in *Otobothrium crenacolle*, as a small structure covered with hairs, situated on the bothridia. Beyond these, and Schiefferdecker's (1874) interpretation of flame-cells as nerve endings, there are no references to sense-organs in the literature of cestodes, in so far as that is known to the writer.

In *Gyrocotyle* the whole acetabulum functions much as does the proboscis of the rhabdocelean *Proboscidea*, as a highly efficient organ of exploration, or one might say of touch. While the whole surface of the acetabulum is richly innervated, there are on the margin of the opening of the acetabulum two ridges with a peculiar and significantly rich nerve supply, and two shallow pits in which lie flat plates of nervous tissue, end-organs of a pair of heavy branches from the anterior lateral stem above referred to.

1. *The Sensory Ridges or Papillae*.—These lie one on each side of the latero-dorsal margin of the acetabular opening. A nerve from the anterior lateral stem spreads out within each "papilla," its branches running to the base of the very thin limiting membrane.

2. *The Sensory Pits (sens. pits, pl. 36, figs. 23, 25)* lie farther laterad than the papillae, and on the opposite or ventral surface of the acetabular margin. They consist of a definite depression, covered with a differentiated membrane, immediately beneath which lies a plate of nervous tissue, formed by a very heavy branch from the anterior longitudinal nerve. This does not break up but ends abruptly as a plate of nervous tissue

immediately beneath the limiting membrane of the pit. These pits stain an intense blue when the living animal is treated with methylen blue. They take up the stain quickly and hold it for several hours after removal from the staining medium. The function of these pits is totally unknown, but the presence of central nervous tissue immediately beneath their surface indicates their possession of some sensory function.

E. GENERAL DISCUSSION.

This investigation was undertaken and carried out in the hope of obtaining evidence which would definitely settle the question of antero-posterior orientation. This evidence was sought along three lines: (1) morphological relationships of organs, in themselves and compared with other platyhelminths; (2) behavior of the living animal; (3) embryological history. The writer has unfortunately failed to find any extra-uterine embryological material, and has no evidence from this source to offer. The fact that *Chimaera colliei* can not be kept in aquaria, even large ones, with any measure of success (Dean, 1906, p. 16) makes the life-history a hard problem to attack. I am convinced that we have thus far no hint whatever as to the intermediate host of *Gyrocotyle*. The occurrence of decaying, sexually mature forms in *Mactra edulis* has, it seems, no bearing on this question. The youngest forms reported, the only immature ones in fact, are the young individuals found by Lönnberg in the spiral valve of *C. monstrosa*. This fact indicates that the worm enters the host in a sexually immature condition. The fact that no hatched embryos have been found in the intestinal contents of *Chimaera* indicates that *Gyrocotyle*, like other cestodes, has at least two hosts. Further than this we know nothing of its life-history.²

Conclusive morphological and functional evidence bearing on the question of orientation has been found in abundance. In the course of this work, evidence bearing on certain other questions

² The discovery by Hungerbühler (1910) of cysticercoids in the parenchyma of *Gyrocotyle rugosa* is a recent addition to our knowledge of the embryology of the genus. The embryo resembles the ten-hooked embryo already figured by Spencer as an extra-uterine embryo. Its position (near the uterine pore) suggests that the wall of the uterus may have given way in that region in the preparation of the specimen.

of interest to students of the phylum has been found; this will be briefly discussed before proceeding to consider the main problems of orientation.

I. CUTICULA.

The question of ectodermal origin of the "cuticula" or limiting membrane of the body, and the significance of the "subcuticular cells" in the trematodes and cestodes has been recently reviewed by Professor Pratt (1909). Blochmann's theory, regarding the subcuticular cells as a sunken epithelial layer, and the limiting membrane as a true cuticula, such as is found in arthropods and annelids, Pratt considers completely discredited by various pieces of embryological and morphological evidence. He considers the "cuticula" to be nothing but a closely matted layer of parenchyma fibres, from which the nuclei have disappeared. The observations made on *Gyrocotyle* seem to bear out this view of the limiting membrane. Of particular interest are the conditions of the vagina, receptaculum seminis and uterus. Here the lining of these ducts is in direct continuity with the cuticula at their openings; there is a gradual transition from this cuticular lining to one of comparatively loose-matted fibres and indefinite boundaries, containing unmistakable parenchyma nuclei and passing on its inner surface indistinguishably into a typical parenchymatous net in which lie muscle fibres. This same transition can be seen on the inner surface of the folds of the posterior rosette. Furthermore, nowhere in *Gyrocotyle* have I found a definite layer of epithelial cells. Such tissue, described by Lönnberg for the ducts of the reproductive system, resolves itself in favorable preparations and under high magnification into the dense parenchymatous layer, fibrillated and without cell-walls, above described.

One statement made by Pratt in support of this view of the cuticula as not associated with the subcuticular cells is not borne out by conditions in *Gyrocotyle*. He says: "If now the cuticula is the product of the underlying subcuticular cells, we should expect to find some special development of them beneath the hooks and spines, especially where these are very large, just as in the integument of insects a cuticular hair or scale is invariably

situated over the enlarged hypodermal cell which produces it. Nothing of the sort exists in trematodes and cestodes. The subcuticular cells beneath the hooks and spines do not differ in size, number or arrangement, from the adjacent cells and in the monogenetic trematodes, which are often provided with gigantic hooks, no subcuticular cells at all are present."

In *Gyrocotyle* the subcuticular layer of cells is much increased in thickness in the neighborhood of a spine and is closely related to it.

A question of far greater difficulty is that of the function of the subcuticular cells. If not related to the formation of the cuticula, what is their function? Pratt makes two suggestions; first that they are secretory in function, forming an antibody for the protection of the worm from the chemical action of the medium in which it lives. This is supported by the fact that these cells are altogether lacking in monogenetic trematodes. A second suggestion (see Looss, 1894), is that these cells constitute an undifferentiated embryonic layer, from which new cells of various tissues are formed during the lifetime of the animal. The only evidence in support of this theory is the statement that in certain individuals known to be of advanced age, the subcuticular layer was greatly reduced.

The glandular theory finds no definite support in the conditions in *Gyrocotyle*. The unmistakable gland cells here present are found as above noted in the central core of the body, not in relation to the peripheral layer. The statement made by previous investigators that the subcuticular layer gives rise on the inner surface of the rosette folds to gland cells has not been verified in the writer's preparations. However, this does not militate against the possible glandular nature of these cells. The intense staining reaction of the cytoplasm of at least some of these cells recalls the appearance presented elsewhere by unmistakable gland cells.

Looss's suggestion seems hardly susceptible of proof or disproof. It is difficult to believe that the layer of cells so closely related in position to the cuticula, varying in thickness with its thickness and increasing in the region of special cuticular structures such as spines, should be totally unrelated to the body-

covering. The conditions of *Gyrocotyle* indicate very clearly that the subcuticular layer is related to the cuticular musculature, and that some at least of its cells are to be considered the myoblasts of the cuticular muscles. There is much in the literature of the subject in harmony with this suggestion; Blochmann (1896) shows in his diagrammatic cross-section of *Ligula* myoblasts lying near the subcuticular layer. He was able to distinguish these cells from the rest of the subcuticular layer. This the writer is unable to do in *Gyrocotyle*. The fact that the cuticular musculature always increases with the thickness of the cuticula, disappearing as the cuticula thins out and passing into the fibrous nucleated layer above described, lends support to the suggestion. In the lining of the receptaculum seminis and the posterior end of the vagina, no subcuticular cells can be seen. These ducts are surrounded by simple nucleated muscle fibres. In the early coils of the uterus, where this same nucleated fibrous lining is found but where cilia are also present, the cilia pass through the fibrous layer and are in connection with scattered nuclei lying just beneath the fibrous lining. Further along the course of the uterus, where a definite non-nucleated fibrous lining has appeared, beneath which lies a cuticular musculature, the subcuticular layer appears, just as it does beneath the cuticular musculature of the body-covering. All the facts available indicate that at least a large part of the subcuticular cells are related, not to the cuticula, but to the cuticular musculature as myoblasts. The subcuticular cells in the neighborhood of the spines are probably related to the protractor musculature of these structures.

II. ORIENTATION.

The question of antero-posterior orientation of cestodes is one of peculiar difficulty. Their endoparasitic and attached mode of life makes it impossible, in general, to settle the matter by the test ordinarily applied, that of the direction of locomotion. The usual custom, reflecting the influence of Leuckart, has been to regard the scolex end as anterior, the free end as posterior. Many early workers, among them Perrier, Grassi, and Blanchard, reversed this orientation, looking on the scolex as

the posterior end. In the Cestodaria, conflicting views as to the orientation of the various genera have long existed, and in the genus *Gyrocotyle* the question never has been conclusively settled. It is of peculiar importance for the problem of cestode orientation in general that these relations should be well established in *Gyrocotyle*, for there is no functional antero-posterior orientation in the adult merozoic cestode and the problem there is one of comparative morphology and phylogenetic development. Since *Gyrocotyle* is in every respect a primitive, relatively simple form, parasitic in one of the most ancient of vertebrates, it seems reasonable to assume that this cestode may give some hint as to the extremity at which the ancestral cestode most probably developed its organ of firm attachment. Observations of the living animal have shown that in *Gyrocotyle* there is still a definite functional antero-posterior orientation, due to the fact that it is not a permanently attached form but is still capable of locomotion.

Diesing (1855) regarded the acetabular end of *Gyrocotyle* as anterior, but his grounds for this decision are not clear. Working with a few poorly preserved specimens, he had little on which to base his conclusions. Wagener (1852), who did careful work on the living animal and on sections, had proposed the same orientation on the basis of the active exploring movements of the acetabulum in the living animal, and of the location of a bridge commissure of the central nervous system at the base of the acetabulum. This orientation was followed by succeeding investigators up to Spencer (1889), who reversed it on the strength of the discovery of a similar and much heavier bow-commissure at the rosette extremity. He did not observe living material. Lönnberg, working on a large quantity of living and preserved material, followed Spencer in regarding the rosette as anterior, basing this decision on the behavior of the living animal (the stretching out of the rosette and funnel into a long canal which performed exploring movements and is directed forward in locomotion, according to his observation), on the great development of its nervous system in the funnel region, and the greater abundance of ganglionic cells in that as compared with the acetabular commissure, on the direction of the spinules,

which point toward the acetabulum; and also on the fact that the worm is always attached to the rosette extremity, since "cestodes always attach by the head end." Haswell (1902) rejects Lönnberg's and Spencer's view on orientation on the basis of homologies in position between the reproductive organs of *Gyrocotyle* and of merozoic cestodes, to which in his opinion it is very closely related. "The end which bears the sucker is seen as the result of such a comparison, to correspond to the scolex end in the segmented cestode." This homology I regard as unjustifiable, as will be pointed out later. Benham (1891), comparing the reproductive organs of *Gyrocotyle* with those of *Amphilina* and the heterocotylean trematodes, concludes that the acetabulum of *Gyrocotyle* corresponds to the anterior sucker of the trematodes, while the rosette organ and its peculiar proboscis possibly represents the posterior caudal disc of the latter class.

An examination of the literature of the genus thus shows that the orientation of *Gyrocotyle* has been made on the following grounds:

1. Behavior of living animal.
2. Cephalization of the nervous system.
3. Homologies of the reproductive organs with similar structure in the merozoic cestodes and in the trematodes.
4. Direction of spines.

Conclusions based on a consistent and constant functional orientation of the living animal in locomotion and general movements are unquestionably well grounded. Conclusions resting on the cephalization of the nervous system assume that the nervous system will be centralized and most richly developed in the head region. This is true for worms in general and for all platyhelminths which retain in any marked degree the power of moving from place to place. In the trematodes there takes place, however, a remarkable development of ring-commissures in connection with the development of powerful organs of attachment. This is especially noticeable in the large posterior terminal sucker of the heterocotylean trematode (pl. 47, fig. 79). It seems very probable that in a permanently attached form, like the cestode, in which the most powerful and highly specialized musculature of the body is centered in the organ of attachment,

there will be found in that region the greatest and most highly developed mass of the nervous system, quite independent of whether the attached end is the homologue of the ancestral anterior or cephalic extremity or not. Therefore, I am inclined to question conclusions as to orientation based on "cephalization" of the nervous system, unless confirmed by other unquestioned evidence.

The third basis on which the question has been decided, the homologizing of the reproductive organs and openings with those of trematodes or merozoic cestodes, can obviously only be applied in the direction of trematodes as long as the orientation of merozoic cestodes themselves is in question. Furthermore, antero-posterior relations among these structures are fixed and constant for trematodes; while among cestodes the most astonishing variations present themselves.

The direction of the spines is not at all a decisive piece of evidence inasmuch as spines may be quite as useful to the animal if directed anteriorly and serving as a means of attachment, as if directed posteriorly and serving as aids to locomotion.

Wagener's orientation of *Gyrocotyle*, regarding the acetabulum as anterior, the rosette as posterior, is justified in my opinion on the following grounds:

1. This is the functional orientation of the living worm. The rosette end is relatively quiescent while the acetabular end is exceedingly active in exploring movements, is directed anteriorly in well-defined progressive locomotion, and leads in all righting-up movements. The rosette end never leads in locomotion except when shoved backward by the doubling under of the active acetabular end, and performs no movements other than a slight rolling from side to side. This mode of behavior agrees with that described by Wagener (1852) in his original account of *Gyrocotyle urna*; but is totally at variance with Lönnerberg's (1891) observations on the same form. This discrepancy is discussed above.

2. The position of the reproductive openings in *Gyrocotyle* as compared with that in the heterocotylean trematodes homologizes the rosette with the posterior sucker. The birth-pore of *Gyrocotyle* is probably, according to Goto's (1891) view of the

uterus in cestodes, the homologue of the female copulatory duct in the Heterocotylea; and the vagina is the homologue of the heterocotylean uterus. This gives exactly similar anterior and posterior relations to the openings of the ducts, the penis-openings being very slightly anterior to the vaginal opening, and the birth-pore lying most posteriorly and some distance to one side of the other two.

3. Further morphological evidence in support of this orientation may be adduced as follows: In the first place there are two pairs of abundantly innervated antero-lateral sensory areas, comparable in structure and location to similar areas in planarians and certain heterocotylean trematodes. In the second place the structure of the central nervous system, when compared with that of the heterocotylean trematodes, affords morphological support to this orientation. The anterior commissure, giving off sensory branches, the main and secondary longitudinal nerve strands, the eight posterior branches and a posterior ring commissure are all common and similarly placed in *Gyrocotyle* and the heterocotylean, as for example in *Tristomum molae*, whose nervous system was described by Lang (1882), (pl. 47, fig. 79). There is added in *Gyrocotyle* the delicate median portion of the bridge commissure and the second ring commissure, which may well have arisen in *Gyrocotyle* in correlation with the increased mass and complexity of the musculature of the posterior organ of attachment, the rosette. Thus a comparison of the nervous system and the position and innervation of the organ of attachment of *Gyrocotyle* with the heterocotylean compels us to homologize the rosette with the posterior sucker of the trematode.

The development of two bridge commissures at the two extremities of the body, approximately equal in abundance of ganglion cells but the anterior supplied with a well-developed median part which is very faint in the posterior one, indicates the manner in which the evolution of the nervous system of the merozoic cestode has taken place. This is, briefly, by the degeneration of the anterior commissure associated with the reduction in the locomotor and sensory functions of the animal, and the great development of the posterior commissure and its

stems and rings, associated with the development of the powerful musculature of the organ of attachment, the scolex.

That this is in harmony with the course of development elsewhere in the phylum is shown by consideration of the probable construction of the nervous system of the primitive turbellarian-like ancestor and the changes it has undergone. Throughout the phylum there is remarkable uniformity in the ground-plan of the nervous system. The primitive structure in the free-living Turbellaria is a sub-dermal plexus of fibres and ganglion cells with a marked concentration of these at the anterior end, and an increase in their number and size on the ventral or creeping surface. This differentiates in two directions; first in the segregation from the plexus of from six to eight longitudinal strands, with irregular transverse connecting fibres; and second, in the increase in size of the main bridge-commissure or brain, and in the development of secondary commissures in the region of the brain and in the neighborhood of specially developed musculature, notably in the pharynx and in organs of attachment. This is to be seen in the remarkable development of the posterior commissure in the heterocotylean in connection with the development of the posterior sucker as the principal organ of attachment. Further, two of the longitudinal nerve-strands, the ventral, become more highly developed than the rest. In the trematodes there are two longitudinal strands, connected near the anterior extremity by a bridge-commissure rich in ganglion cells from the region of which arises a pair of sensory nerves. There are in addition numerous peripheral longitudinal strands and an indefinite number of cross-nerves, anastomosing among themselves to form irregular ring-commissures about the body. In the posterior region, in close relation to the large sucker, is developed a complicated system of commissures and rings. From this type the nervous system of *Gyrocotyle* has been derived. The longitudinal strands are the same in both; there are however two bridge-commissures in *Gyrocotyle*. But the sensory function of the acetabulum and the forward direction of that extremity in locomotion, together with the well-developed nature of that commissure throughout as compared

with the delicate median thread of the rosette bridge-commissure, all point to its unmistakable homology with the anterior commissure of trematodes, and so with the typical "brain" of the Turbellaria.

The posterior commissure with its accompaniments of complicated rings and connectives has plainly been developed in connection with the musculature of the funnel-shaped rosette-scolex. This complex development of nervous structure in connection with a highly developed musculature is strikingly shown throughout the phylum. The ventral nerve stems, in connection with the ventral creeping muscles, become heavier, more profusely branched, than their homologues near the dorsal surface. The great complexity of the nervous system connected with the posterior sucker of the heterocotylean has already been referred to. The development of a posterior commissure, in itself rather weak, but surrounded by a complex system of rings and connectives such as is found in the rosette of *Gyrocotyle*, is exactly what would be expected in connection with the development of a complicated and powerful organ of attachment.

The comparison of the nervous system of *Gyrocotyle* with that of the merozoic cestodes shows two main longitudinal stems in both. These are more or less sharply differentiated but always sufficiently clearly marked to be distinguished from the weaker longitudinal stems, of which there are four or eight, corresponding to the eight peripheral nerves of *Gyrocotyle*. Near the free margin of the proglottid, which must be regarded as anterior, these longitudinal stems are connected by a transverse commissure, in close connection with the transverse canal of the excretory system. In the scolex there is a heavy ganglionic bridge-commissure, joining the longitudinal stems, lying midway between the dorsal and ventral surfaces of the body. Peripheral to this and in contact with it only at the points where the longitudinal stems enter the commissures, is a more or less complete ring-commissure. This ring reaches its most perfect development in the Taeniadae, but is present in an incomplete form in *Ligula*, in the Tetrarhynchidae, and in the Tetraphyllidea. Distal to this commissure and ring is found a more or less clearly developed ring joined to the former by numerous connectives,

usually six or eight in number. This ring appears in a rudimentary form in the Tetracystellidae and in the Tetracystellidae; it is well established and clearly marked in the Taeniidae and the Dibothriidiata.

It is at once evident that the nervous system of the rosette in *Gyrocotyle* is much more easily homologized with the nervous system of the merozoic cestode scolex than is the nervous system of the acetabular region. There are two serious objections to attempting to derive the nervous system of the cestode scolex from the acetabular bridge-commissure and its anterior rings. In the first place, the rosette and funnel constitute an efficient organ of attachment, so strikingly like the scolices of many Tetracystellidae in mode of adhesion and probable developmental history—being formed by partial fusion of the walls of a trough, and later differentiation of the ends of the tube thus formed—that it seems irrational to suppose that two structures of such fundamental similarity could have been developed independently in two groups of organisms as closely allied as are the merozoic and the monozoic cestodes. The acetabulum, on the contrary, never functions as a sucker or organ of attachment; there seems to be no possible relationship between this structure and any of the familiar types of cestode scolex. There is every reason, on the basis of function, derivation and structure for regarding the rosette as a scolex of the phyllidian type. In the second place, there is no “starting-point” for the formation of a ring about the acetabular commissure, no matrix out of which to differentiate the complex rings and connectives of the nervous system of the scolex. Such a matrix is, however, afforded by the numerous anastomosing branches and the two irregular rings and their connectives, seen in the rosette extremity.

These facts, with other considerations previously given, justify the homologizing of the scolex of the merozoic cestode with the rosette of *Gyrocotyle*, a posteriorly situated organ of attachment. This conclusion implies a functional reversal of the nervous system of the ancestral flatworm in the course of its development into a merozoic cestode. The greatest mass of nervous tissue, cephalized in the primitive flatworm, comes to lie in the posterior region of attachment of the cestode. The anterior

commissure disappears and the ring grows weak with the assumption of the sessile habit and the disappearance of sense-organs; while the posterior commissure develops with the increase in efficiency and complexity of the organ of attachment.

The orientation of cestodes here suggested has been advanced by several investigators, on more or less substantial grounds, from Perrier to the present day. This contention has been based for the most part on embryological evidence, especially with reference to the hexacanth onchosphaeres so characteristic of cestodes. The well-established fact that the embryonic hooks are at the extremity of the cysticercus opposite to the one on which the organ of attachment is developed, and the further fact that the hook-bearing part of the onchosphaere is directed forwards in the movement of the embryo, affords good ground for seriously questioning, if not altogether denying, the generally accepted identification of the scolex as "head." Barrois (1889) maintains that the anterior part of the scolex is that extremity which bears the embryonic hooks; that this part of the scolex gives rise to the first proglottis, which is therefore to be regarded as the "Kopftheil" of the primitive animal. Furthermore, the establishment of a zone of growth in the "neck" of the strobila suggests very strongly the penultimate "zone of growth" in annelids, with which the "neck" of the cestode is homologized if the scolex is recognized as posterior. A full presentation of the evidence in favor of this orientation, derived from embryological and comparative anatomical considerations such as the above, was given by Cohn (1907). He remarks that the present orientation of cestodes has been regarded as self-evident, incapable of proof; and proceeds to show that, aside from the habitus of the worm, there is no evidence in favor of this view. In his own words: "Meine These ist, dass dem Geschlechtstiere der Cestoden ein Kopf überhaupt fehlt, und sein Hinterende zu einem Haftorgane—dem Scolex—umgebildet ist." He regards the hook-bearing tail-like appendage of the cysticercoids as the homologue of the ancestral anterior extremity of the worm; this is discarded, leaving the posterior organ of attachment and the intermediate growing region of the body to constitute the adult cestode. "Wir haben in den Proliferationsfähigen Scolices also

Tiere, die ohne ein wahres Vorderende, d. h. einen Kopf zu besitzen, mit dem äussersten Hinterende sich an der Darmwand fixieren und mit ihren relativ vordersten Körperende frei in den Darm hineinhängen." He then proceeds to show that, first, the presence of a differentiated intermediate portion between the anterior and posterior segments of the body, secondly, the detachment of the posterior segment and its transformation into the sexually mature animal, and lastly, the location of the growing-zone in the penultimate region of the body, are conditions whose analogues can be readily found in other worms and also in echinoderms, bryozoans, etc. On the last and probably most important point, the location of the growth-zone, he sums up the evidence very briefly as follows:

"Ob wir also die normalen Wachstumserscheinungen, ob wir Regeneration oder die der autotomischen Teilung vorausgehenden Prozesse der Segmentvermehrung betrachten; überall finden wir dass sich die Wachstumzone beiden genannten Tieren an äussersten Hinterende des Körpers befindet. Bei der von mir vorgeschlagenen Orientierungen der Cestoden schaffen wir also in bezug auf die Wachstumsverhältnisse keinen Ausnahmefall sondern erhalten im Gegenteil erst so die Möglichkeit, das Wachstum der Cestoden durch Proliferation am Collum mit demjenigen anderer Vermes konform aufzufassen."

These considerations, arising from facts of comparative embryology and morphology of the invertebrates, taken together with those arising from a study of the morphology of the primitive genus *Gyrocotyle*, afford a warrant for serious question of the validity of the generally accepted orientation of cestodes. Furthermore, they constitute a more or less successful effort to take this question out of the realm of "self-evident" hypotheses incapable of either proof or disproof where, as Cohn pointed out, it has too long existed. Further embryological research, especially on such forms as *Amphilina* and *Gyrocotyle*, is greatly to be desired; from this field the final word on the question must be obtained. All the facts now at hand, however, seem to show that this decision will be in direct opposition to the generally accepted belief, and will place the organ of attachment in cestodes at the posterior extremity of the strobila.

F. SUMMARY.

1. The genus *Gyrocotyle* is composed of the following species: *G. rugosa*, *G. urna*, *G. nigrosetosa*, *G. fimbriata*. These are distinguished on the basis of the following specific characteristics:

- (1) Character of folds of terminal rosette.
- (2) The ratio between the distance from the opening of the uterus to the tip of the acetabulum, and the distance from the opening of the uterus to the level of the opening of the penis.
- (3) Character of lateral frills.
- (4) Presence and distribution of spines.
- (5) Size of tail-rosette.
- (6) Presence of hooked embryo in uterine eggs.
- (7) Presence of an eversible cirrus, adapted to self-impregnation.
- (8) Spinules lining ejaculatory duct.
- (9) Opereculated uterine eggs.

2. The normal habitat of the sexually mature individual is in the spiral valve of the intestine of some species of the family Chimaeridae. Reported occurrences of *G. rugosa* in bivalve molluscs are probably accidental. Nothing is known of intermediate host or life-cycle of the parasite.

3. The functional orientation of *Gyrocotyle fimbriata* directs the acetabulum anteriorly, the rosette posteriorly. This is in agreement with Wagener's observations on the living *G. urna*, but in exact opposition to Lönnberg's observations on the same form. The worm is capable of definitely directed locomotion and is very active under favorable conditions. The exploring function of the acetabulum is strongly in evidence. The posterior rosette functions strictly as an organ of attachment. The acetabulum never functions as an organ of attachment.

4. This functional orientation is borne out by evidence from the structure of the central nervous system and by the presence on the margin of invagination of the acetabulum of a pair each of sensory pits and sensory papillae, abundantly innervated by heavy branches from the central nervous system.

5. The acetabular portion of the nervous system is developed in connection with the acetabular sense organs and with the power of locomotion in a definite direction. It corresponds to the "brain" of Turbellaria and to the anterior ganglionic commissure in Trematoda.

6. The rosette portion of the nervous system is developed in connection with the development of a powerful posterior organ of attachment, and is comparable to the posterior ring-commissure in the posterior sucker of a heterocotylean trematode.

7. The rosette of *Gyrocotyle* is in structure and function a true scolex, and corresponds to that organ in merozoic cestodes. This correspondence is strikingly shown in a comparison of the nervous system of the rosette of *Gyrocotyle* and that of the scolex of the merozoic cestodes.

8. On the basis of this evidence from comparative morphology and of other evidence previously adduced from the embryology of merozoic cestodes, it is proposed to regard the cestode scolex as a posteriorly situated organ of attachment, the "neck" or growing region as the antepenult region corresponding to the antepenult segment in annelids, and the proglottis as the intermediate region of the body. The anterior extremity has completely disappeared, according to this view.

9. The limiting-membrane in *Gyrocotyle* consists of a surface layer, composed of delicate fibres in a homogeneous matrix, and immediately beneath this a layer of transverse and a layer of longitudinal muscle fibres, non-nucleated. These are connected by fine processes with a layer of large cells lying in the parenchyma of the body, the subcuticular cells. Some at least of these cells are to be regarded as myoblasts of the cuticular musculature. There is no ground for regarding them as sunken epidermal cells. There is no trace in any of the tissues of the body of an epithelial layer of cells. The lining of the genital ducts is a meshwork of fibres in a homogeneous matrix, with nuclei scattered through it. This passes by gradual transition into the non-nucleated condition described for the limiting membrane of the body.

10. The muscle fibres of *Gyrocotyle* are all nucleated except those of the cuticular musculature. The latter are attached by

delicate processes to deeper-lying myoblasts (in the subcuticular layer).

11. The processes of cell-division in the maturation of the ovum are mitotic. A large "nucleolus" is formed within the nucleus and extruded into the cytoplasm. This process can easily be mistaken for an amitotic figure.

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Transmitted April 25, 1910.

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DESCRIPTION OF PLATES.

All figures are drawn with a Zeiss camera lucida, unless otherwise stated.

PLATE 33.

Figs. 1-4. Changes in form of living *Gyrocotyle*, as seen by Lönnerberg (1891, Taf. III, figs. 34, 35, 36, 37). Fig. 1, the *Ligula*-like form; fig. 2, rosette extended into long tube; figs. 3 and 4, form ordinarily assumed by animal.

Figs. 5 and 6, Diesing's figures of *Gyrocotyle rugosa*. (Diesing 1855, Taf. 1, figs. 17, 20.)

Figs. 7, 8, 9. Sketches of the acetabulum of a living specimen. Figs. 7, 9, extended; fig. 8, contracted.

acet.—acetabulum.

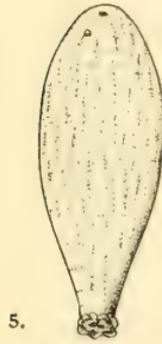
p. op.—penis opening.



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2.



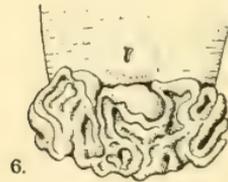
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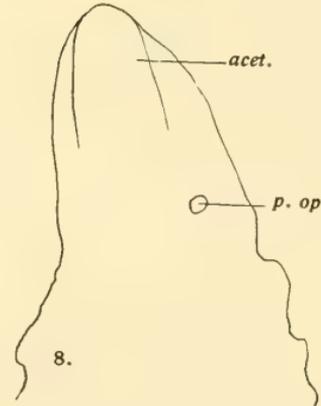
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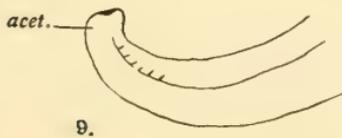
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PLATE 34.

Fig. 10. *Gyrocotyle fimbriata*, ventral. Flattened, stained in borax-carminé, cleared in cedar-oil. Showing arrangement of spines at posterior extremity. Spines at anterior extremity not shown. $\times 4$.

Fig. 11. *G. urna*, dorsal. Stained flattened specimen. Showing size and character of folds of posterior rosette, and collar of spines about the neck of the rosette. $\times 4$.

Fig. 12. *G. fimbriata*, dorsal. Stained flattened specimen. $\times 4$.

Fig. 13. *G. urna* (var.), ventral. Showing distribution of spines over whole surface. $\times 7$.

Figs. 14, 15. *G. fimbriata*. Showing canal-opening, with proboscis inverted, fig. 14, and everted, fig. 15. Sketch without camera.

Fig. 16. Sagittal section of longitudinal nerve-stem, showing sheath-cells, branch-nerves, and ganglion-cells of the first order. Iron haematoxylin-erythrosin. $\times 100$.

acet.—acetabulum.

can. op.—canal opening.

gang. 1st.—ganglion cell of the first order.

gen. notch—genital notch.

n. b.—nerve branch.

n. fib.—nerve fibre.

p. op.—penis opening.

par.—parenchyma.

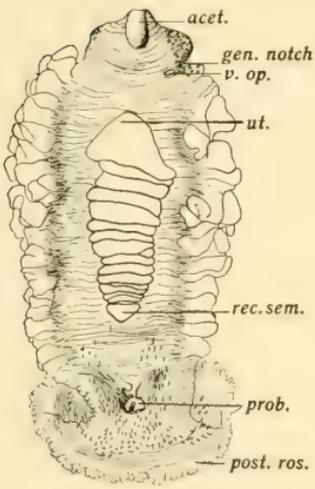
post. ros.—posterior rosette.

prob.—proboscis.

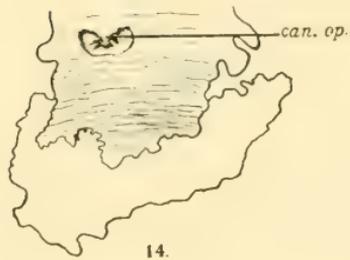
rec. sem.—receptaculum seminis.

sh. c.—sheath cell.

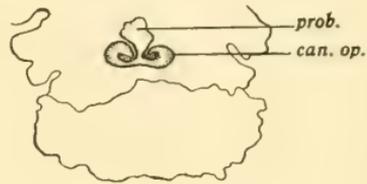
ut.—uterus.



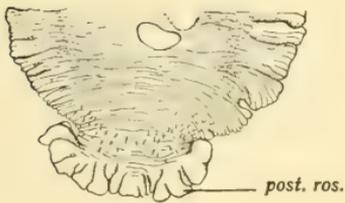
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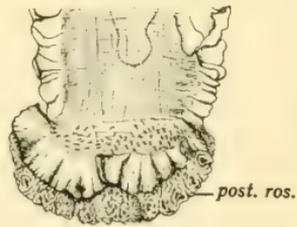
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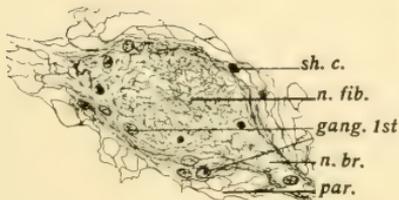
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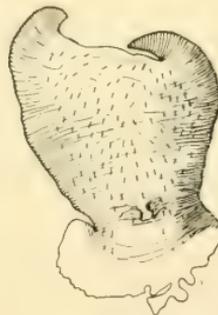
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PLATE 35.

Fig. 17. *Gyrocotyle fimbriata*. Diagram of the nervous system of the posterior extremity. From Kofoid and Watson (1910, fig. 3).

Fig. 18. Diagram of the arrangement of muscle-layers in the saggital section.

Fig. 19. Diagram showing track made by living specimen across dish. Distance traversed, about 14 cm.; four contractions.

Fig. 20. Sketch of network of excretory canals in the lateral fold as seen in a living specimen. Zeiss-Greenough binocular.

Fig. 21. Diagram, reproductive system, typical heterocotylean trematode. (After Benham, 1891, p. 51.)

cut.—cuticle.

cut. trans.—cuticular transverse muscle.

cut. long.—cuticular longitudinal muscles.

dist. r. comm.—distal ring commissure.

ex. can.—excretory canal.

in. long.—inner longitudinal muscle.

in. trans.—inner transverse muscle.

lat. f.—lateral fold.

lat. long. conn.—lateral longitudinal connective.

marg. ex. sin.—marginal excretory sinus.

med. long. conn.—median longitudinal connective.

out. long.—outer longitudinal muscle.

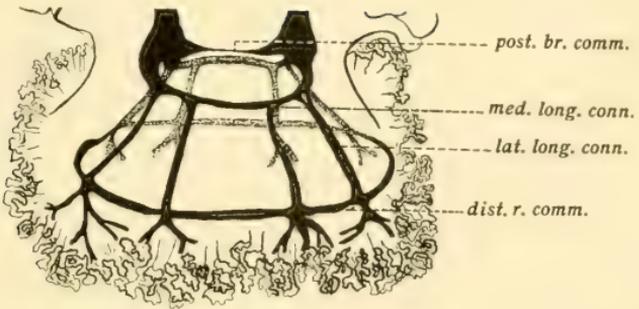
out. trans.—outer transverse muscle.

post. br. comm.—posterior bridge commissure.

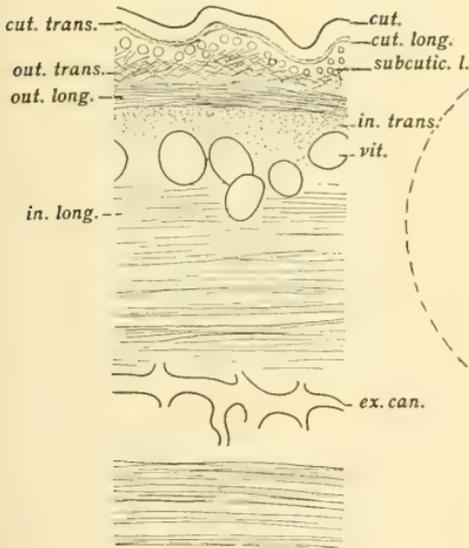
subcutic. l.—subcuticular layer.

vit.—vitellaria.

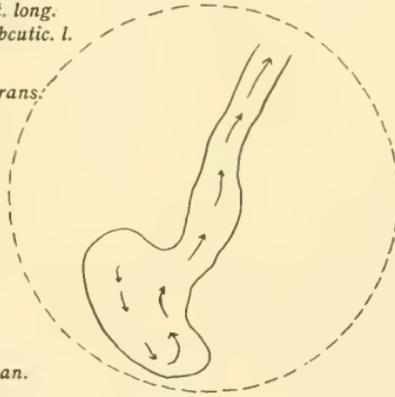
v. op.—vaginal opening.



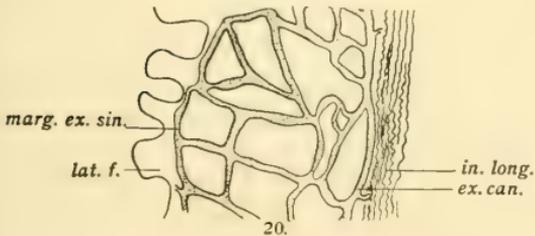
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18.



19.



20.



21.

PLATE 36.

Figs. 22, 23. *Gyrocotyle fimbriata*, anterior extremity, ventral and dorsal. Showing sensory pits and arrangement of spines. From preserved specimen. $\times 13$.

Fig. 24. *G. urna* (var.). Sketch from life. Lateral view, expanded. Showing spines, lateral fold and posterior rosette.

Fig. 25. *G. fimbriata*. Dorsal half of sagittal section of tip of acetabulum, showing sensory pit. Borax-carmin, Lyon's blue. $\times 430$.

Fig. 26. *G. fimbriata*. Sketch, life, acetabular extremity. Showing anterior excretory ring and deeper-lying ciliated canals.

Fig. 27. *G. fimbriata*. Sagittal section just laterad of the acetabulum. Showing anterior longitudinal nerve stem, with branches and anterior ganglionic knot. No histological detail; position of giant-cells within ganglion knot marked by small circles.

acet. op.—acetabular opening.

ant. ex. r.—anterior excretory ring.

ant. gang. kn.—anterior ganglion knot.

ant. lat. n. st.—anterior lateral nerve stem.

cil.—cilia.

cut.—cuticula.

ex. can.—excretory canal.

gen. notch—genital notch.

lat. f.—lateral fold.

par. nuc.—parenchyma nucleus.

p. op.—penis opening.

post. ros.—posterior rosette.

sens. pit—sensory pit.

sp.—spine.

test.—testis.

ut. po.—uterine pore.

test. n.—testicular nerve.

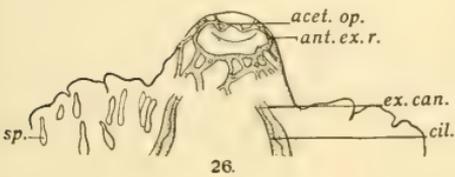
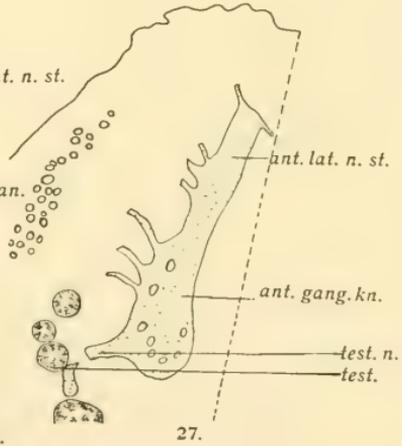
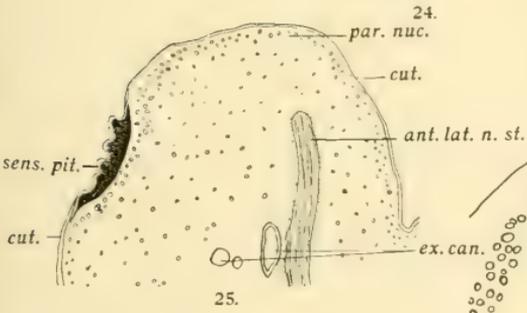
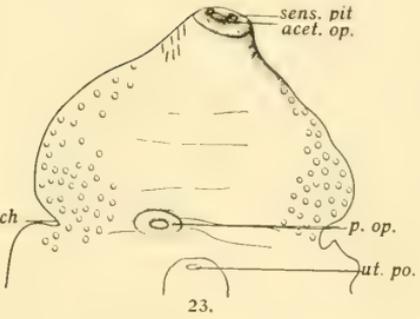
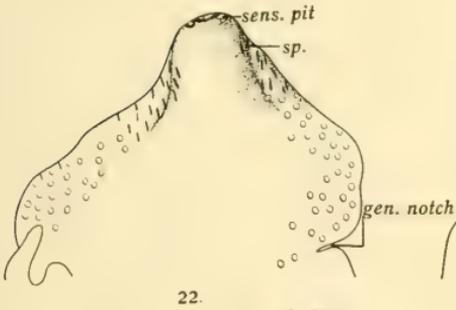


PLATE 37.

Figs. 28, 29. *Gyrocotyle fimbriata*. Spines, from acetabular group. Teased out. $\times 1000$.

Fig. 30. *G. fimbriata*. Spine, from neck of rosette. From specimen stained in borax-carmin and cleared in cedar-oil. Showing direction of spine and attachment of muscles. $\times 430$.

Fig. 31. *G. fimbriata*. Spine from neck of rosette. From same specimen as fig. 30. Drawn in situ. $\times 430$.

Fig. 32. Spines from margin of anterior end, in front of genital notch. Teased out. $\times 1000$.

Fig. 33. *G. fimbriata*, transverse section. Cuticula absent. Showing muscles of spine. $\times 430$. Iron haematoxylin.

Fig. 34. Same as fig. 33. Showing structure of socket of spine. $\times 1000$.

Fig. 35. Spine from neck of rosette. $\times 1000$.

musc. fib.—muscle fibre.

par. felt—parenchyma felt.

par. nuc.—parenchyma nucleus.

protr. m.—protractor muscle.

retr. m.—retractor muscle.

sp.—spine.

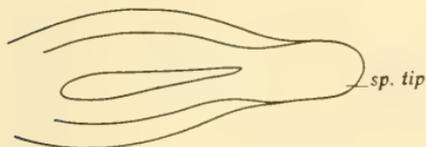
sp. base—spine base.

sp. sock.—spine socket.

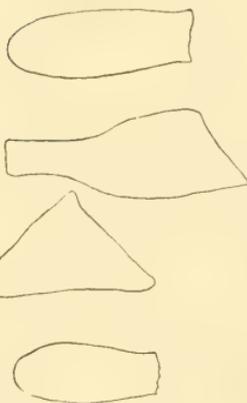
sp. tip—tip of spine.



28



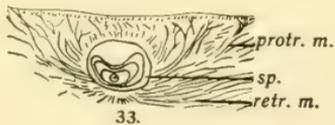
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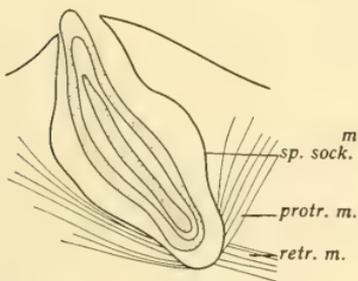
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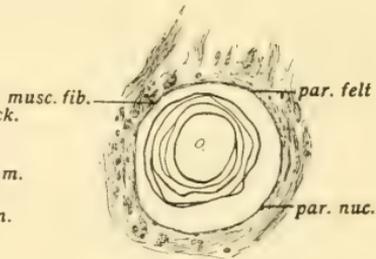
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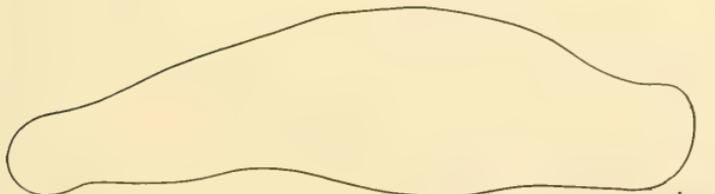
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35

sp. base

PLATE 38.

Fig. 36. *Gyrocotyle rugosa*, from Spencer (1889, pl. 1, fig. 1). To show size and character of lateral folds and posterior rosette and position of genital pores. $\times 1.5$, based on Spencer's reported magnification of 3 which is possibly an error.

Fig. 37-41. Eggs of *G. fimbriata*. Figs. 37-40, from decayed or macerated specimens; fig. 41, from living worm. $\times 500$.

acet.—acetabulum.

ant. br. comm.—anterior bridge commissure.

long. n. st.—longitudinal nerve stem.

operc.—operculum.

p. op.—penis opening.

post. br. comm.—posterior bridge commissure.

post. ros.—posterior rosette.

prob.—proboscis.

rec. ov.—receptaculum ovarum.

rec. sem.—receptaculum seminis.

ut. po.—uterine pore.

vag.—vagina.

vag. op.—vaginal opening.

vas def.—vas deferens.

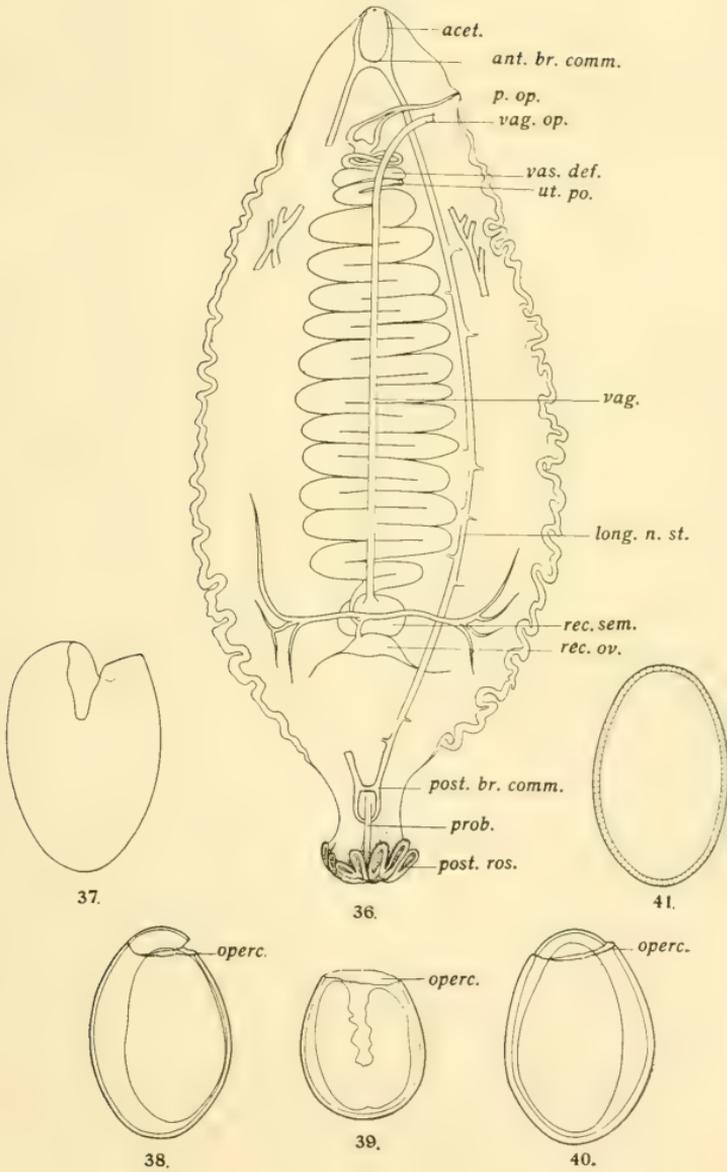


PLATE 39.

Fig. 42. *Gyrocotyle fimbriata*, dorsal. Specimen flattened, stained in borax-carminé; cleared in cedar-oil. $\times 13$.

acet.—acetabulum.

acet. op.—acetabular opening.

ant. br. comm.—anterior bridge commissure.

ant. lat. n. st.—anterior lateral nerve stem.

gen. notch—genital notch.

lat. f.—lateral fold.

long. n. st.—longitudinal nerve stem.

ovar.—ovary.

p. op.—penis opening.

pen. pap.—penis papilla.

post. br. comm.—posterior bridge commissure.

post. gang. kn.—posterior ganglion knot.

post. ros.—posterior rosette.

prox. r. comm.—proximal ring commissure.

rec. sem.—receptaculum seminis.

ros. n.—“neck” of rosette.

sh. gl.—shell gland.

ut. po.—uterine pore.

vag.—vagina.

vas def.—vas deferens.

vit. d.—vitelline duct.

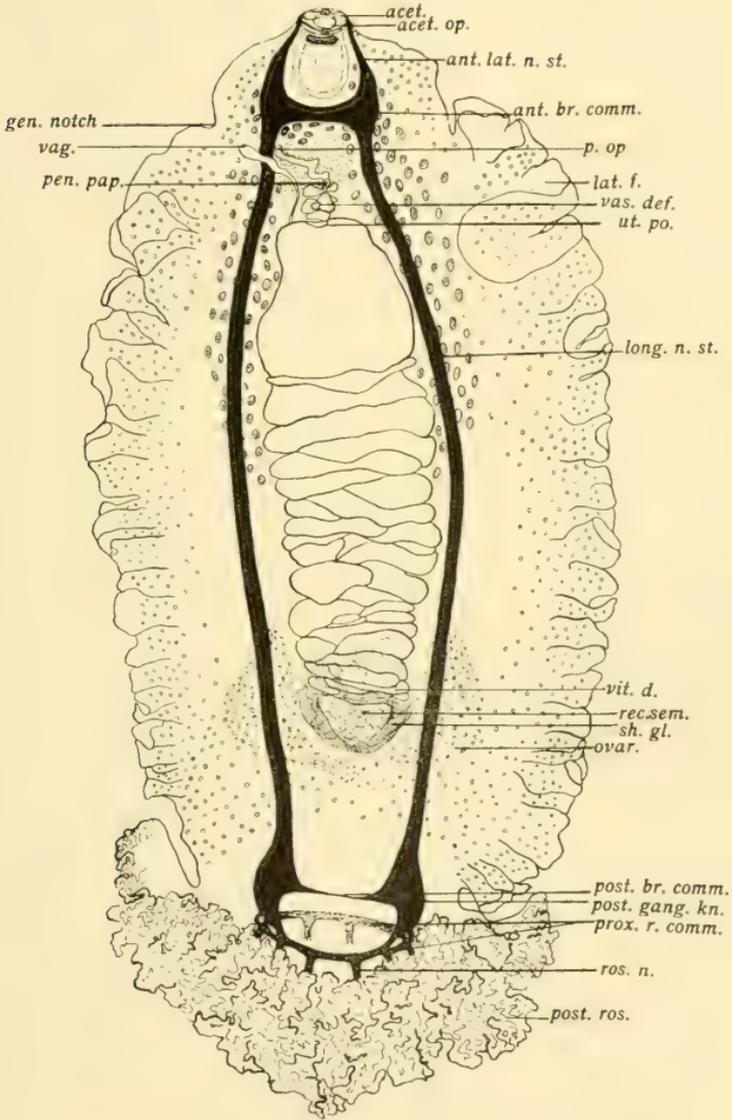


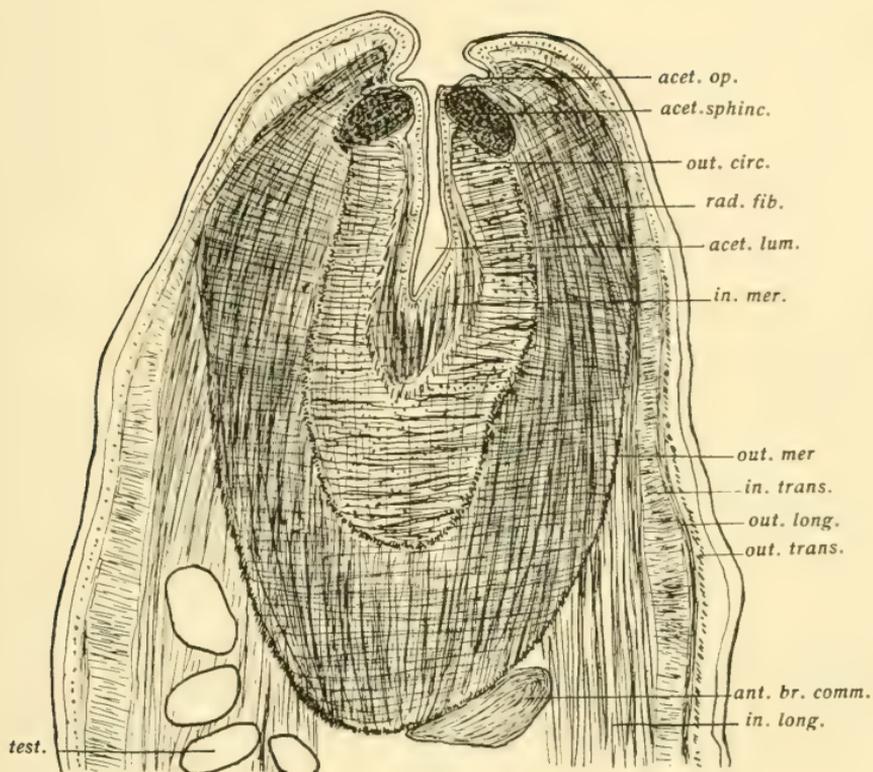
PLATE 40.

Fig. 43. *G. fimbriata*, sagittal section. To show structure of acetabulum and attachment of inner longitudinal muscles. Borax-carmine, Lyon's blue. $\times 100$.

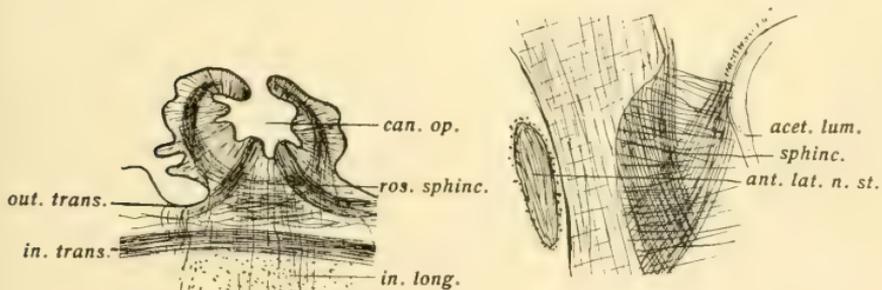
Fig. 44. Diagram, showing musculature of canal opening.

Fig. 45. Same as fig. 43, showing detail of acetabular sphincter. $\times 430$.

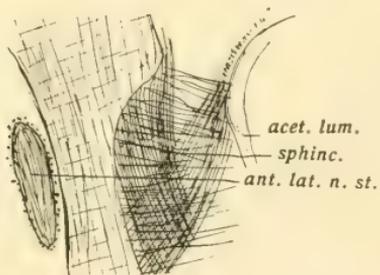
acet. lum..—acetabular lumen.
acet. op..—acetabular opening.
acet. sphinc..—acetabular sphincter.
ant. br. comm..—anterior bridge commissure.
ant. lat. n. st..—anterior lateral nerve stem.
can. op..—canal opening.
in. long..—inner longitudinal muscle.
in. mer..—inner meridional muscle.
in. trans..—inner transverse muscle.
out. circ..—outer circular muscle.
out. long..—outer longitudinal muscle.
out. mer..—outer meridional muscle.
out. trans..—outer transverse muscle.
rad. fib..—radial fibre.
ros. sphinc..—rosette sphincter.
sphinc..—sphincter.
test..—testis.



43.



44.



45.

PLATE 41.

Fig. 46. *Gyrocotyle fimbriata*. Same specimen as fig. 42. Ventral. Showing vagina and vaginal opening, vesicula seminalis, penis-papilla and ejaculatory duct. $\times 100$.

Fig. 47. Egg from fifth coil of uterus. Showing single ovum surrounded by numerous yolk-cells. Delafield's haematoxylin. $\times 1000$.

Fig. 48. Same, tenth coil of uterus. Showing division of ovum and disintegration of yolk cells. Note disappearance of nuclei of yolk cells. $\times 1000$.

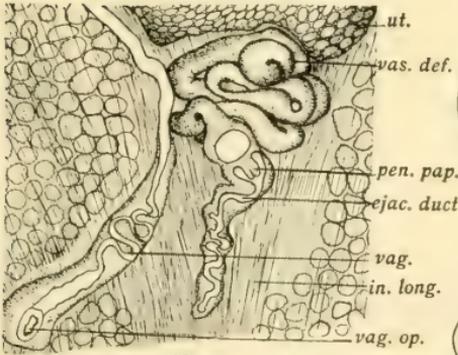
Fig. 49. Yolk cells in vitellarian follicle. Note reduction of cytoplasm and formation of yolk-platelets. $\times 1850$.

Fig. 50. Spermatozoa from receptaculum seminis, showing head, tail and aerosome. $\times 1850$.

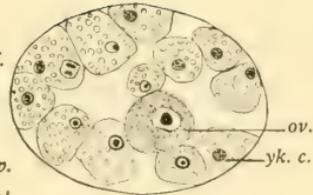
Fig. 51. Ovum in afferent oviduct; note shadow of yolk nucleolus. $\times 1500$.

Figs. 52, 53, 54. Follicle of ovary. Showing syncytial ova and various stages in the formation and extrusion of the yolk-nucleolus. $\times 1500$.

cyt. r.—cytoplasmic rim.
ejac. duct—ejaculatory duct.
in. long.—inner longitudinal muscle.
ov.—ovum.
pen. pap.—penis papilla.
sptz.—spermatozoa.
ut.—uterus.
vag.—vagina.
vag. op.—vaginal opening.
vas def.—vas deferens.
yk. c.—yolk cell.
yk. gr.—yolk platelets.
yk. nucleo.—yolk nucleolus.



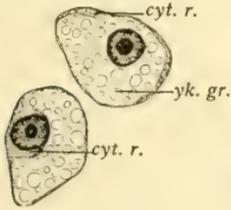
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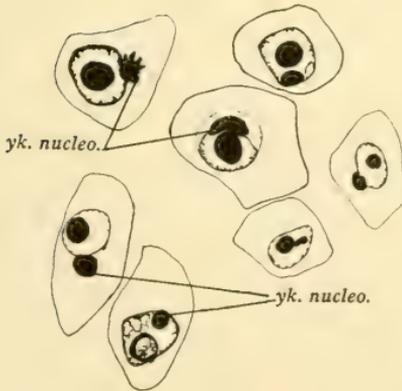
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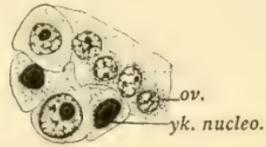
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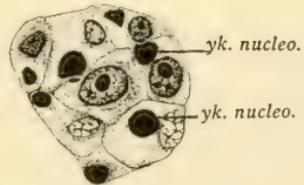
51.



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52.



53.

PLATE 42.

Fig. 55. *Gyrocotyle fimbriata*. Transverse section, showing cuticula and cuticular musculature. Iron haematoxylin. $\times 1500$.

Fig. 56. Showing structure of muscle fibres of the inner circular and inner longitudinal layers. $\times 1850$.

Fig. 57. Showing sagittal (upper) and outer transverse (lower) muscle cells. $\times 1850$.

Fig. 58. Frontal section of cuticula and cuticular musculature. Cut through a fold of body-covering, in the plane of the fibres of the cuticular musculature. $\times 1850$.

Fig. 59. Showing wall of receptaculum seminis, and undifferentiated nucleated muscle fibres lying in the parenchyma of which it is composed. $\times 1850$.

cut.—cuticula.

cut. long.—cuticular longitudinal muscle.

cut. trans.—cuticular transverse muscle.

ext. cut. l.—external cuticular layer.

in. long. fib.—inner longitudinal fibre.

in. trans.—inner transverse muscle.

in. trans. fib.—inner transverse fibre.

nuc.—nucleus.

out. long.—outer longitudinal muscle.

out. trans.—outer transverse muscle.

out. trans. fib.—outer transverse fibre.

par. felt—parenchyma felt.

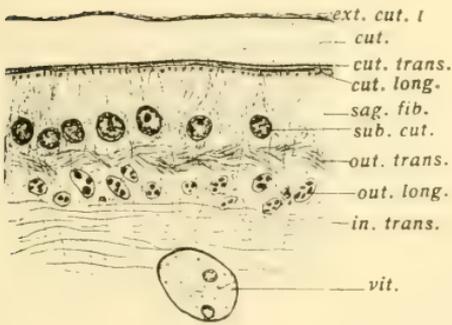
par. nu.—parenchyma nucleus.

sag. fib.—sagittal fibre.

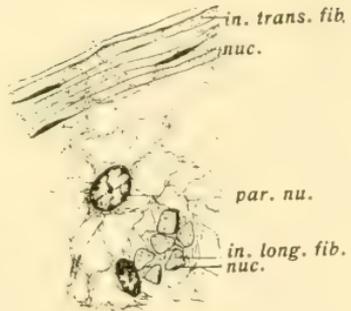
sub. cut.—subcuticula.

undif. musc. fib.—undifferentiated muscle fibre.

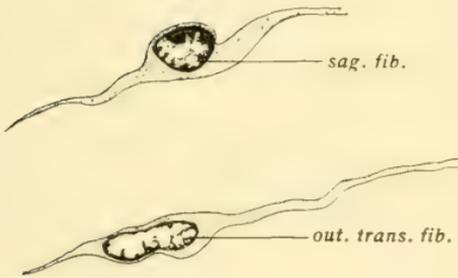
vit.—vitellaria.



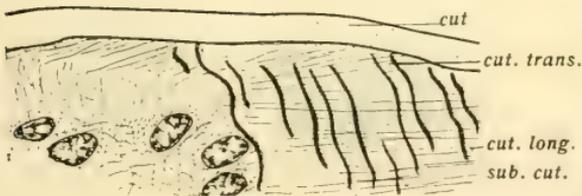
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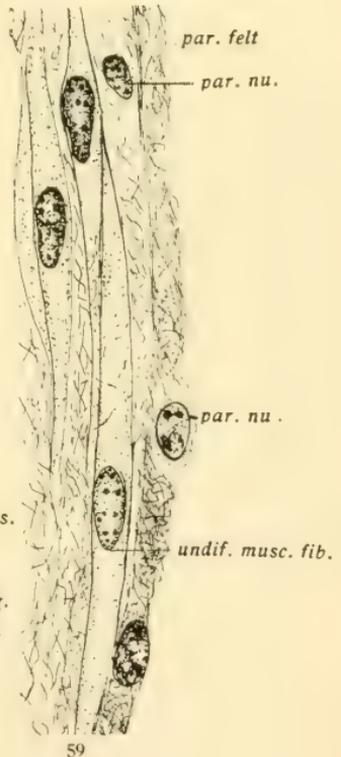
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58



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PLATE 43.

Fig. 60. *Gyrocotyle fimbriata*. Transverse section through ciliated excretory canal. Showing circular muscle coat. Iron haematoxylin. $\times 1000$.

Fig. 61. Longitudinal section through ciliated excretory canal (taken at one side of attachment of cilia). Showing circular muscle coat. Iron haematoxylin. $\times 1000$.

Figs. 62, 63. Flame cells. $\times 1500$.

Fig. 64. Cells of prostate gland. $\times 1500$.

Fig. 65. Sagittal section through penis papilla and ejaculatory duct. $\times 100$.

can.—canal.

cil.—cilia.

circ. musc. l.—circular muscle layer.

ejac. duct.—ejaculatory duct.

fl.—flame.

long. musc. l.—longitudinal muscle layer.

in. long.—inner longitudinal muscle.

par.—parenchyma.

par. nu.—parenchyma nucleus.

pen. pap.—penis papilla.

prost. d.—prostate duct.

prost. gl.—prostate gland.

rad. musc. f.—radial muscle fibre.

spinl.—spinule.

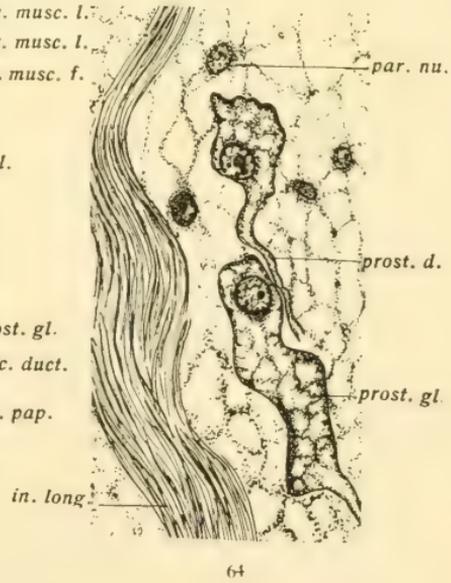
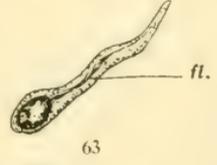
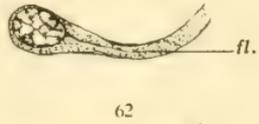
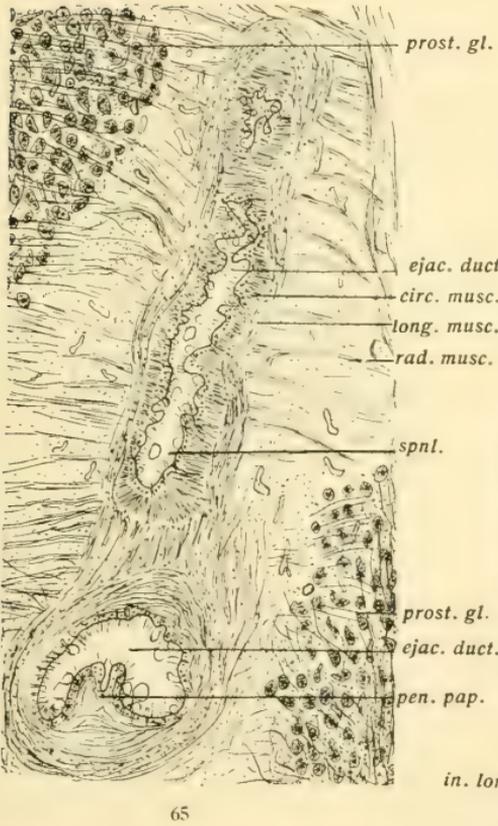
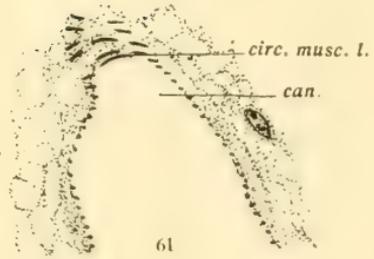
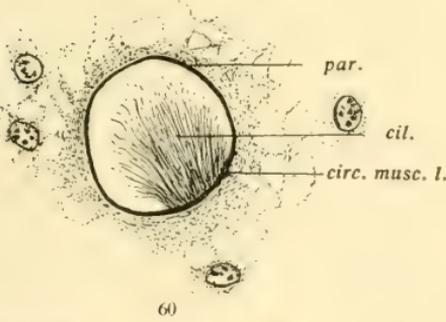


PLATE 44.

Fig. 66. *Gyrocotyle fimbriata*. From posterior ganglionic knot. Showing ganglion cells of first order and a ganglion cell of the second order ("giant cells"). $\times 800$.

Fig. 67. Cross section of longitudinal nerve stem, at region from which a branch to the ovary is given off. $\times 800$.

Fig. 68. Cells of shell-gland. $\times 1500$.

Fig. 69. Diagram of receptaculum seminis and the ducts which unite to form the uterus.

duct. sem.—ductus seminalis.

ef. vit. d.—efferent vitelline duct.

gang. 1st.—ganglion-cell of the first order.

intrac. d.—intra-cellular duct.

n. br.—branch nerve.

par.—parenchyma.

par. nuc.—parenchyma nucleus.

rec. ovar.—receptaculum ovarum.

rec. sem.—receptaculum seminis.

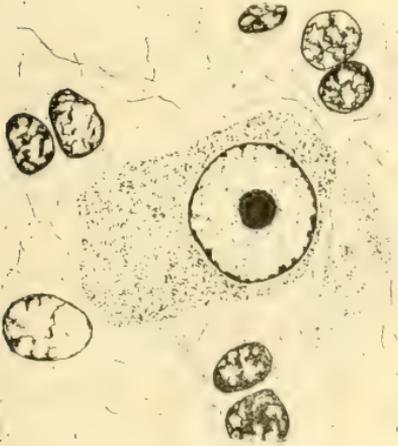
sag. fib.—sagittal fibre.

sh. gl.—shell gland.

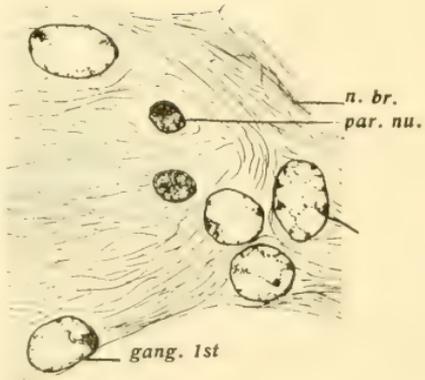
ut. c.—uterine coil.

vit. d.—vitelline duct.

yk. res.—yolk reservoir.



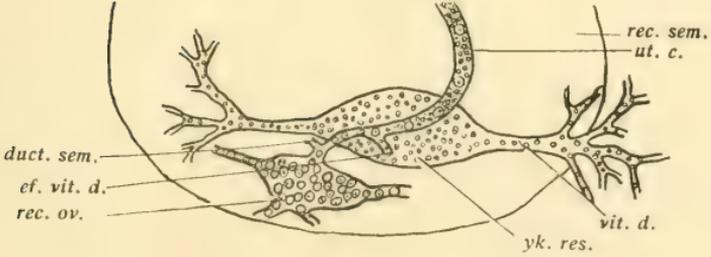
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68



69

PLATE 45.

Figs. 70, 75. *Gyrocotyle fimbriata*. Sagittal section, nearly median. Diagrammatic. $\times 13$.

Figs. 71, 72, 73. Transverse sections, showing (71) emergence of ductus seminalis from receptaculum seminis; (72) fusion of the efferent vitelline duct with the efferent oviduct, which thus becomes the uterus. $\times 100$.

Fig. 74. Sagittal section through dorsal half of neck of funnel. Showing contrast between cuticula of funnel cavity and of the surface of the body. $\times 1000$.

acet.—acetabulum.

cut.—cuticula.

duct. sem.—ductus seminalis.

ef. ovd.—efferent oviduct.

ef. vit. d.—efferent vitelline duct.

ejac. duct.—ejaculatory duct.

ex. can.—excretory canal.

in. long.—inner longitudinal.

lat. long. conn.—lateral longitudinal connective.

long. n. st.—longitudinal nerve stem.

mus. bd.—muscle bundle.

oot.—ootype.

ovar.; *ov.*—ovary.

post. ros.—posterior rosette.

pros. gl.—prostate gland.

rec. ovar.—receptaculum ovarum.

rec. sem.—receptaculum seminis.

subcutic. l.—subcuticular layer.

sh. gl.—shell gland.

test.—testis.

ut.—uterus.

ut. c.—uterine coil.

vag.—vagina.

vit.—vitellaria.

vit. d.—vitelline duct.

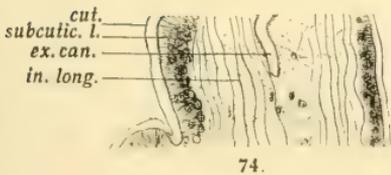
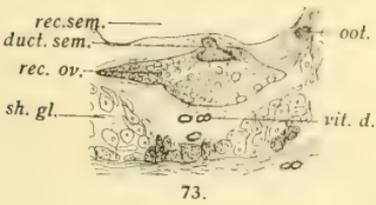
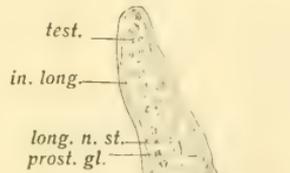
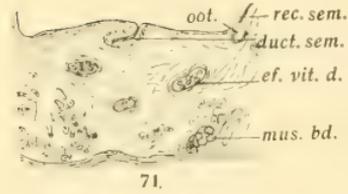
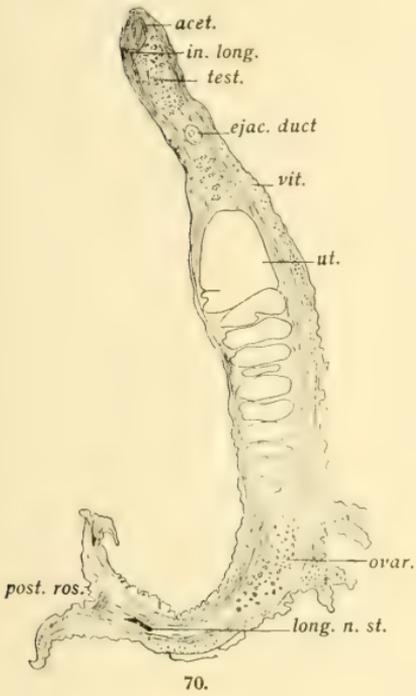
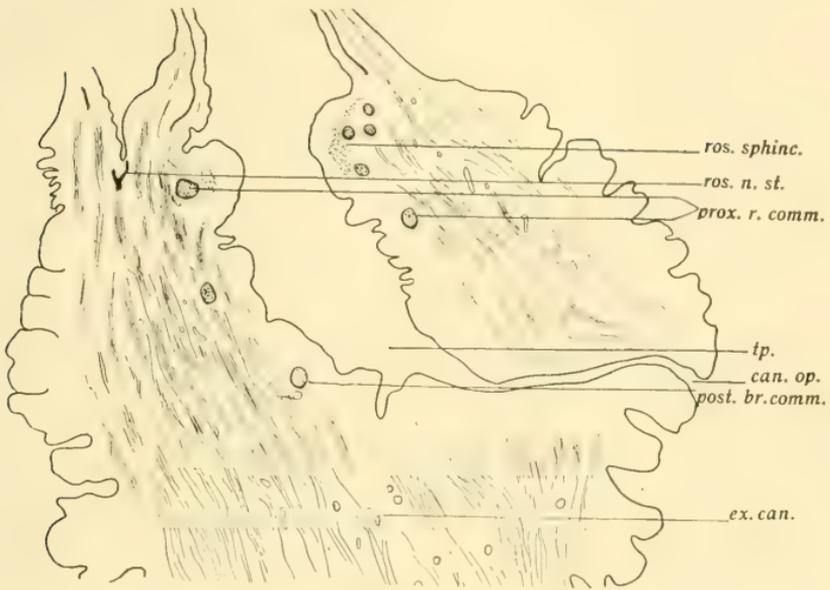


PLATE 46.

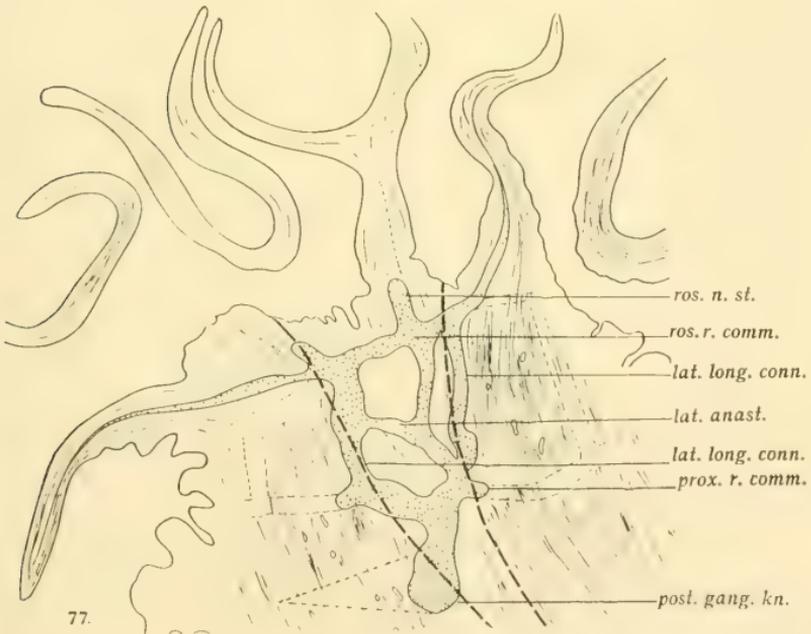
Fig. 76. *Gyrocotyle fimbriata*. Median sagittal section, posterior extremity. Showing funnel, canal, funnel-opening, canal-opening and sections of the ring commissures of the nervous system of the posterior extremity. $\times 100$.

Fig. 77. Same, to left of median. Reconstruction of five sections, showing lateral view of nervous system. Faint dotted lines indicate course of nerves as shown in the neighboring sections; heavy dotted lines indicate position of funnel with reference to the central nervous system. $\times 100$.

- can. op.*.—canal opening.
ex. can..—excretory canal.
lat. anast..—lateral anastomosis.
lat. long. conn..—lateral longitudinal connective.
post. br. comm..—posterior bridge commissure.
post. gang. kn..—posterior ganglion knot.
prox. r. comm..—proximal ring commissure.
ros. n. st..—rosette nerve stem.
ros. r. comm..—rosette ring commissure.
ros. sphinc..—rosette sphincter.
tp..—tope.



76.



77.

PLATE 47.

Fig. 78. Nervous system of *Moniezia expansa*, after Tower (1900).

Fig. 79. Nervous system of Triclad; after Lang (1881).

Fig. 80. *G. nigrosetosa*, Haswell (1902, pl. VII, fig. 1).

Fig. 81. Same, egg, showing operculum. Haswell (1902, pl. VII, fig. 7).

ant. br. comm.—anterior bridge commissure.

ant. gang. kn.—anterior ganglion knot.

ant. r. comm.—anterior ring commissure.

dist. r. comm.—distal ring commissure.

lat. long. conn.—lateral longitudinal connective.

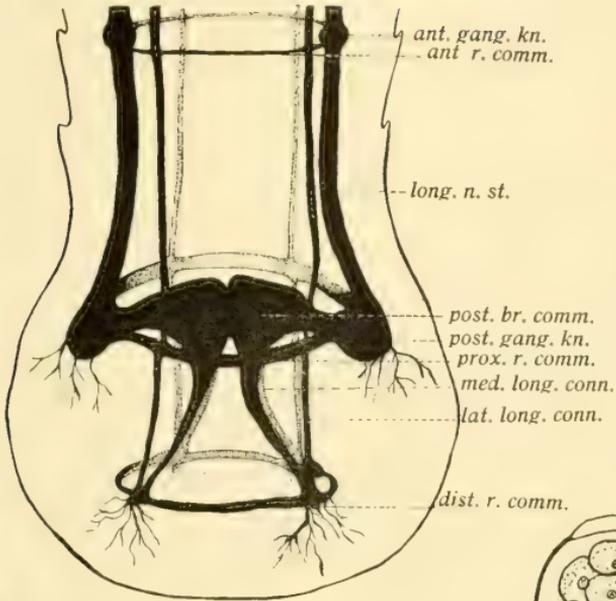
long. n. st.—longitudinal nerve stem.

med. long. conn.—median longitudinal connective.

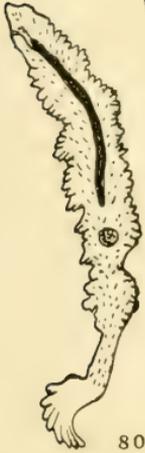
post. br. comm.—posterior bridge commissure.

post. gang. kn.—posterior ganglion knot.

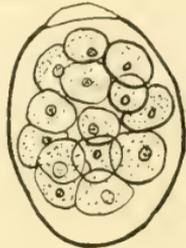
prox. r. comm.—proximal ring commissure.



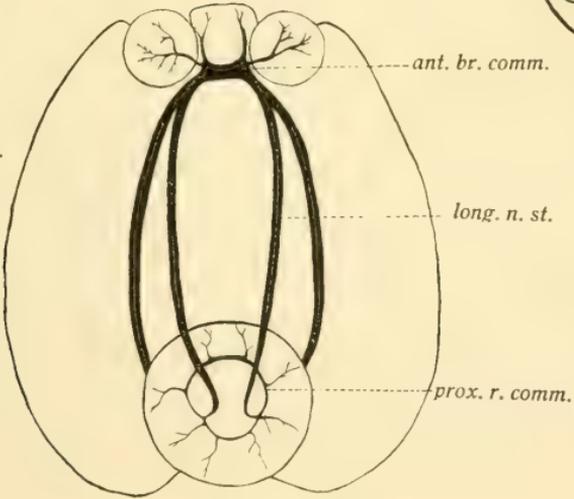
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PLATE 48.

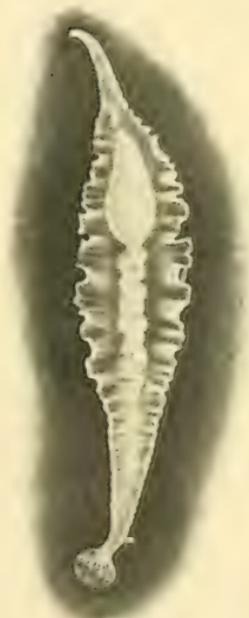
Figs. 82, 83. Photographs of living specimens of *G. fimbriata* and *G. urna* (var.) All in state of contraction. About natural size.

Figs. 84, 85. *G. urna*, from Wagener (1852, pl. 14, figs. 1, 2).



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ERRATA.

- Page 18, *For Gen. Tiaropsidium* n. gen. *read Gen. Tiaropsis*, subgen. *Tiaropsidium* n. subgen.
 Page 19, line 2. *For genera read subgenera.*
 Page 22, line 9. *For browni read diegensis.*
 Page 43, *For Amphiuira verrilli* sp. nov., *read Amphiuira diastata* sp. nov.
 Page 56, *For Amphiuira verrilli* sp. nov., *read Amphiuira diastata* sp. nov.
 Explanation of pl. 2, fig. 8. *For Ophiura read Ophiura.*
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 Page 142, Explanation of pl. 16. *For Fig. 31, read Fig. 32.*
 Page 169, line 14. *For Ceratphyllum read Ceratophyllum.*
 Page 177, line 17. *For The read This.*
 Page 178, line 9. *For seeds read needs.*
 Page 182, line 3 from bottom. *For Gonyaulaux read Gonyaulax.*
 Page 183, line 15. *For posterodorsal read postero-dorsal.*
 Page 195, line 7. *For 1.02591 read 1.02481.*

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