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ERRATA.

P. 251, line 31: *For* fuchsin-orange G-anilin blue, *read* fuchsin-orangeG -anilin blue.

P. 259, under Zalesky 1866: *For* Bd. J 1, *read* Bd. 1; *for* Saeyler, *read* Seyler.

P. 264, under description of fig. 16: *For* ×1650, *read* ×825.

P. 266, under description of figs. 21, etc.: *For* ×1850, *read* ×925.

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THE HYDROIDA

OF THE

PACIFIC COAST OF NORTH AMERICA

BY

HARRY BEAL TORREY

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THE HYDROIDA

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PACIFIC COAST OF NORTH AMERICA,

WITH ESPECIAL REFERENCE TO THE SPECIES IN THE COLLECTION OF THE UNIVERSITY OF CALIFORNIA.

BY

HARRY BEAL TORREY.

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*Two species should be added, though found too late to be given their proper places in text or tables. One, a Bougainvillia, was growing with *T. crocea*, in Oakland Creek. It is probably the *B. mertensi* of A. Agassiz, ('65), which for reasons stated below (p. 29) I had identified with *Bimeria franciscana*. The size and habit of the two species are similar. There are many medusae attached to the stem of the Bougainvillia, each of the larger ones having four pairs of tentacles and eight eye spots. The other newly found species is *Clytia bicophora Ag.* It was growing on stems of *T. crocea*, where it has been found on the eastern coast. It has not been recorded previously from the Pacific Coast. Blastostyles with medusae. Both species were collected September 26.

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Relation of Form and Habit to Environment (*Syncoryne mirabilis*, p. 31; *Tubularia crocea*, p. 44; *Campanularia urceolata*, p. 54; *Obelia commissuralis*, p. 57).
Development and Regeneration of Tentacles; Taxonomic Significance (*Clava leptostyla*, p. 30; *Hydractinia milleri*, p. 35; *Corymorpha palma*, p. 41; *Tubularia crocea*, p. 45).
Orientation (*Corymorpha palma*, p. 39; *Sertularia furcata*, p. 66; *S. argentea*, p. 68).
Response to Tactual Stimulation (*Corymorpha palma*, p. 41).
Origin of Branches and Gonothecae within Hydrothecae (*Sertularella dentifera*, p. 61; *S. halecina*, p. 62; *Plumularia goodei*, p. 76).
Haleciid with Free Medusa (*Campalecium medusiferum*, p. 48).

THE HYDROIDA

OF THE

PACIFIC COAST OF NORTH AMERICA,

WITH ESPECIAL REFERENCE TO THE SPECIES IN THE COLLECTION OF THE UNIVERSITY OF CALIFORNIA.

The scope of this paper has broadened since its preparation was begun. It was intended at first to embody the species of hydroids collected off the southern coast of California during the summer of 1901 by the University of California. To obtain a proper view of these species, however, especially from the standpoint of their distribution, not only was it found necessary to consider all the known species of the western coast of North America, but all the previous collections of the University were overhauled and a number of new species brought to light. As a consequence, 140 western species have been distinguished. Of these, 102 are represented in the University of California collections, 55 (39%) are restricted to this region, and 20 (14%) are new.

While the lack of collections from the deeper waters along our shore would make any attempt to monograph the West Coast Hydroida premature on my part even were it not unnecessary in view of the enormous task of monographing the Hydroida of North America which is now engaging the energies of Professor C. C. Nutting, I have thought that a key to the known species would be at least a convenience at this time, the more so because there are not likely to be any considerable additions in the near future to the list of littoral species, which are the most accessible and for that reason form the great majority of the total number. In the body of the paper all the species in the University of California collection are treated, with the exception of those

from the Alaska coast, an account of which Professor Nutting ('01), has recently published.

If there is one thing more than another which the preparation of this paper has brought emphatically to my attention, it is the great necessity for long-continued observations on the growth and development of hydroids under natural and artificial conditions. Unfortunately the systematist is forced to rely for his determinations almost exclusively upon skeletal characters, which are peculiarly variable. Size, habit, branching, length of branches and internodes, thickness of perisarc, shape and ornamentation of hydrothecæ, kind and amount of annulation, number of tentacles on the hydranth and on the medusa at the time of liberation—all these are subject to often perplexing variations. This leaves little doubt that when proper measures are taken for the observation of living animals the number of species will be materially decreased.

It is mainly through experimentation that the natural conditions of life will be analyzed, and it is only by a thorough investigation of the latter that true affinities can be established. Some of the many causes which affect the lives of hydroids directly have been suggested in the course of the paper. In the cases of *Sertularia furcata* and *S. argentea*, gravity seems to be a factor of importance in determining the direction of growth and the position of the hydrothecæ on the stem. In *Gonothyræa clarki* and *Campanularia pacifica*, malnutrition, or some other unfavorable condition not yet known, produces a peculiar attenuation of branches and perisarc, possibly by directly stimulating the coenosarcal cells to division while inhibiting the action of those with a glandular function. It is equally desirable to know the factors which determine the position of the gonosome in such forms as *Obelia commissuralis*, *Plumularia goodei*, and *Sertularella halecina*, in which species the gonangia take the place of hydranths.

There are other sorts of questions which can receive as yet but doubtful answers, such as the causes of the seasonal distribution of some species, *e.g.*, *Tubularia crocea*, which dies out in San Francisco Bay during the winter months, though it flourishes the year round at San Pedro; here the result is probably referable to changes in temperature.

It is important to discover the relative variability of species, their plasticity or adaptability, what characters are affected directly by the conditions of the environment, what are more stable or not affected at all. So I have tried to bring into this paper as much pertinent ecological material as possible. Most of the western species have been described from preserved specimens, and in many cases there are no records of environmental features, such as depth, temperature, character of the bottom, etc. The depth and temperature, whenever known, are given in the table of distribution. The records are necessarily incomplete, and form a rather insecure basis for generalizations at present.

The develópment of some species, especially with reference to the appearance of the tentacles, has been briefly considered, being of much taxonomic importance. In connection with some species, especially *Corymorpha palma*, I have described certain activities, phenomena of orientation, and processes of regeneration, some of the points which have appeared to me to be of general interest.

Distribution. Of the 140 species on the western coast of North America, 54 (39%) are restricted to this region. Of the remaining 85 species, 24 (17%)* are found on the eastern coast of North America, 11 (8%) in Greenland, 36 (25.7%) in Asia, 5 (3.6%) in South Africa, and 6 (4.3%) in New Zealand and Australia. The presence of 11 of the foreign species is recorded for the first time.

The great center of distribution is northern. *Halicornaria producta* is a single exception to the rule, having been collected in Australia and San Diego, California, only. The South African species are circumboreal. Three of the New Zealand species are circumboreal, the other two probably so, since they are found also in Great Britain. Of the foreign species, 4 do not pass the Aleutian Islands from the north; 14 do not pass Sitka, Alaska; 15 reach, but do not pass Puget Sound; 13 are found in Southern California, 4 being peculiar to that region. The northern character of the hydroid fauna is shown by the tables,

* The percentages are based on the total number.

according to which 69 species (49%) occur north of Sitka, 96 (68.5%) north of Puget Sound.

The only geographical barrier of any magnitude is Alaska Peninsula. The fauna of Alaska north of the peninsula is distinguished from that south of it by the absence of any representatives of the *Haleciidae*, *Lafœidae* and all the families of the *Gymnoblastea* except three species of *Pennariidae*, which are restricted to that region; also by the small number of species (2) of *Campanulariidae*, in representatives of which family the fauna of Alaska south of the peninsula is so rich. The fauna of the Aleutian Islands belongs essentially to that of Alaska south of the peninsula. Of the nine species distributed between Kyska Island and Akutan Pass, none occurs north of the islands, although five occur in the Southern Alaska region.

From Alaska Peninsula to San Diego there are no abrupt transitions in the fauna. It is possible, however, for purposes of comparison, to divide this great region into four sub-regions. The first extends from Alaska Peninsula south to Sitka. It possesses a large number of species (59, 18 of which are peculiar to it) belonging mainly to the *Campanulariidae* and *Sertulariidae;* there are relatively large numbers of *Haleciidae* (7) and *Lafœidae* (6). The second sub-region includes the fauna of Puget Sound, Vancouver Island and vicinity. There are 50 species, of which 10 are peculiar to the region; 22 are *Campanulariidae*, of which 10 are found in the first sub-region; 14 are *Sertulariidae*, 9 of which are found in the first sub-region; 5 are *Haleciidae*, of which but one is found in Alaska and one south of Puget Sound. The two species of *Lafœidae* are Alaskan; the four species of *Plumulariidae* includes the single Alaskan species. Both first and second sub-regions contain families of *Gymnoblastea*, though no species are common to the two. The third sub-region comprises San Francisco Bay and vicinity, including Monterey Bay. There are here no representatives of the *Lafœidae* and *Haleciidae*. Six species are peculiar to it, all of which are *Gymnoblastea*, including a *Clava* and a new *Hydractinia*. The fourth sub-region comprises Southern California, south of Point Conception. The fauna contains a relatively large number of *Plumulariidae* (12, of which 8 are local) and *Sertulariidae* (14, of

which 7 are local); three of the four species of *Haleciidae* are local; the *Clavidae* and *Hydractiniidae* are without representatives.

The differences in the fauna which have just been outlined are correlated with certain geographical differences. The Japan Current, striking the shore of Alaska, parts into two streams. The larger turns down along the coast of the United States; the smaller turns upward and runs along the southeast shore of the Alaska Peninsula. The shore of this part of the Alaska coast drops precipitously away, so that the current comes close in toward the land. North of the peninsula is the great one hundred fathom plateau, extending many hundreds of miles out from the shore line. On this plateau the hydroids from Northern Alaska have been collected. It is covered by waters much colder than those south of the peninsula. If the warmer waters of the Japan Current reach it, they flow, so far as known, only along its edge.

North of the peninsula, then, is a region whose waters are largely covered with ice for more than half of each year. South of the peninsula begins a vast stretch of coast which is washed by the comparatively warm waters of the Japan Current. This current is probably accountable for the absence of abrupt transitions between the faunal areas which I have tried to schematize above, and the exceedingly long distances to which some of the northern species have been distributed southward. The temperature of the current varies gradually with the latitude, however, and that offers some explanation for the small faunal differences that exist.

Future exploration will doubtless reduce these differences. While the Alaska coast from Unalaska to Sitka has been rather thoroughly explored, practically no collections have been made between Sitka and Vancouver Island. From Puget Sound to San Pedro little is known of the off-shore fauna, though much dredging and shore collecting have been done in Puget Sound and San Francisco and Monterey bays. Little is known of the hydroid fauna on each side of Point Conception, a natural barrier which has decidedly affected the distribution of some groups of animals, notably the molluscs.

TABLE OF DISTRIBUTION.

	West Coast America.												East Coast America.	(Greenland, Iceland, Jan Mayen, and Spitzbergen.	Europe.	Asia.	South Africa.	New Zealand.	Australia.	Bathymetrical Range. In fathoms.	Temperature. ° C.
	Alaska N. of Peninsula.	Aleutian Islands.	Alaska S. of Peninsula.	Puget Sound Region.	California. Humboldt Region.	San Francisco Reg.	Monterey Bay.	Santa Barbara.	San Pedro Region.	San Diego Region.											
Gymnoblastea																					
Bougainvillidae																					
Atractyloides formosus Fewkes																				0, 42	
*Bimeria annulata (Nutt.)			+			+				+											
formosa (Fewkes)							+														
* franciscana						+														0—1	
gracilis Clark															B					0—1	
* nutans Wright			+																	0—1	
* robusta									+						B					0—1	
*Perigonimus repens Wright				+																	
Clavidae						+															
*Clava leptostyla Ag.						+							M								
Corynidae																					
*Coryne brachiata Nutt.			+																		
*Syncoryne eximia Allman			+				+								N						
* mirabilis Ag.				+		+		+							Sp					0—1	
Eudendridae																					
*Eudendrium californicum				+		+										N				0—1	
* rameum Pallas									+						++					0—D	—1.0
* ramosum Linn.							+													1—50	
* vaginatum Allman			+												B						

TABLE OF DISTRIBUTION—*Continued.*

| | West Coast America. | | |

TABLE OF DISTRIBUTION—*Continued.*

| | West Coast America. | | |

TABLE OF DISTRIBUTION—*Continued.*

	West Coast America.																					
					California.																	
	Alaska N. of Peninsula.	Aleutian Islands.	Alaska S. of Peninsula.	Puget Sound Region.	Humboldt Region.	San Francisco Reg.	Monterey Bay.	Santa Barbara.	San Pedro Region.	San Diego Region.	East Coast America.	Greenland, Iceland, Jan Mayen, and Spitzbergen.	Europe.	Asia.	South Africa.	New Zealand.	Australia.	Bathymetrical Ranges, in fathoms.	Temperature. °C.			
*Campanularia regia Nutt.			+																			
rigida (A. Ag.)						+																
* ritteri Nutt.			+															20				
* speciosa Clark			+															6—20				
* urceolata Clark			+	+		+												0—18				
* verticillata (Linn.)			+								+		+					20—50				
* volubilis Linn.				+		+			+		N		N					0—100	—0 to 13			
Gonothyraea gracilis Sars				+																		
* clarki nom. nov.	+		+	+		+					M		N					0—30				
* inornata Nutt.			+																			
*Obelia borealis Nutt.			+																			
* commissuralis McCr.						+					M							0—1				
* dichotoma Linn.			+	+					+	+	M		B	N				0—24	—1.0 to 13			
* dubia Nutt.			+																			
fragilis Calk.				+																		
gelatinosa (Pallas)				+							M											
* genieulata (Linn.)						+				C	SMN		+			+		0—42				
gracilis Calk.				+																		
griffini Calk.																						
longissima Hincks											M			N				5—80				
* plicata Hincks			+	+									B									

TABLE OF DISTRIBUTION—*Continued.*

	West Coast America.																				
						California.															
	Alaska N. of Peninsula.	Aleutian Islands.	Alaska S. of Peninsula.	Puget Sound Region.	Humboldt Region.	San Francisco Reg.	Monterey Bay.	Santa Barbara.	San Pedro Region.	San Diego Region.	East Coast America.	Greenland, Iceland, Jan Mayen, and Spitzbergen.	Europe.	Asia.	South Africa.	New Zealand.	Australia.	Bathymetrical Range, in fathoms.	Temperature. °C.
Obelia surcularis Calk				+															
*Clytia caliculata (Hincks)			+	+							N		B					0—15	
* compressa (Clark)			+															3—20	13
?johnstoni (Alder)			+	+							+		+			+		0—D	
*Calycella syringa (Linn.)			+	+		+				+		IG	B	N				1—100	to 12
*Campanulina rugosa Nutt.			+																
*Hebella pocillum (Hincks)	+		+								N		B					15	
Incerta sedis: Thaumantias inconspicua Forbes				+									B						
Lafoeidae																			
*Filellum serpens Nutt.			+									I	B	N				12—100	—0.8
*Grammaria immersa Nutt.																			
*Lafoea adhaerens Nutt.			+																
* dumosa (Fleming)		+	+	+							+	Sp	N					12—450	
* fruticosa M. Sars		+	+								+	IG	N	N				6—35	1.6
* gracillima (Alder)			+	+					+		+	Sp	+					15	
Sertulariidae																			
Dynamena group																			
*Sertularia desmoidis									+	+								1—40	13
* furcata Trask						+	+	+	+	+								0—25	9.5 to 13
? pumila (Linn.)											+		+		+	+		0—2	

TABLE OF DISTRIBUTION—*Continued.*

	West Coast America.										East Coast America.	(Greenland, Iceland, Jan Mayen, and Spitzbergen.	Europe.	Asia.	South Africa.	New Zealand.	Australia.	Bathymetrical Range, in fathoms.	Temperature ° C.
	Alaska N. of Peninsula.	Aleutian Islands.	Alaska S. of Peninsula.	Puget Sound Region.	California.														
					Humboldt Region.	San Francisco Reg.	Monterey Bay.	Santa Barbara.	San Pedro Region.	San Diego Region.									
Hydrallmania group																			
*Hydrallmania distans Nutting				+					+					N	+			35	
falcata (Linn.)				+							+		+						
franciscana Tr.						+													
Selaginopsis group																			
*Selaginopsis cylindrica (Cl.)			+															0—15	
* mirabilis (Verr.)			+	+										E					
Sertularella group																			
* Sertularella clarki Mereseh.	+								+		S							10—60	
* conica Allman									+										
* dentifera									+				B					0—1	
* * fusiformis Hincks						+												5—12	12
* * haleyina										+								1—9	10 to 12
* hesperia																			
nana Hartlaub				+									J					0—112	
* pinnata (Clark.)	+																	0—30	
* polyzonias (Linn.)	+			+											+				
* saccata Nutting	+																		
* tenella (Alder)										+			B			+		0—19	10
* * triuspidata (Alder)				+									GI	N				4—40	—0.8
* tuigida (Trask)				+														0—42	13

TABLE OF DISTRIBUTION—*Continued.*	West Coast America.																		
					California.														
	Alaska N. of Peninsula.	Aleutian Islands.	Alaska S. of Peninsula.	Puget Sound Region.	Humboldt Region.	San Francisco Reg.	Monterey Bay.	Santa Barbara.	San Pedro Region.	San Diego Region.	East Coast America.	Greenland, Iceland, Jan Mayen, and Spitzbergen.	Europe.	Asia.	South Africa.	New Zealand.	Australia.	Bathymetrical Range, in fathoms.	Temperature. ° C.
Thuiaria group																			
Sertularella albida K.	+		+											E					
*Sertularia argentea E. & S.				+	+	+					N	G	N		+			0 50	
* cupressoides Cl.	+																	6 - 13	
* fabricii Lev.			+	+															
* filicula E. & S.	+		+	+		+	+		+	+	N		B					0—25	to 12
* greenei Murray				+	+	+	+	+											
* incongrua									+										
* similis Cl.	+		+	+														8 - 15	
tenera Sars	+											I	N	N				4 40	—1.6
* thuiaroides Cl.	+		+															11—24	
* traski									+										
* variabilis Cl.	+		+	+				+						N				0 112	—1.0
*Thuiaria coei Nutting		+																	
* costata Nutting			+																
* elegans Nutting																			
* gigantea Clark	+		+															0 - 10	
plumosa Clark	+													N				10—30	
robusta Clark	+													N				0—33	—1.0
* turgida Clark		+	+											N				0 -28	0.0

TABLE OF DISTRIBUTION—*Continued.*

	West Coast America.											East Coast America.	Greenland, Iceland, Jan Mayen, and Spitzbergen.	Europe.	Asia.	South Africa.	New Zealand.	Australia.	Bathymetrical Range, in fathoms.	Temperature. ° C.
	Alaska N. of Peninsula.	Aleutian Islands.	Alaska S. of Peninsula.	Puget Sound Region.	California. Humboldt Region.	San Francisco Reg.	Monterey Bay.	Santa Barbara.	San Pedro Region.	San Diego Region.										
Plumulariidae																				
*Aglaophenia diegensis										+									1—7	12
* inconspicua										+									5	12
* pluma (Linn.)										+				+		+			1—40	12
* struthionides (Murray)						+	+	+	+	+									0—32	13
*Antenella avalonia										C										
*Halicornaria producta (Bale)										+									1 2	12
Nuditheca dalli (Clark)		+																		
*Plumularia alicia									+	+									5—25	10—13
echinulata, var., Calk.			+											B						
* goodei Nutt.							+	+											1—10	
* lagenifera Nutt.		+	+				+		+										1—20	
* [lagenifera septifera]										[+]										
* plumularoides Clark	+									+									8—25	
* setacea (Ellis)			+		+	+	+	+	+	+				+					0—25	12
virginiae Nutt.								+												
Totals	20	9	59	50	3	28	14	9	23	29	24	11	36	15	5	5	1			

The letters in the table have the following significance: B, Great Britain; C, Catalina Island; D, deep water; E, eastern; G, Greenland; I, Iceland; J, Jan Mayen; M, middle; N, northern; S, southern; Sp, Spitzbergen. The species preceded by an asterisk are represented in the collection of the University of California; those which are not followed by a proper name are new.

CONDENSED TABLE SHOWING THE NUMERICAL DISTRIBUTION OF SPECIES OCCURRING ON THE WEST COAST OF NORTH AMERICA.

	West Coast North America.											General Distribution.						
	Species peculiar to locality.	Alaska North of Peninsula.	Aleutian Islands.	Alaska South of Peninsula.	Puget Sound Region.	Humboldt Region.	San Francisco Region.	Monterey Bay.	Santa Barbara.	San Pedro Region.	San Diego Region.	East Coast North America.	Greenland, Iceland, Spitzbergen, and Jan Mayen.	Europe.	Asia, North and East.	South Africa.	New Zealand.	Australia.
Alaska North of Peninsula	2	20	.....	13	6	.....	2	1	1	1	2	6	2	6	8	1	.....	.....
Aleutian Islands	3	.....	9	5	1	.....	.....	.....	.....	.....	.....	2	3	2	3	.....	.....	.....
Alaska South of Peninsula	18	13	5	59	22	1	6	3	2	4	4	12	9	18	9	2	1	.....
Puget Sound Region.	10	6	1	22	50	2	14	6	6	8	7	13	7	19	6	1	2	.....
Humboldt Region	.....	.....	.....	1	2	3	3	2	2	.....	.....	1	1	1	.....	1	.....	.....
San Francisco Region	5	2	.....	6	14	3	28	8	6	7	8	9	3	9	1	1	2	.....
Monterey Bay	1	1	.....	3	6	2	8	14	4	6	6	1	.....	4	.....	.....	.....	.....
Santa Barbara	1	1	.....	2	6	2	6	4	9	3	3	2	1	2	2	1	.....	.....
San Pedro Region	7	1	.....	5	9	.....	7	6	3	23	8	5	.....	5	.....	.....	.....	.....
San Diego Region	8	2	.....	5	8	.....	9	6	3	9	29	2	.....	7	1	1	2	1

TABLE SHOWING THE DISTRIBUTION BY FAMILIES OF THE WEST COAST HYDROIDS.

	Bougainvilliidae, incl. Bimeriidae.	Clavidae.	Corymidae.	Eudendriidae.	Hydractiniidae.	Pennariidae, including Tubulidae and Corymidae.	Haleciidae.	Campanulariidae, including Campanulinidae.	Lafoeidae.	Sertulariidae.	Plumulariidae.
Alaska North of Peninsula	.....	.....	.....	.....	.....	3	.....	2	.....	14	1
Aleutian Islands	.....	.....	.....	.....	.....	.....	.....	1	2	5	1
Alaska South of Peninsula	2	.....	2	1	.....	1	7	21	6	18	1
Puget Sound Region	1	.....	1	.....	.....	1	5	22	2	14	4
Humboldt Region	.....	.....	.....	.....	.....	1	.....	.....	.....	2	.....
San Francisco Region	3	1	1	1	1	3	.....	9	.....	7	2
Monterey Bay	1	.....	1	2	.....	1	.....	1	.....	4	4
Santa Barbara	.....	.....	1	.....	.....	.....	.....	.....	.....	4	4
San Pedro Region	1	.....	.....	1	.....	2	1	4	1	9	4
San Diego Region	2	.....	.....	.....	.....	1	3	5	.....	7	9

KEY TO THE HYDROIDA OF THE WESTERN COAST OF NORTH AMERICA.*

1. No true hydrothecae or gonangia ..... Gymnoblastea 2
1. True hydrothecae and gonangia present ..... Calyptoblastea 25
2. Tentacles in proximal and distal sets ..... Pennariidae 3
2. Filiform tentacles in one whorl 8
2. Tentacles scattered 20
3. A single nutritive polyp, rooted in the sand; perisare rudimentary ..... Corymorpha 4
3. Several nutritive polyps from a common hydrorhiza ..... Tubularia 5
4. About 40 prox. tentacles; body a coral red C. (Rhizonema) carnea[1]
4. Not more than 30 prox. tentacles; stem colorless ..... C. palma (p. 37)
5. Gonophores with laterally compressed processes 6
5. Gonophores with conical or tentaculate processes 7
5. Gonophores with conspicuous radial canals; no processes ..... T. indivisa[1]
6. With 4 processes, 32-34 proximal and 50-60 distal tentacles ..... T. borealis[1]
6. With 6-10 processes and 25 proximal tentacles ..... T. crocea (p. 43)
7. 4 tentaculiform processes on female gonophore, as long as gonophore; proximal tents. 22-25 ..... T. marina (p. 46)
7. 3-5 tentaculiform processes on gonophores, half as long as gonophores; proximal tents. 40-50 ..... T. harrimani[2]
7. Processes conical; proximal tents. 18-20 ..... T. larynx[3]
7. Proximal tents. 30–40 ..... T. tubularoides[4]
8. Hydranths of two sorts; large sterile and small fertile, each with clavate proboscis; spiral zooids; hydrorhiza encrusting, with tubular spines ..... Hydractiniidae Hydractinia milleri (p. 34)
8. Hydranths of one sort 9
9. Proboscis trumpet-shaped ..... Eudendriidae Eudendrium 10
9. Proboscis conical ..... Bougainvilliidae 13
10. Hydrocaulus annulated throughout 11
10. Hydrocaulus not annuluated throughout 12
11. Height of colony 2 inches or less; female gonophores usually without tentacles ..... E. vaginatum[2]
11. Height of colony 4-5 inches; female gonophores with tentacles ..... E. californicum (p. 32)
12. Stem and principal branches polysiphonic ..... E. rameum (p. 33)

*Some of the species in the key are described in this paper, others in papers mentioned in their several synonymies; descriptions of the rest may be found in the papers to which the indices after the specific names refer, which have been selected with especial reference to their accessibility.

12. Stem polysiphonic at base only; principal branches simple ..... E. ramosum (p. 34)
13. Unbranched ..... Atractyloides formosa[3]
13. Branched 14
14. Gonophores fixed sporosacs ..... Bimeria 15
14. Gonophores free medusae ..... Perigonimus 19
15. Stem polysiphonic 16
15. Stem simple 17
16. Stems several inches long, robust ..... B. robusta (p. 29)
16. Stem less than an inch long ..... B. nutans[4]
17. Stems annulated throughout ..... B. annulata (p. 28)
17. Stems not annulated throughout 18
18. Hydranth with 10-12 tentacles ..... B. gracilis[6]
18. Hydranth with 14-16 tentacles; hydrorhiza creeping over base of stem ..... B. franciscana (p. 28)
19. Branches not annulated; tentacles 4-12 ..... P. repens (p. 29)
19. Branches slightly annulated; tentacles 10-16 ..... P. (?) formosus[5]
20. Tentacles filiform; fixed sporosacs ..... Clavidae
Hydrocaulus rudimental; hydranths claviform; gonophores proximal to tentacles ..... Clava 21
20. Tentacles capitate ..... Corynidae 22
21. More than 20 tents.; color red ..... Clava leptostyla (p. 30)
22. Gonophores free medusae ..... Syncoryne 23
22. Gonophores fixed sporosacs; tents. of one sort ..... Coryne 24
23. Tentacles 20-30; colony 2 or more inches high ..... S. eximia (p. 31)
23. Tentacles 16; colony ½ in. to 1½ in. high ..... S. mirabilis (p. 31)
24. Branches regularly annulated throughout ..... C. brachiata[2]
25. Hydrotheeae saucer-shaped; hydranth with conical proboscis ..... Haleciidae 26
25. Hydrotheeae campanulate, pedunculate, with partial septum at base ..... Campanulariidae 33
25. Hydrotheeae tubular, without basal septum, margin smooth, no operculum ..... Lafoeidae 60
25. Hydrotheeae well developed, sessile; nematophores absent ..... Sertulariidae 66
25. Hydrotheeae well developed, sessile, borne on one side of stem or branch only; nematophores present ..... Plumulariidae 92
26. Gonophores medusoid ..... Campalecium 27
26. Gonophores fixed sporosacs ..... Halecium 28
27. Rim of hydrotheca strongly everted; hydranth with 24-28 tentacles; gonophore with 4 tentacles ..... C. medusiferum (p. 48)
28. Non-fascicled 29
28. Fascicled 32
29. Annulated 30
29. Not annulated 31
30. Hydrotheeae usually half as deep as broad; gonotheeae very much compressed ..... H. annulatum (p. 49)
30. Annulated or corrugated, unbranched or irregularly branched; about 20 tentacles ..... H. corrugatum[7]
30. Sparsely and irregularly annulated; irregularly branched; parasitic; 23-30 tentacles ..... H. ornatum[2]

30. Stem geniculate, pedicels taking the place of stem joints; gonothecae annulated, with annulated pedicels ..... H. speciosum[2]
31. Branched, 1½ inches high; hydrothecae on internodes sessile, not reaching beyond distal node; rim not everted....H. kofoidi (p. 49)
32. Densely and irregularly branched, often three branches from same shoulderlike process; hydrothecae sub-alternate, rim everted ..... H. densum[3]
32. Bushy, principal branches pinnate; rim of hydrothecae not everted; gonothecea ovate, female surmounted by two hydranths.. H. halecinum[3]
32. Stem and branches polysiphonic, stiff; hydrothecae everted; gonothecae compressed, spiny ..... H. muricatum[5]
32. Each internode of branches with one or two proximal annulae, with distal hydrothecae reaching beyond end of internode; ultimate branches geniculate ..... H. nuttingi (p. 50)
32. Flabellate colony; hydranth small, 20 tentacles, pedicels from proximal part of internode ..... H. reversum[2]
32. Thick stem and branches fascicled with many tubes, branching profusely; hydranths numerous, crowded, in whorls and clusters, with 10 tentacles; rim of hydrotheca non-everted..... H. robustum[2]
32. Stout, coarse, ultimate branches divided into wedge-shaped internodes; gonothecae with orifice on one side..... H. scutum[6]
32. Hydrothecae everted; male gonotheca a circular disk, with peduncle with one or two annulae ..... H. wilsoni[3]
33. Non-operculate 34
33. Operculate; operculum of numerous small triangular pieces 58
34. Gonophores sessile; sporosacs ..... Campanularia 35
34. Gonophores sessile, medusoid ..... Gonothyraea 48
34. Gonophores free medusae 49
34. Hydrothecae tubular, smooth margin, hydranth with conical proboscis ..... Hebella 57
35. Stems branched 36
35. Stems unbranched 42
36. Stems fascicled 37
36. Stems simple 40
37. Pedicels of hydranths in whorls of 4 to 6, at regular intervals..... 38
37. Pedicels of hydranths alternating in one plane 39
38. Hydrotheca with 10-12 blunt denticles; base rounded..... C. circula[1]
38. Hydrotheca with 12 sharp denticles; tapering to base..... C. verticillata[8]
39. Colony often 200 mm. long, densely branching; hydrotheca with 10 bicuspid teeth, hydranth with 26 tentacles ...C. pacifica (p. 53)
39. Colony 5-10 mm. long; hydrotheca with 11-12 moderate teeth; hydranth with 20-24 tentacles ..... C. fascia (p. 52)
40. Colonies small, with few branches, which are parallel to the parent stem 41
40. Hydrotheca small, funnel-shaped, with even rim..... C. exigua[8]
40. Stems unbranched except for the hydrotheca pedicels, which are short and regularly alternate, giving the colony the aspect of a Sertularian ..... C. rigida[4]
41. Length of hydrotheca, .65–1.00 mm.; breadth, .36-.45 mm.; 14-15 teeth on margin ..... C. denticulata (p. 51)
41. Length of hydrotheca, .5 m.; breadth, .25 m.; margin with 9-10 teeth ..... C. attenuata[3]

42. Margin of hydrotheca smooth 43
42. Margin of hydrotheca denticulate 44
43. Hydrotheca broadly campanulate; gonotheca with about 10 annulae ..... C. integra[6]
43. Hydrotheca large, cylindrical, delicate; long slender pedicel with 1 distal and 2 or 3 proximal annulae only ..... C. ritteri[2]
43. Hydrotheca very large, tubular, urceolate, with everted margin; hydranth with 20 tentacles ..... C. regia[2]
44. Hydrotheca with longitudinal striations 45
44. Hydrotheca unstriated 47
45. Hydrotheca small, tubular; striations due to deep longitudinal flutings and continuous with 7-10 sharp teeth ..... C. kincaidi[7]
45. Striations continuous with interdenticular spaces 46
46. Hydrotheca deep, tapering to pedicel, margin with 10-12 square-topped teeth; gonotheca elongate, with numerous large annulae ..... C. hincksi (p. 53)
46. Hydrotheca large, delicate, depth to breadth as 3:2, sides parallel, base hemispherical; 12-14 rounded teeth ..... C. lineata[7]
46. Hydrotheca large, deeply campanulate, urceolate, with short pedicel; 10 low, blunt teeth; striations in distal quarter..C. speciosa[1]
47. Rim of hydrotheca usually everted, with 12-15 low teeth or crenations; gonotheca smooth, compressed, with small terminal aperture ..... C. everta (p. 51)
47. Hydrotheca deep, cylindrical, with 12 blunt marginal teeth; gonothecae fusiform ..... C. fusiformis (p. 52)
47. Hydrotheca variable, margin often reduplicated, with 12-15 rounded teeth; gonotheca fusiform ..... C. urceolata (p. 54)
47. Hydrotheca small, tubular, margin often reduplicated, with 9 moderate teeth ..... C. volubilis (p. 54)
48. Hydrotheca deep, margin with 10 square-topped or bicuspid teeth; gonophores with tentacles but without radial canals ..... G. clarki (p. 55)
48. Hydrotheca deep, with 10-11 sharp teeth; gonophores with radial canals and tentacles ..... G. gracilis[3]
48. Hydrotheca funnel-shaped, with smooth margin; gonophore without radial canals or tentacles ..... G. inornata[2]
49. Medusae with 4 tentacles when liberated ..... Clytia 50
49. Medusae with 16 or more tentacles when liberated ..... Obelia 51
50. Hydrotheca campanulate, with even margin and usually thick walls; gonotheca irregularly ovate, with wide aperture ..... C. caliculata[5]
50. Hydrotheca usually with thick walls; margin slightly crenate; gonotheca broadly ovate, compressed ..... C. compressa (p. 58)
50. Hydrotheca with 13-15 marginal teeth; gonotheca with a single constriction in the middle ..... C. johnstoni
51. Margin of hydrotheca dentate or undulating 52
51. Margin smooth 53
52. A line running from each depression in the margin half way to the base ..... O. dubia[2]
52. Stem fascicled; margin of hydrotheca with bicuspid teeth ..... O. gelatinosa[8]
52. Stem fascicled, branches sub-verticillate; margin of hydrotheca with shallow undulations ..... O. longissima[8]

53. Stem fascicled 54
53. Stem not fascicled 55
54. Stems interwoven, often of great length (18 in.); hydrotheca funnel-shaped ..... O. borealis[2]
54. Stem and larger branches fascicled; branching profuse; hydrothecae broadly campanulate, slightly everted ..... O. plicata[5]
54. Stem and branches long, flexuous; perisarc delicate; length of hydrotheca, 5 m.; breadth, 4 m.; tentacles 22-24 ..... O. fragilis[3]
55. Hydrotheca polygonal at margin 56
55. Single geniculate stem; pedicels usually on shoulders reinforced by a thickening of the perisarc; medusa with 24 tentacles ..... O. geniculata (p. 58)
55. Dimensions of hydrotheca: length, .36 m., .32 m.; breadth, .34 m., .19 m.; hydranth with 28 tentacles ..... O. gracilis[3]
55. Colony much branched; diaphragm in hydrotheca single, with down-turned edges; hydranth with 24 tentacles; medusa with 24 tentacles, 6-8 medusae being borne at one time ..... O. griffini[4]
55. Colony 25 mm. high, branches relatively long, alternate; margin of hydrotheca slightly everted, diaphragm a simple shelf; medusa with 28 tentacles ..... O. surcularis[3]
56. Branches sub-verticillate; medusa with 16 tentacles at liberation ..... O. commissuralis (p. 56)
56. Branching irregular; medusa with 20-24 tentacles at liberation ..... O. dichotoma (p. 57)
57. Hydrotheca larger below, narrowing slightly above, then expanding to the orifice ..... H. pocillum[3]
58. Branched, annulated throughout; long slender converging teeth form operculum; free bell-shaped medusa ..... Campanulina rugosa[2]
58. Unbranched, hydrotheca tubular, pedunculate, opercular pieces distinct from hydrothecal teeth ..... Calycella syringa[5]
59. Stem short, sparely branched or not at all; hydrotheca .60-.65 m. long, with 7 large teeth ..... Thaumantias inconspicua[3]
60. Stem fascicled 61
60. Stem not fascicled; hydrauth curved, decumbent, attached for $\frac{2}{3}$ its length ..... Filellum serpens[5]
61. Hydrothecae free or partially immersed ..... Lafoea 62
61. Hydrothecae partially adnate to axial tube, completely inclosed by peripheral non-thecate tubes ..... Grammaria 65
62. Hydrothecae short or sessile 63
62. Hydrothecae pedunculate 64
63. Colony encrusting ..... L. adhaerens[2]
63. Colony erect, hydrothecae short, stout ..... L. dumosa (p. 59)
64. Hydrotheca long, slender, delicate, with slender twisted pedicel $\frac{1}{4}$ its length ..... L. gracillima (p. 60)
64. Hydrotheca stouter; pedicel annulated, $\frac{1}{5}$-$\frac{1}{4}$ length of hydrotheca ..... L. fruticosa[5]
65. Hydrothecae in 8-9 rows, spirally arranged ..... G. immersa[2]
66. Hydrothecae in one row, several to an internode ..... Hydrallmania group 67
66. Hydrothecae in two rows 68
66. Hydrothecae in three or more rows ..... Selaginopsis group 91
67. Distal end of hydrotheca not reaching beyond proximal third of next one above; 3-5 to an internode ..... H. distans (p. 70)

67. Mouth of hydrotheca reaching beyond middle of next one above; hydrothecae crowded, often more than 5 to an internode..H. falcata[9]
67. Hydrothecae flask-shaped, much narrowed distally..H. franciscana[9]
68. Hydrotheca alternate, one to an internode ..... Sertularella group 69
68. Hydrothecae in pairs, one pair to an internode.....Dynamena group 75
68. More than two hydrothecae to an internode..... ..... Thuiaria group 77
69. Margin of hydrotheca dentate 70
69. Margin of hydrotheca entire, everted, hydrotheca tubular.. .... S. halecina (p. 61)
69. Margin of hydrotheca smooth or bilabiate; hydrothecae distant ....

79. Aperture semilunar 84
80. Hydrotheca abruptly narrowed distally, aperture round 81
80. Hydrotheca not abruptly narrowed distally, aperture round or oval 83
81. Hydrothecae sub-opposite to alternate; orifice of gonotheca large, round, with a number of teeth projecting downward ..... Sertularia variabilis[1]
81. Hydrothecae alternate; gonotheca widest in middle, tapering to both ends, aperture small, terminal 82
82. Gonotheca smooth ..... Sertularia filicula (p. 68)
82. Gonotheca with about five conspicuous longitudinal ridges ..... Sertularia costata[2]
83. Hydrotheca tubular, deeply immersed, with round aperture, opposite on branches; gonotheca with three or five lodgitudinal ridges ..... Thuiaria turgida[1]
83. Hydrothecae subalternate, deeply immersed, curving outward, oval aperture; stem and branches stout; gonotheca ovate; large terminal aperture ..... Thuiaria gigantea[1]
84. Branches spirally arranged, hydrothecae sub-opposite to alternate, distal end of alternate reaching beyond base of next; gonotheca bimucronate ..... Sertularia thuiaroides[1]
84. Branches pinnate, distal end of alternating hydrotheca barely reaching base of next ..... Sertularia traski (p. 69)
85. Hydrothecae opposite on branches, curved strongly outward ..... Sertularia similis[1]
85. Hydrothecae alternate on branches 86
86. Hydrothecae on main stem 87
86. No hydrothecae on main stem; even number of alternating branches to an internode, hydrothecae deeply immersed ..... Sertularia cupressoides[1]
87. Gonotheca with two horns or spines 88
87. Gonotheca without horns or spines 90
88. Hydrotheca never completely immersed 89
88. Hydrotheca completely immersed in median portion of branches only; hydrocaulus largest distally; gonotheca with two truncate spines ..... Thuiaria robusta[1]
88. Hydrotheca always completely immersed; aperture toward stem; gonothecae very long, bicornuate, in single row on upper side of branches ..... Thuiaria plumosa[1]
89. Aperture well defined; gonothecae constantly bimucronate ..... Sertularia argentea (p. 67)
89. Aperture less clearly defined; gonothecae only occasionally bimucronate ..... Sertularia fabricii[3]
90. Gonotheca with bottle-shaped distal end, small round aperture; hydrotheca with two prominent teeth; stems densely clustered ..... Sertularia greenei (p. 69)
90. Gonotheca ovate, round aperture; colony one-half inch high, stem flexuous, hydrotheca free for distal half ..... Sertularia tenera[7]
91. Hydrothecae tubular, almost completely immersed ..... Selaginopsis cylindrica[1]
91. Hydrothecae immersed for half their length, narrowing distally ..... Selaginopsis mirabilis[1]
92. Nematophores movable 93
92. Nematophores fixed 101
93. Hydrocladia borne on erect stems ..... Plumularia 94

93. Hydrocladia borne directly on stolon .....Antenella avalonia (p. 74)
94. Hydrocladial internodes thecate and non-thecate 95
94. Hydrocladial internodes thecate only 98
95. Nodal septa transverse; supra calycine and intermediate nematophores present 96
95. Nodal septa alternately transverse and oblique; hydrocladia alternating; hydrothecae free for half their length..... P. alicia (p. 75)
96. Never more than two intermediate internodes; hydrotheca as deep as longer diameter, front forming an angle with stem ..... P. setacea (p. 79)
96. Often more than two intermediate internodes; longer diameter of hydrotheca greater than depth, front parallel with stem 97
97. Septal ridges moderate, usually two on each intermediate internode ..... P. lagenifera (p. 77)
97. Septal ridges heavy, never more than one on each intermediate internode ..... P. lagenifera septifera (p. 78)
98. Nematophores monothalamic 99
98. Nematophores dithalamic: depth of hydrotheca about half its greater diameter; gonothecae fusiform ..... P. virginiae[12]
99. Margin of hydrotheca slightly recurved 100
99. Margin of hydrotheca not recurved; gonothecae on stem or stolon, with numerous long spines ..... P. echinulata[5]
100. Cauline internodes with one to three branches each; gonotheca oval, borne in place of hydrocladium ..... P. goodei (p. 76)
100. Cauline internodes each with one branch; gonothecae axial, without spines..... P. plumularoides (p. 78)
101. Stem fascicled; hydrocladia branched; no marginal teeth; gonothecae unprotected ..... Nuditheca 102
101. Stem simple 103
102. Hydrotheca without anterior constriction; gonotheca with two or three nematophores at base ..... N. dalli[12]
103. Gonothecae protected by corbulae, each of which is a modified hydrocladium; no hydrotheca at base of each gonangial leaf..... Aglaophenia 104
103. Gonothecae unprotected; no septal ridges in hydrocladial internodes; an anterior intertheeal ridge..... Halicornaria 107
104. Hydrotheca with 11 irregular teeth .....A. struthionides (p. 73)
104. Hydrotheca with 9 teeth 105
105. Median tooth recurved 106
105. Median tooth not recurved.....A. pluma (p. 73)
106. Hydrocladial nodes well marked; mesial nemataphore reaches mouth of hydrotheca..... A. inconspicua (p. 72)
106. Hydrocladial nodes weak; mesial nematophore does not reach mouth of hydrotheca ..... A. diegensis (p. 71)
107. No marginal teeth..... H. producta (p. 75)

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1. Clark ('76, 1).
2. Nutting ('01, 1).
3. Calkins ('99).
4. A. Agassiz ('65).
5. Fewkes ('89).
6. Clark ('76, 2).
7. Nutting ('99).
8. Hincks ('68).
9. Trask ('54).
10. L. Agassiz ('65).
11. Kirchenpauer ('84).
12. Nutting ('00).
13. Mereschkowsky ('78).

Systematic Discussion.

GYMNOBLASTEA.

Hydroida without true hydrothecae or gonothecae. Gonophores when free, usually furnished with eye-spots, gonads on wall of manubrium.

Fam. Bougainvilliidae.

Atractylidæ, Hincks, Brit. Hydr. Zooph., 1868, p. 87.

Trophosome. Hydranth with a single verticil of filiform tentacles around the base of a conical or dome-shaped proboscis.

Gonosome. Gonophores in the form of fixed sporosacs or free medusæ.

There is, it appears to me, as little advantage in separating this family into two (*Bimeriidæ*, *Bougainvilliidæ*) on the basis of the free or fixed character of the gonophores, as there is in dividing the *Corynidæ* into two families on the same grounds. I have ventured, therefore, to restore the family *Atractylidæ*, as Hincks understood it, changing the name, however, for reasons which Allman has fully set forth ('71, p. 299). The oldest genus in the family thus constituted is *Bougainvillia*, for which reason I have given its name to the family.

Bimeria. Wright.

Bimeria. T. S. Wright, Edin. N. Phil. Jour., 1859, n. s., X., p. 109. Hincks, Brit. Hydr. Zooph., 1868, p. 103. Allman, Gymnobl. Hydr., 1871, p. 297.

Garveia. T. S. Wright, Edin. N. P. Jour. 1859, p. 109. Hincks, Brit. Hydr. Zooph., 1868, p. 101. Allman, Gymnobl. Hydr., 1871, p. 294. Nutting, Proc. Wash. Ac. Sc., 1901, III., p. 166.

Trophosome. Colony branching, hydranth fusiform with conical proboscis, and invested with perisarc which may cover the tentacles and proboscis proximally.

Gonosome. Gonophores sporosacs, never borne on body of hydranth.

The original diagnosis of *Bimeria* was based upon specimens of *B. vestita* Wright, which up to the present time has been the only species definitely referred to the genus, with the exception of a species from San Diego, Cal., described by Clark ('76), under the provisional name of *Bimeria* (?) *gracilis*.

The character which distinguishes the trophosome of *Bimeria* from that of *Garveia* in the diagnosis of Hincks ('68) and All-

man ('71) is the continuation of the perisarc so as to invest the proximal portion of each tentacle. Allman adds that the perisarc also covers the hypostome to within a short distance of the mouth.

I have examined specimens of *Garveia annulata* Nutting from the collection which contained the type of his species, and find that they are similar in all respects to a hydroid from the entrance of San Francisco Bay. These San Francisco specimens were carefully examined to determine the presence or absence of perisarc on the tentacles. It was extremely difficult to make out the distal limit of the perisarc. It is certainly attached to the cœnosarc, thinning away distally very gradually. Soaking in caustic potash destroyed more than the distal half of each tentacle, and demonstrated that the basal portion of each was sheathed in delicate perisarc, as shown in Fig. 1, Pl. I. Repeatedly have I seen the perisarc continue upon the bases of the tentacles in the expanded living hydranth. It is by no means an "opake brown" (Hincks, '68, p. 103) nor is it so conspicuous and its distal limit so clearly marked as in Allman's figure of *B. vestita* ('71, Pl. XII). But these cannot be considered differences of generic importance. Neither do I think that the extent of the perisarc offers any longer a proper criterion for the separation of the two genera. The tentacles of *B. vestita* are alternately elevated and depressed; those of *G. nutans* and the present species are not. This character by itself, however, is not even of specific importance.

While the trophosomes do not offer distinguishing characters, the gonosomes of these genera are held to be distinct for two reasons: first, the gonophore is "borne on the summit of a true branchlet, where it takes the place of the hydranth on an ordinary branchlet" (Allman); second, the perisarc of this branchlet expands below the gonophore into a sort of cup (Nutting). The Alaska and San Francisco specimens agree in possessing gonophores, some of which are completely covered with perisarc, as in the typical *Bimeria*, and lack the proximal cup-like expansion, while others are left half naked by the rupture and retraction of their perisarcal covering, and still others possess what approximates the cup-like expansion that Nutting describes.

The "branchlets" on which the gonophores are borne are no less like peduncles than those of the *B. vestita* which Allman figures. They are similar to hydranth-bearing branches in color, diameter and the transverse wrinkling of the perisarc characteristic of the species.*

In the gonosome, then, as in the trophosome, *G. annulata* is intermediate between the types of *Bimeria* and *Garveia*, possessing and combining the essential characters of each. It seems no longer desirable, therefore, to retain both generic names. Originally both appeared on the same page of one of T. S. Wright's papers (1859, p. 109), with *Bimeria* first. This name will consequently take precedence.

Bimeria annulata Nutting.

Pl. I. Figs. 1, 2, 3.

Garveia annulata, Nutting, Proc. Wash. Ac. Sc., 1901, III, p. 165.

Distribution. Santa Catalina I., Cal., 42 fathoms; San Francisco Entrance, Cal., between tides. Yakutat and Sitka, Al. (Nutting).

Bimeria franciscana, sp. nov.

Plate I. Fig. 4.

Trophosome. Stems rising to the height of about 70 mm. in dense clusters from a tangled hydrorhiza which creeps over the bases of the stems for a few millimeters. Branches arise at short intervals in all planes; some may be more than half as long as the main stem. On these are borne secondary branches, which have hydranths. All secondaries borne on the *distal side* of the branches, alternately to right and left. Hydranths fusiform with 14–16 tentacles; conical hypostome.

Perisarc of the main stem moderately thick, smooth, without annulæ. On the branches it is much thinner and roughened by irregular wrinkles which extend to hydranths. A few more or less definite annulæ at the origin of the branches and branchlets. Body of each hydranth invested with perisarc. Color brown throughout.

Gonosome. Sporosacs with very short peduncles borne irregularly on secondaries and ultimates in the proximal half of the colony in abundance. Female with prominent spadix and one or two ova. Invested with a layer of perisarc.

Distribution. San Francisco Bay, between tides.

* The annulation of the stem is by no means so regular and prominent as the figure in Nutting's paper (1901, Pl. XVI, fig. 1) would lead one to suppose, nor are the gonophore stalks there shown typical for all colonies.

This is in all probability the hydroid that A. Agassiz ('65, p. 152) suggests may be the hydrarium of *Bougainvillia (Hippocrene) mertensii*. There is nothing in his notice to indicate that he saw the gonosome on the hydroid, and that would account for a mistake in referring a free medusa to a form with fixed sporosacs. His brief description, so far as it goes, answers well for the present species. So far as I know, there is no *Bougainvillia* in San Francisco Bay.

Bimeria robusta, sp. nov.

Pl. I. Figs. 5, 6, 7.

Trophosome. Hydrorhiza encrusting. Stems and larger branches stout, polysiphonic. Colony may be 13 cm. long, longest branches 4 cm. or even 6 cm. long. The latter arise irregularly. Hydranth pedicels from these, or from secondaries which are always short (6–8 mm.) and may bear 2-4 hydranths. All branches rather closely associated. Perisarc wrinkled throughout, investing the hydranth body and possibly bases of the tentacles.

Hydranths fusiform, with conical proboscis, the largest with 11 tentacles, rarely 12, in one case 16. Five tentacles are longer and often stouter than the others, subequal, suberect, and belong to the first whorl. The tentacles of the second whorl, alternate with these, are shorter, subequal, and bend downward.

Gonosome. Absent.

Distribution. San Pedro, Cal. Covered with diatoms and Tentaculifera. Growing in company with *Endendrium rameum* and *Tubularia crocea*, on the float at the ferry landing.

This species is placed provisionally in the genus *Bimeria* until the character of the gonosome shall have been determined.

Perigonimus Sars.

Trophosome. Hydrocaulus branched or simple, rooted by a filiform hydrorhiza. Hydranth fusiform with conical hypostome.

Gonosome. Free medusæ, with either two or four marginal tentacles with bulbous bases but without ocelli.

Perigonimus repens (Wright), Hincks.

Atractylis repens, Wright, Proc. Roy. Phys. Soc. Ed., I, p. 450.

Perigonimus repens, Hincks, Brit. Hyd. Zooph., 1868, p. 90.

Perigonimus repens, Calkins, Proc. Bot. Soc. N. H., 1899, XXVIII, No. 3, p. 339.

Distribution. Sausalito, Cal., between tides. Townsend Harbor, Wash. (Calkins). Great Britain (Allman).

A single colony covering the shell of *Nassa mendica*. Some of the medusæ were about ready for liberation (March 25, 1895).

Fam. Clavidæ.

Trophosome. Hydranths clavate or fusiform, with scattered filiform tentacles.

Gonosome. Gonophores fixed sporosacs.

Clava, Gmelin.

"*Trophosome.* Hydrocaulus rudimental and consisting of very short tubular processes from the free surface of a hydrorhiza which is composed of creeping tubes, either distinct or adnate to one another by their sides, and invested, as well as the rudimental hydrocaulus, by an obvious perisarc. Hydranths claviform.

"*Gonosome.* Sporosacs springing from the body of the hydranths at the proximal side of the tentacles." Allman, '71.

Clava leptostyla Ag.

Pl. I. Figs. 5, 8, 9, 10, 11, 12.

Clava leptostyla, Ag., Contr. N. H. U. S., 1862, IV, p. 218.

Distribution. San Francisco Bay, Cal. Massachusetts Bay (Agassiz). Great Britain (?) (Hincks). Between tides.

Found the year round, with sporosacs, in Oakland Harbor, (brackish water). The sexes of this species are ordinarily separate, but occasionally a colony will be found with individuals of both sexes, one predominating greatly, however; instances of hermaphroditic gonophores have been met with also.

Regeneration. This species regenerates readily. Pieces cut from a hydranth may produce hydranths at each end. (Figs. 8,9). The basal portion of the hydranth, if left attached to the stolon, will produce tentacles and a mouth. The development of the tentacles on one such piece was followed. During the night after the animal was sectioned four tentacles appeared at the same level (Fig. 10), and, to judge by their equal length, simultaneously. The next four appeared simultaneously just proximal to and alternating with these (Fig. 11). The third four appeared simultaneously, proximal to these directly in line with those of the first quartette (Fig. 12). The scattering of the tentacles evidently takes place later.

According to Allman's observations on *C. squamata*, the tentacles appear on the fixed planula in the same way; so that

there is in *Clava* a certain correspondence of methods of regeneration and normal development. This correspondence is not necessarily true for all hydroids, (*e.g.*, *Tubularia*, *p.* 46), which makes it important to determine the factors which lie behind the differences wherever they exist.

Fam. Corynidæ.

Trophosome. Hydranths spindle shaped, with scattered capitate tentacles, and a conical proboscis.

Gonosome. "Fixed sporosacs, or medusæ with a very long manubrium, four marginal tentacles and four sense bulbs with eye-spots." Nutting, 1901, p. 164.

Syncoryne.

Trophosome. Characters of the family.

Gonosome. "Free medusæ with a very long manubrium, four margina tentacles and four sense bulbs with eye-spots." Nutting, 1901, p. 164.

Syncoryne eximia Allman.

Coryne eximia, Allman, Ann. N. H., 1859 (3), IV, p. 141.
Syncoryne eximia, Allman, Ann. N. H., 1864, (3), XIII, p. 357. Nutting, Proc. Wash. Ac. Sc., 1901, III, p. 166.

Distribution. Pacific Grove, Cal. Juneau, Al. (Nutting). Gt. Britain (Allman). Lofoten Is., Norway (Sars).

Fragment of stem. No gonophores. Dec. 19, 1896.

Syncoryne mirabilis Ag.

Coryne mirabilis, Ag., Contra N. H. U. S., 1862, IV, p. 185.
Coryne rosaria, A. Ag., Ill. Cat., 1865, II, p. 176.

Distribution. San Francisco Bay, between tides, Atl. U. S. (Ag. and Clark). Spitzbergen (Marktanner—Turn.).

It does not seem to me that a separation of the western representative of this species from the eastern is advisable. The trophosomes agree in all points, and it is doubtful whether the medusæ are distinguishable.

As Agassiz has said concerning *S. mirabilis*, it lives either in the open sea or in brackish water in equal abundance. Corresponding with these extremes of habitat it lives in San Francisco Bay under two forms. The one grows at the entrance of the bay, upon rocks which are exposed to the breakers of the

open ocean; the other has been found upon wharf piling on the eastern shore of the bay, where the water is comparatively quiet, usually muddy and brackish. The former has the more vigorous appearance; the perisarcal tube is firm and is filled by the coenosarc; the stems reach the height of an inch, and may branch three or four times. The latter has a more delicate perisarc, from which the attenuated coenosarc has shrunk away. The branching is not profuse, but the branches are longer and are matted together in tangled masses not characteristic of the other form. The colonies from the Bay entrance possessed numerous medusæ Dec. 14, 1895. There were a few medusæ on colonies collected at West Berkeley (bay form) August, 1894.

Fam. Eudendriidæ.

Trophosome. Branching hydrocaulus, invested with perisarc. Hydranths more or less ovate with a single whorl of filiform tentacles; proboscis abruptly differentiated from the body.

Gonosome. Gonophores fixed sporosacs.

The integrity of this family can no longer rest solely upon the shape of the proboscis. In *Hydractinia milleri* the proboscis represents a condition transitional between the conical and trumpet shaped types. In combination, however, with the non-fusiform hydranth and the branching hydrocaulus, the limits of the family are still sufficiently well marked.

Eudendrium.

Trophosome. Same as for family.

Gonosome. Male gonophores polythalamic, borne on body of hydranth in a whorl proximal to tentacles. Female gonophores monothalamic, less regularly distributed on hydranth body or stalk.

Eudendrium californicum, sp. nov.

Pl. II. Figs. 13, 14.

Trophosome. Stem stout, simple, reaching 140 mm. or more in length, in clusters of 6 or 8 from an encrusting platelike hydrorhiza. Each ascends in a very loose spiral, giving rise to branches at moderately frequent intervals in all planes. These branches first bend away from the stem at a wide angle, turning upward near the tip. The branches are usually less than 20 mm. long, of nearly the diameter of the stem and branching similarly, though their branches (secondaries) tend to bend toward the distal end of the colony. Hydranths, with 20–22 tentacles, borne on secondaries, though one fertile hydranth may appear at times near the base of a primary. Color of hydranths flesh pink.

Gonosome. Perisarc annulated regularly in narrow annulæ on stem and branches, extending as a thin expansion upon the bodies of the hydranths to the bases of the tentacles. Very dark brown, may be almost black. Female gonophores monothalamic, crowded on the body of the hydranth immediately proximal to the tentacles; each gonophore usually with one ovum to which its orange color is due. Male gonophores dithalamic, in two or three whorls just proximal to tentacles; a delicate pink with small green spadix. Gonophores of both sexes invested with perisarc.

Distribution. Entrance of San Francisco Bay; Tomales Bay, Cal.; Pacific Grove, Cal., between tides.

This species resembles *E. vaginatum* closely, but differs in the distinctly narrower annulation of the perisarc, and the habit, which is much freer and more graceful, though the branches are quite rigid. The annulation agrees perfectly with that figured by Clark ('76) for a hydroid from Santa Cruz; this, with his description and the fact that *E. californicum* occurs both north and south of Santa Cruz, removes any doubt in my mind that his species is identical with the latter, rather than with *E. vaginatum*. It is probable that *E. pygmæum* Clark ('76) is a synonym of *E. vaginatum*, as Nutting suggests.

Colonies with female gonophores were collected during November, December, January; male gonophores were seen in January, 1902.

It is clear from Fig. 14 that the gonophores are borne on young but fully formed hydranths which may not lose their tentacles as the gonophores develop. Often the gonophores become so numerous as to crowd the tentacles, which are then usually more or less concealed; but in no case that I have examined are they wanting.

Eudendrium rameum Pallas.

Tubularia ramea, Pallas, Elenchus Zoophytorum, p. 83.
Eudenrium rameum, Johnston, Brit. Zooph., 1847, p. 45.

Distribution. San Pedro, Cal. Mediterranean, Norway, Great Britain (Allman). Jan Mayen (Marktanner-Turneretscher).

The hydroid which I have referred to this species, hitherto unrecorded for the Pacific Coast, reaches a length of 11 cm. The stem is polysiphonic, the perisarc heavy and brown. Branches appear irregularly but tend to lie in one plane, more or less alternate. Secondary branches approximately alternate, in planes

at an angle of 120°. Tertiaries arise similarly on secondaries and may branch. All branches with 2–5 rings at the base, though not always sharply marked. Hydranths usually on the distal side of the branches; tentacles 24–27, in one whorl; prominent nettle cells in a close spiral on each tentacle; hypostome trumpet shaped.

Gonosome absent (December, 1901).

Growing at the surface, on a float at the ferry landing.

Eudendrium ramosum Linn.

Tubularia ramosa, Linn., Syst. Nat., ed. X.

Eudendrium ramosum, Ehrenberg, Corallenth. des r. Meeres. Abh. Berl. Ac., 1832, p. 296. Allman, Gym. Hyd., 1871, p. 332.

Distribution. Pacific Grove, Cal. Great Britain (Allman). Adria, Rovigno, Jan Mayen (Mark. T.)

The gonosome is not present, but the trophosome agrees in all details, save size, with the description and figure in Allman's monograph. Length of tallest stem 35 mm.

Not previously reported from the Pacific Coast.

Fam. Hydractiniidae.

Trophosome. Two sorts of persons: clavate or cylindrical naked hydranths arising from the encrusting hydrorhiza, with a circlet of filiform tentacles and a conical or clavate proboscis; spiral zooids, usually at the edge of the colony. Hydrorhiza may be beset with spiny processes.

Gonosome. Sporosacs borne upon more or less specialized hydranths.

Hydractinia Van Ben.

With the characters of the family.

Hydractinia milleri, sp. nov.

Pl. II. Figs. 15, 16, 17, 18, 19, 20.

Trophosome. Sterile hydranths with 8-20 filiform tentacles, which in contraction may be seen to be arranged in closely approximated alternating series of four each around the base of a clavate (in contraction subconical) proboscis. Larger ones 3-5 mm. long (preserved specimens). Spiral zooids at the edges of the colony about as long as the sterile hydranths, but much more slender; end knobbed, the whole structure resembling a very long tentacle. Processes from the encrusting hydrophyton, tubular without spinules or coenosarcal investment, ½-1 mm. in length.

Gonosome. Fertile hydranths, usually not more than one half as long as sterile ones and more slender, with 3-8 filiform tentacles around the base of a long clavate proboscis, with a terminal mouth. Sporosacs borne on hydranth about midway between base and tentacles. Male sporosacs

spherical with small spadix; female smaller, slightly elongated, with distally extended spadix, and containing one, or at most, two eggs.

Distribution. San Francisco Entrance; Tomales Bay, Cal.

This hydroid grows commonly in patches sometimes several square inches in extent on rocks exposed to the breakers of the open sea, between tidal limits. The color of the hydranth and male gonophore is a very delicate pink; the female gonophores are of a faint orange due mainly to the yolk in the egg. The perisarc of the hydrophyton is of a dark horn color. Each gonophore has a separate origin from the fertile hydranth. I have never seen more than four on the same hydranth.

This species is readily distinguished from the eastern *H. polyclina* and European *H. echinata* by the tentacles on the fertile hydranths, the smooth tubular processes from the hydrorhiza, and the small number of eggs in the female gonophore. The sterile hydranths are much stouter than those of *H. polyclina*, with which I have compared them. The species is related closely to the *Stylactis fusicola* (Sars) of Allman. The latter has all the characters of *Hydractinia* save the spiral zooids and the coenosarcal covering of the hydrorhiza—both of which characters might have been easily overlooked. Sars originally described the species as a *Podocoryne*, from which genus it is excluded by the possession of fixed sporosacs. I feel, however, that Allman was hardly justified in removing it to his genus *Stylactis*.

The arrangement of tentacles in series of four each is of considerable interest. These series evidently represent successive generations of tentacles—though four do not appear simultaneously in all cases at least, since at the edge of a colony young hydranths often may be seen with three or five tentacles not of a uniform size.

This development in quartettes I have repeatedly observed in regenerating hydranths of *C. leptostyla*, and the same thing occurs in the egg development (Allman). In a recent paper Paul Morgenstern ('01, p. 567) shows that the first four tentacles in *Cordylophora*, a near relative of *Clava*, appear in twos at the same level. This is true also for *Syncoryne (Coryne) mirabilis* Ag. I have found that the regenerated distal tentacles in

Corymorpha palma appear similarly to those in *Clava* up to the number of twelve at least. In embryos of *Tubularia* the first tentacles to be developed are two in number and opposite. The distal tentacles develop in fours. In regenerating, however, both proximal and distal tentacles appear in considerable numbers simultaneously and in a peculiar manner. Possibly the conditions under which regeneration takes place have determined the method of regeneration in this case. There is a wide discrepancy here between this method and the one employed by the related *Corymorpha*, where the distal tentacles appear in fours and as buds, not ridges. The appearance of the tentacles in *Hydra* has been variously reported. In one case, in a *Hydra* bud two opposite tentacles appeared simultaneously, then a single dorsal one, followed by a ventral one, completing the quartette.

Another form is worthy of note in this connection — the *Bimeria robusta* of San Pedro. The tentacles of the budding hydranths in this species appear in *fives*, there being usually two complete whorls of five tentacles each, and another with from one to three. In the adult condition the whorls are almost indistinguishable except by the habit of carrying the tentacles alternately raised and depressed. I venture to suspect that the related *Perigonimus* may develop on this plan, a view supported by Allman's figure of *P. repens*. There may be here a criterion for the determination of larger groupings of far more moment than the fixed or free habit of the gonophores.

But it is quite impossible at present to establish certain phylogenies on this basis. I shall refer more in detail to the growth of tentacles in discussing the species concerned.

The exceptional shape of the proboscis of *H. milleri* should be emphasized, as it is of some taxonomic importance. It is usually long, and especially prominent in the fertile hydranths where it is set off from the body of the hydranth by a narrowed base and is swollen distally. Even in cases of extreme contraction, which are common among the sterile hydranths, this swollen extremity preserves its identity (Pl. II, Fig. 18). In no case have I seen what might be called a typically conical proboscis. The shape is clearly intermediate between the conical and the trumpet shaped types, the latter of which is so characteristic of the *Eudendriidæ*.

Fam. Pennariidæ.

"Hydrocaulus branched or unbranched. Hydranths much enlarged proximally with one ring of large filiform tentacles about the base and with another set of capitate or filiform tentacles distributed irregularly or regularly. Proboscis conical, short, and not distinctly limited but passing gradually into the hydranth. Gonophores in the form of medusæ or of sporophores." (Calkins, '99, p. 335, translated from Schneider, '97.)

Corymorpha.

Trophosome. Hydranths solitary, rooted by filamentous processes; with several whorls of closely set distal and one whorl of larger proximal filiform tentacles. Cavity of stalk in the shape of a number of superficial longitudinal canals of equal size. Perisare thin, non-supporting.

Gonosome. Gonophores borne between proximal and distal tentacles, medusiform, fixed or free, with four radial canals and one to four tentacles, all of which may be rudimental.

Corymorpha palma, sp. nov.

Pl. II. Fig. 21.

Trophosome. Stem 2–4 inches long, rooted in the sand by a dense tangle of filamentous processes and covered by perisare proximally for $\frac{1}{3}$ or $\frac{1}{4}$ its length. Thickest near proximal end, tapering gradually into a narrow neck which supports the hydranth. Hydranth with 18–30 proximal tentacles in one whorl, with a span of an inch or less; distal tentacles more than twice as numerous, more or less irregularly placed around the mouth in several whorls.

Gonosome. Gonophores medusoid, permanently fixed to peduncles springing from the base of the proboscis just within the whorl of proximal tentacles; each with a ring canal, four radial canals, and a manubrum at least twice as long as the bell, without a mouth; tentacles, wanting; velum may be present or absent.

Distribution. San Pedro, Cal., throughout the year; between tides.

This species resembles the eastern *C. pendula* closely, but differs in lacking all but the merest rudiments of tentacular processes on the medusa bell, which is much shorter, relatively to the manubrium, than in *C. pendula*. Nor is the color a "bright pink" (Agassiz), it being an extremely delicate pink, if it can be said to have any color at all in hydranth and stem. The endoderm of the gonophores is usually furnished with green color bodies.

I was long in doubt as to whether the gonophores ever became free. On individuals collected in summer and winter months,

gonophores were always present in various stages of development ranging from the earliest appearance of buds to medusoids with long manubrium and pulsating bell. This pulsation seemed to indicate that the medusa was ready for liberation and was attempting to free itself. Yet these apparent struggles for liberty have continued, in aquaria, for more than ten days, without success. The bell finally shriveled away, leaving entirely naked the long mouthless manubrium. I have never seen a medusa detach itself nor were they seen to my knowledge in the tow taken daily in San Pedro Harbor during the latter part of May, and the entire months of June and July, 1901, although I have seen eggs on the manubrium of different attached medusæ during the same months.* The individuals examined in December had no sexual cells, which makes it probable that the breeding season is limited to the warmer months of the year.

The perisarc surrounding the lower part of the stem is thin and flexible; this invested portion of the stem is more transparent than the rest, and its ectoderm contains very few scattered nettle cells, compared with the many that appear at once as soon as the distal edge of the perisarc is passed and cover the rest of the stem.

C. palma inhabits sand and mud flats between tides, often thickly covering patches many square yards in extent. The filamentous rootlets by which it is anchored, arise as outpocketings on the proximal coenosarcal canals, under the perisarc. These small processes, or frustules (Allman), may occur regularly in pairs on each canal, or they may be more or less scattered or alternately arranged. There are usually not more than eight pairs on each canal, rather closely associated. The proximal ones are longest. Each process in elongating grows downward for some distance, closely applied to the stem in the manner of a stolon as though responding to a thigmotactic stimulus. The enlarged

* Since this paper was sent to press eggs of Corymorpha have been laid in the the laboratory (in May, June, and July, 1902). They drop from the manubrium of the attached medusa, and stick by their adhesive coat to whatever they first touch. There is no free swimming larva. Often the young are clustered on the root filaments of old hydroids. The new species of Tubularia recently described by Hargitt (Am. Nat., July, 1902) is undoubtedly based on such clusters of young individuals of Corymorpha. Buds of the peduncles which support the medusoids appear very early. I shall describe the development more fully in another paper.

free end is connected by a much attenuated stalk to the place of origin. It finally turns outward, investing itself with perisarc and may attain to the length of an inch, penetrating between and adhering to sand grains. The longest processes are usually nothing but perisarc, the attenuated coenosarc having disappeared.

The characteristic attitudes of the expanded hydroid are somewhat different from those of *C. pendula*. It is oftenest perfectly erect, in quiet water, the plane of the tentacles being slightly tilted from the horizontal. It may bend downward, however, in which case the arching includes the greater part of the stem. I have never seen it assume the pendulous attitude shown in Agassiz's figures of *C. pendula*.

Orientation. A few simple experiments demonstrated that the erect posture of the stem was assumed in response to a geotropic stimulus. To determine relatively the specific gravity of different parts of the polyp, the basal tufts of sand-incrusted filaments were cut from several polyps and the latter were placed in an aquarium. They sank directly to the bottom, distal (hydranth) end foremost. Then several other polyps, together with two polyps with proximal filaments removed, were put into a jar filled with water so that all but a small bubble of air was excluded when sealed. When the rooted polyps had assumed erect postures the jar was transferred to a dark closet and tilted at an angle of 45°, the polyps remaining parallel to the sides of the jar. In an hour all the polyps had become erect. The jar was righted, and within another hour the polyps had oriented themselves again in line with the pull of gravity. The polyps without basal filaments did not change their position materially during the whole experiment, without doubt because they lacked a proximal point of support.

There was no difference in the result when the experiment was performed in the light or in darkness. To determine whether light exercised a directive influence, several polyps were exposed before a window, so screened that the light came from one direction only. At the end of three hours, no effect on their attitudes was visible. Light thus appears to be without influence as an orienting factor, and the following experiment was performed in the day light.

Two individuals were suspended by a string so that the stems pointed directly downward. Within seven hours both had assumed horizontal positions. At the end of thirty hours one was bent sharply upon itself so that the distal four-fifths of the stem was vertical, the knot by which the animal was tied interfering with the assumption of a vertical position by the entire stem; the other polyp was extended upward at an angle of 45°. On the following day both were as nearly vertical as the knot would allow; and so they remained until released several days later.

To determine whether the sensitiveness to the stimulus of gravity was local or general, three polyps were transversely sectioned, the first just below the hydranth, the second half way down the stem, the third near the base. They were placed in the dark in an airtight jar, which was set at different angles as in the first experiment. Like results followed. Each piece responded, the shortest taking the longest time to become erect, the longest one the shortest time, but all finally arranging themselves in line with the pull of gravity.

To determine whether the muscles of the stem or the vacuolated endoderm cells (skeletal cells) respond to the stimulus of gravity, the following experiments were made. An individual was decapitated, and cuts were made on one side at three levels, half through the column, thus destroying the continuity of the muscle layer on that side in three places. The muscles contracted between the wounds, causing them to gape; the gaps were soon filled by skeletal cells. The column bent toward the side opposite the wounds showing the greater potency of the uncut muscle layer. When, however, it was laid upon the bottom of the aquarium, wounded side uppermost, it assumed an erect posture in about an hour—moving toward the muscularly weaker side.

Another individual was cut in a similar manner, though there were eight or ten cuts, alternately on one side and the other. These cuts interrupted the continuity of the muscle layer on the entire circumference except for very short distances. The column lay quite limp on the floor of the aquarium immediately after the operation. Within two hours, however, it had stiffened into an erect posture, though the wounds had not closed.

These experiments seem to demonstrate what was suggested by the slowness of the orientation of the normal individual and the method of lengthening the stem by increasing the turgescence of the skeletal cells (since the diameter may increase at the same time) viz., that the skeletal cells alone are susceptible to geotactic stimulation, the muscles producing only such comparatively rapid movements as the contraction of the tentacles and the proboscis, and the bending of the column away from the perpendicular against the stimulation of gravity.

Response to tactual stimulation. A vigorous stimulus, such as a pinch by forceps, results in a contraction of the stem within two seconds, whether the stimulus is applied to a tentacle or the proboscis or the proximal or distal portion of the stem itself. Only that part of the stem contracts that is not invested in perisarc, though the perisarc seems to be too thin to be an effective hindrance to contraction in the basal region. The fact may be formulated in this way: A vigorous stimulus applied in any region of the body produces a definite localized response. The phenomenon reminds one forcibly of the behavior of *Mimosa* under stimulation, and is due to the same immediate cause—a change in the turgescence of certain large vacuolated cells, which in *Corymorpha* form the axis of the stem.

A stimulus too slight to produce any reaction when applied to the stem, may be effective with a tentacle. The tentacle may respond at once and independently of all the others, by shortening slightly, and waving toward the proboscis. This reaction is the same, whether the stimulus be applied to the tip or base, upper or lower side. If the stimulus be increased, all the tentacles may contract, without any evidence of response in the stem.

These reflex movements indicate the presence of a co-ordinating mechanism which appears to have adaptive value for the prehension of food and for protection.

Regeneration. C. palma regenerates certain lost parts with great readiness. Pieces of the stem produce remarkable cases of hetermorphosis, which will be considered in another paper. A few of the facts connected with the regeneration of the hydranth may be mentioned here.

Proximal and distal tentacles appeared on several regenerating

pieces of the stem in the following manner: The proximal tentacles, averaging about twenty-four in the adult, arose as buds, in two series. The tentacles of the first series appeared simultaneously to the number of seven to fourteen, the number being conditioned apparently by the diameter of the stem and the number of canals in it; a tentacle arose on each canal. The tentacles of the second series appeared singly, between the tentacles of the first series, some time after the latter.

The distal tentacles are filiform in the adult, and are scattered and more numerous than the proximal ones; in small regenerating pieces they are somewhat capitate at first and arranged more or less regularly in whorls of four (quartettes), each whorl being proximal and alternating with the one immediately preceding it. The tentacles of the several whorls did not develop simultaneously. They may appear one at a time, in no order that I have yet determined; but their arrangement in quartettes in the first two or three whorls seems to be certain.

The bearing of these observations upon the question of the affinities of *Corymorpha* is important. The young regenerated hydranth of *C. palma* is essentially identical in form with young hydranths of *Pennaria* and *Tubularia.** Each possesses a flask-shaped body, a whorl of filiform proximal tentacles and one or more quartettes of capitate distal tentacles. This agreement supports the view of Schneider, which has been adopted by Calkins ('99), and with which I am in accord, that the *Tubularidæ* and *Pennaridæ* should be united to form but a single family, since the capitate or filiform character of the distal tentacles offers hardly sufficient ground on which to base a distinction between families. The *Tubularidæ* as here used include both the *Corymorphidæ* and *Hybocodonidæ* of Allman ('71) and later authors. For the *Hybocodonidæ* have been distinguished from the *Tubularidæ* only by the possession of free swimming medusae, those of the latter family being permanently attached. The difference is of minor importance. Moreover, *Tubularia couthouyi* and *Corymorpha palma* should hardly be placed in distinct families on account of differences in extent of perisarc, and character

*With the uncertain *Vorticlava* Alder and *Acharadria* Wright also, which lack the gonosome and are probably immature forms.

of root filaments, the only respects in which they differ conspicuously. It is because of the transitional condition of these filaments in such forms as *Tubularia couthouyi* that we are able confidently to interpret those of *Corymorpha* as homologous with the creeping hydrorhiza of other forms.

It may be mentioned that peripheral canals and a solid endodermal axis are present in *T. couthouyi* and *T. indivisa*, as well as in *Corymorpha*. This condition seems to be a direct adaptation to size, since all three species have exceptionally large diameters.

Tubularia Linn.

Trophosome. Hydrocaulus usually unbranched and rising from a creeping hydrorhiza; both completely invested with perisare. Hydranth with two sets of filiform tentacles.

Gonosome. Gonophores fixed, more or less medusoid.

Tubularia crocea (Ag.).

Pl. II. Figs. 22, 23.

Parypha crocea, Agassiz, Contr. N. H. U. S., IV, 1862.
Parypha microcephala, A. Agassiz, Ill. Cat., II, 1865.
Tubularia crocea, (Ag.), Allman, Gymn. Hydr., 1871.

Distribution. San Francisco Bay, San Pedro Harbor, San Diego Bay, Cal. Eastern U. S. (Ag.).

This species is essentially a brackish water, harbor form. It has been recorded already for San Francisco, Cal., by Alex. Agassiz, in his Illustrated Catalogue ('65) under the name of *Parypha microcephala*. Agassiz distinguished it from *P. crocea* in the belief that it had a more slender stem and smaller head. Numerous observations on the living animals from Oakland Harbor, at different times of the year, have demonstrated to me that these characters are not constant; and I cannot find any others upon which to base a separation of the western from the eastern form. According to observations made at San Pedro during December, on living animals, the tentacular processes on the female gonophores are eight in number, though they may vary greatly in size and shape, appearing at times as little more than small welts about the bell mouth. L. Agassiz says of the male gonophores: "The male medusoids never have any tentacles, nor do they deviate from an almost perfectly spherical

shape." Fig. 15, Pl. XXIII of his work, however, shows a raised welt at the edge of the bell mouth, divided by radial wrinkles into a number of rudimentary processes. Fig. 22 of the present paper represents a male gonophore drawn at San Pedro from life, on which there are eight unmistakable flattened tentacular processes. It does not represent the condition in all male gonophores, however, for these tentacular processes vary in size almost to the vanishing point. The shape of the bell is not constant, either, though varying far less than that of the female gonophores. All of these variations in size and shape are due either to different degrees of contraction—which applies especially to the tentacular processes; or to the nature of the contents—which applies especially to the shape of the gonophores. The female gonophores are less symmetrical than the male only when they become distorted by the growth of the contained embryos, which often number four or even more.

I have seen actinulæ liberated at Oakland in September and at San Pedro in July, August and December. Specimens dated May 10, 1898, in the University of California collection, have heavily loaded male gonophores.

In midwinter, headless stems only are found ordinarily in Oakland Harbor. At the same time of year the species is growing luxuriantly at San Pedro where it is found the year round. The difference is perhaps to be explained by a difference of habit. The headless stems in Oakland Harbor are attached to fixed supports, such as the piles of wharves and bridges, sometimes as many as three feet above mean low water mark. Consequently they are exposed to the air at least once a day, at ebb tide. On the other hand, the San Pedro colonies which grow so luxuriantly the year round are attached as a rule to floating timbers, unused barges and other floating supports; consequently they are never uncovered at ebb tide. It is possible that the severity of the diurnal change to which the Oakland colonies are subjected during the winter is the cause of the loss of the hydranths. Whether well formed colonies continue below mean low water through the winter I cannot say positively, but so far as I have been able to see from the surface at low tide, they do not. If they do not, then it is probable either that the temperature of water is too low

for them, or that they do not grow during any season below mean low water mark. From their prevalence on floating supports, near the surface and hence near the oxygen supply—usually a position of great advantage in harbor water, so constantly fouled with sewage and other dirt—I suspect the latter to be the more probable alternative.*

A word might be added with reference to S. F. Clark's species, *Tubularia elegans*, collected on the piles of a wharf in San Diego Bay. Clark's description would suffice for *T. crocea*, with two exceptions: 1. There are "about thirty tentacles in the proximal set" in *T. elegans*, while I have never seen more than twenty-five by actual count in *T. crocea*. 2. Instead of several flattened tentacular processes around the mouth of the gonophore, there are four conical tubercles crowning the larger gonophores, which Clark has figured.

The first difference is of little consequence, since "about thirty" might mean twenty-five. The second is more important, and I would not have been led to doubt the validity of Clark's species, had I not found in the University of California collection several colonies of *T. crocea* from Coronado. In some of the female gonophores, the tentacular processes are much contracted and might be judged without careful observation to be conical and fewer in number than they really are. Clark's material was very poor, being in "the same delapidated condition" as a *Bimeria* (?) packed with it, whose "hydranths and sporosacs especially were in a very worn and mutilated state." These facts make it evident that Clark's figure is rather diagrammatic and that he did not have sufficiently well preserved material to be certain of the tentacular processes. For these reasons I am of the opinion that *T. elegans* will prove to be a synonym of *T. crocea* Ag.

Regeneration. Regeneration of pieces of the stem occur in the way already known for *T. mesembreanthemum*. Both distal and proximal sets of tentacles first appear as welts or ridges on

*Since every colony arises from a single actinula, its position must be determined by the influences that control the movements of the actinula during its free existence. It would be interesting to know whether these influences include any of the tropisms, for instance, geotropism and chemotropism (with respect to oxygen.)

the coenosarc. The proximal set has about one-half (12) its adult number; the distal approximating their final number quite closely (15–18). This regenerative process, interesting to the naturalist because among other reasons it occurs constantly in nature, is doubly so because it departs so widely from the method of development of the tentacles in the egg embryo. In the latter the tentacles arise as buds, not ridges. The distal tentacles appear in successive alternating whorls of four each (quartettes). The proximal arise in a less orderly fashion, one or two at a time; probably a secondary modification of the quartette type, since the first two tentacles are opposite, and the actinula has a symmetrical eight tentacle stage. Both proximal and distal tentacles are capitate for a time, which is true also for *Pennaria* and the regenerated distal tentacles of *Corymorpha*. The questions of relationship which these facts suggest have been considered in another place (p. 42).

There is at present no explanation for this difference between regeneration and embryonal development. Driesch ('01) has seen the tentacles appear as ridges on a small naked piece of Tubularia stem which seems to exclude the possibility that confinement within the perisarc might be the determining factor. The question needs further investigation however.

Tubularia marina, sp. nov.

Pl. III. Figs. 24, 25.

Trophosome. Stems rising in clusters, from a creeping hydrohiza to a height of 30–50 mm.; moderately stout, unbranched, increasing in diameter distally; more or less annulated; annulæ more frequent and regular in proximal half. Hydranths with 22–26 proximal and 18 distal tentacles.

Gonosome. Colonies dioecious. Gonophores in about ten pendulous racemose clusters which may be as long as the proximal tentacles, and contain more than twenty gonophores each, in well developed specimens. Male gonophores very broadly ovate with four small apical processes slightly flattened laterally. Female gonophores more narrowly ovate than male, with four stout, stiff tentacles with bulbous bases, sometimes forking near their ends and as long as the gonophore. Actinulæ (S. F.).

Distribution. Trinidad, (June), San Francisco, (Dec., Jan., Feb.) and Pacific Grove, (Dec.) Cal.

This species is easily recognized by the unusually long tentacles on the female gonophores. A. Agassiz, in his Illustrated

Catalogue ('65, p. 196), has mentioned a species of Tubularia which he calls *Thamnocnidia tubularoides*, and which is characterized by the "stoutness of the stem and size of the head, surrounded by as many as from thirty and even forty tentacles in large specimens. Found growing profusely on the bottom of the coal barges which bring coal from Benicia to the Pacific Mail Company's steamers at San Francisco." This description is very meagre, but is sufficient, I think, to show that it does not refer to the species I have just described. *T. marina* is in no sense a harbor species, but grows between tides on the lee side of rocks exposed to the breakers of the open sea. Its head is not noticeably large as compared with *T. crocea*, and the largest number of tentacles I have seen is twenty-six, on one occasion only. The female gonophores are so characteristic that I feel sure they would have been described in Agassiz's notes had he seen them. I have not seen any hydroid in the bay corresponding to his description.

The nearest relative of this species on this coast appears to be *T. harrimani* Nutting, from which it may be distinguished by the much smaller number of proximal tentacles, and the greater length of the tentacles of the female gonophores.

CALYPTOBLASTEA.

Hydroida with true hydrothecæ and gonothecæ. Gonophores when free usually with otocysts; gonads on radial canals.

Fam. Haleciidæ.

Trophosome. Hydrothecæ arranged alternately on hydrocaulus, shallow, saucer-shaped, incapable of containing the large hydranths in contraction, margin smooth; hydranth with conical proboscis and one whorl of filiform tentacles.

Gonosome. Gonophores sporosacs or medusoid.

Whether the Haleciidae are primitive or highly modified Calyptoblastea is a problem that is at present without an altogether satisfactory solution. The hydranth-bearing blastostyles and reduced hydrothecae place them near the Gymnoblastea. The presence of sarcostyles (*Diplocyathus* Allman) and a row of bosses on the inner surface of the theca are characters of the highly specialized Plumulariidae (cf. *P. plumularoides*). Sessile

hydrothecae are characteristic of both Plumulariidae and Sertulariidae. The mode of branching, while exhibiting at times a certain irregularity suggestive of the Gymnoblastea, most nearly approaches the type of branching in the Campanulariidae, which family the Haleciidae further resemble through such forms as *Diplocyathus dichotomous* Allman, in which the hydrothecae have rudimentary stalks, and *Campalecium medusiferum*, described below, in which the gonotheca contains a series of medusoid gonophores.

This union of the characters of the various families of the Calyptoblastea is strong support for the view, which I am disposed to adopt, that the Haleciidae stand nearest of them all to the ancestral Gymnoblastea.

Campalecium, gen. nov.

Trophosome. As in *Halecium*.

Gonosome. Gonothecae each with a blastostyle bearing several medusoid gonophores.

This genus bears a relation to *Halecium* similar to that between Gonothyraea and Campanularia. The distinction is not a sharp one, being based on the degree of degeneration of the gonophores, yet it is serviceable in the absence of intergrading forms.

Campalecium medusiferum, sp. nov.

Pl. III. Figs. 26, 27, 28, 29.

Halecium tenellum, Clark, Trans. Conn. Ac., 1876, III, p. 255.

Trophosome. Stems short (5-10 mm.), sparingly and irregularly branched, rooted by a creeping stolon. Hydrotheca with strongly everted rim. Hydranth large, with low conical proboscis and 24 to 28 tentacles in one whorl.

Gonosome. Gonotheca on short peduncle arising just below a hydrotheca; about three times as long as broad; broadest at distal end which is truncate, tapering gradually to the peduncle. Orifice not determined. Gonophores 2 to 5, in linear series, medusoid, with 4 tentacles developing in pairs which differ in size, and a conical manubrium.

Distribution. Long Beach, Cal., in 6 fathoms. Bottom covered with Nitophyllum. July 6, 1901.

The material consists of a few stems on a stolon which was tangled round the bases of stems of *P. setacea* and *S. halecina*. The skeletal characters agree closely with Hincks's description of

H. tenellum, but the medusoid gonophores constitute an important difference in the gonosome. Whether the gonophores are ever liberated as medusae I have no means of knowing at present. Their development to an advanced stage, however, before definitive sex cells appear (they are not present in any of the gonophores) and before the gonotheca containing them has obtained an external opening, is a condition of affairs usually associated with the formation of free medusae—as yet unknown among the Haleciidae.

The species which Clark ('76) identifies with *Halecium tenellum* Hincks is in all probability *Campalecium medusiferum*.

Halecium.

Trophosome. No sarcostyles. Other characters those of family.

Gonosome. Female blastostyles usually bear two distal hydranths. Gonophores sporosacs.

Halecium annulatum, sp. nov.

Pl. III. Figs. 30, 31.

Trophosome. Stems rising from a creeping stolon to a height of 7 mm.; the longer have two or three regularly alternating branches. Stem and branches more or less regularly annulated throughout. Hydrothecae may be half as deep as broad; margin everted. Sessile hydrothecae alternately on either side of stem or branch; peduncles arising within these carry other hydrothecae which may also give rise to other peduncles.

Gonosome. Female gonothecae broadly ovate, excessively compressed, with terminal aperture. Single gonophore with numerous ova, surrounded by blastostylar processes reaching to gonothecal wall.

Distribution. South of Coronado, Cal.; 10-fathom line; eel grass. Growing on seaweed. July 6, 1901.

Halecium kofoidi, sp. nov.

Pl. III. Figs. 32, 33.

Trophosome. Colony with a thick trunk from which branches arise irregularly, forming a sparse tuft 1½ inches high. The branches may branch again; from these secondaries the ultimate branchlets grow, alternating regularly on either side of the branch. All branches are divided obliquely into internodes of approximately equal length. Each internode usually bears on a shoulder at its distal end a sessile hydrotheca which does not reach beyond the distal internode. Within this hydrotheca another may arise on a short stalk, and within the latter still another on a similar stalk. These stalks are somewhat constricted at the base, and bend away slightly from the stem. Occasionally a stalked hydrotheca arises directly from the internode without the interposition of a sessile hydrotheca. There may be

one or two wavy annulations at its base. Secondary and ultimate branches arise from the bases of hydrothecae.

The wall of the hydrotheca is especially thickened, the interior contour in profile being convex while the outer one is straight. There is a circle of bosses of variable number and arrangement around the inner surface of the wall.

Gonosome. Male gonothecae present. When mature they are long, oval, smooth, three to four times as long as broad, each attached just below a hydrotheca by a short pedicel which may have one or two faint annulations. The base of the gonotheca may have a wavy outline. Small terminal aperture.

Color of stem and base of branches brown. Coenosarc in poor condition.

Distribution. Off Point Loma, San Diego, Cal., bottom of sand and cobbles; harbor in 5 fathoms; Catalina I., in 42 fathoms.

Halecium nuttingi, nom. nov.

Halecium geniculatum, Nutting, Proc. U. S. Nat. Mus., XXI, p. 774.

Distribution. Dredged off Pt. Loma, San Diego, Cal., July, 1901; sandy, cobbly bottom. Puget Sound (Nutting).

The single colony of this species in the collection agrees with Nutting's description in every detail save the number of tentacles (18–24 instead of 16–20), and the fasciculation, which is prominent on the stem, larger branches and bases of the smaller branches; the gonosome is absent also. Several stems of varying lengths, the longest 40 mm., arise from a stolon creeping over a fragment of seaweed frond. On the longest stem two stemlike branches are borne. On each of these and the stem, secondary branches of irregular lengths—none more than 10 mm.—arise alternately on either side in approximately the same plane. These may branch again. The non-fascicled branches are more or less regularly annulated at their bases. Only the ultimates are geniculate. Occasionally they acquire annulations similarly to those of *H. annulatum*, from which they can be distinguished by the larger size of hydranth and diameter of branches.

The specific name given by Nutting had been used already by Norman for a British species of *Halecium* (Rep. Brit. Assn., 1866, p. 196), so I have taken the liberty of substituting Dr. Nutting's own name in its stead.

Fam. Campanulariidae.

Trophosome. Hydrothecae well developed, pedunculate, non-operculate, with septum at base.

Gonosome. Gonophores free medusae or fixed.

Campanularia.

Trophosome. Colony regularly branching or unbranched, simple or polysiphonic; hydrothecae campanulate.

Gonosome. Gonophores fixed sporosacs.

Campanularia denticulata Clark.

Pl. IV. Fig. 34.

C. denticulata, Clark, Proc. Ac. Sc. Phil., 1876, XXVIII, p. 213.

Distribution. San Pedro Harbor, on float at ferry landing. Port Etches, Al,, dredged 10–18 fathoms; clayey mud (Clark).

The San Pedro colonies agree with Clark's description with the one exception that they branch. The Alaska form lacks a gonosome and is probably immature.

The branches bearing hydrothecae are completely ringed, with 5–15 rings. They arise in all planes. Above each axil the main stem has 3–8 rings. Below and opposite the origin of the hydrotheca there is a definite knee. The stem is straight between knees; as a whole not flexuous. Hydranths with 22 tentacles. Hydrothecae .65 mm. x .36 mm.; .75 mm. x .47 mm.; 1.00 mm x .45 mm. Tallest stem 20 mm. Gonosome absent.

Campanularia everta Clark.

Pl. IV. Figs. 35, 36, 37.

C. everta, Clark, Trans. Conn. Ac., 1876, III, p. 253.

Distribution. Catalina I., 42 fathoms; San Diego, 1–24 fathoms, fine sand; Pacific Grove, Cal. San Diego (Clark). Growing on seaweed. July, 1901.

This is an exceedingly variable species. The rim of the hydrothecae may or may not be everted; it is usually, but not always crenate. The wall of the hydrotheca may be very thick or very thin, and is either straight or convex in profile. The stem may be long or short, smooth, wavy or irregularly jointed. A constant feature is the presence of a spherical annula immediately below the theca. The gonotheca is somewhat compressed,

ovate, with a small round terminal orifice. The wall varies in thickness and may be slightly wavy. Acrocysts containing three or four embryos were found on female colonies from Catalina. Male gonothecae are smaller than female.

Transitions between all the forms of hydrothecae can be traced in the same colony. The typical form is different, however, in different localities. As a rule the Catalina specimens have thicker walls than those from Pacific Grove, whose walls are often quite thin; the San Diego material is intermediate in this respect.

C. everta may be distinguished from *Clytia compressa*, which it closely resembles, by the gonosome only. The gonothecae have a much narrower aperture and the gonophores are fixed sporosacs.

Campanularia fascia, sp. nov.

Pl. IV. Fig. 38.

Trophosome. Height of longest stem, 45 mm. Branching irregularly and profusely, forming a coarse, shrubby tuft. Stem and branches polysiphonic; ultimates alone monosiphonic. Perisarc thin throughout, wrinkling easily. Ultimates wavy or ringed, never with more than two hydranths. Shorter hydranth stalks with 8-10 rings; longer with 9-11 at base and 5-8 immediately below hydranth, with wavy interval. Hydrothecae less than twice as long as broad, cylindrical in distal half, tapering gradually to narrow base. Rim with 11-12 moderately sharp teeth. Hydranth with 20-24 tentacles.

Gonosome absent.

Distribution. Pt. Loma, San Diego, Cal.; hard sand bottom. Covered with *Calycella syringa*.

Campanularia fusiformis Clark.

C. fusiformis, Clark, Trans. Conn. Ac., 1876, III, p. 254.

Distribution. Point Reyes Peninsula, growing on *Bimeria annulata;* Dillon's, Cal., on *Sertularia anguina.* Vancouver I., on *S. anguina.* Between tides.

This species resembles *C. urceolata* closely. The hydrothecae are deeper, narrower, with fewer and blunter teeth. The gonotheca often has a long neck. It may be sessile or raised on a peduncle with five or six annulae. Gonophores present July 7, 1898, and August 10, 1892.

Campanularia hincksi Alder.

Campanularia hincksii, Alder, Trans. Tynes. F. Club, 1857, III, p. 127.
Hincks, Brit. Hydr. Zooph., 1868, p. 162.

Distribution. Mouth of San Diego, Cal.; shallow water, shelly bottom. British coasts (Hincks), from 10–20 fathoms to deep water.

In the San Diego specimens the diaphragm is not so heavy as in Hincks's figures. The gonothecae may have 15–18 rings. July 13, 1901.

Campularia pacifica (A. Ag.)

Pl. IV. Figs. 39, 40, 41.

Laomedea pacifica, Agassiz, Ill. Cat., 1865, II, p. 94.

Trophosome. Stems stout, frequently reaching a length of 200 mm.; branching profusely, forming an exceedingly dense and bushy colony. Stem and larger branches polysiphonic; 2-4 annulae above the origin of each branch. Hydrothecae borne on pedicels of moderate length, usually annulated throughout; 5-8 annulae; deep, gradually tapering to base, rim with ten teeth, each with two cusps. Hydranth with 26 tentacles.

Ganosome. Gonothecae elongated, clubshaped, female somewhat broader than male; bottle neck and moderate round aperture. Gonophores fixed sporosacs.

Distribution. San Francisco Bay. Gulf of Georgia, Wash., and San Francisco, Cal. (Agassiz). Bering Str., Avatska Bay, Kamtschatka (Stimpson).

This is a common species in Oakland Harbor the year round, where it flourishes in the brackish and dirty water, attached to the supports of wharves and bridges, between tides. The branches arise in all planes, and with the exception of occasional stem-like branches, are short. Two usually appear at the same point, one at right angles to and much smaller than the other. Both rebranch profusely.

Gonophores are produced from March to November at least. They show no traces of bell. The endoderm of the manubrium is lobed as in *Gonothyræa* and serves as a nutritive organ for the sex cells. There may be six, eight or even more ova in the larger gonophores, which vary in number from four to twelve or fifteen.

Campanularia urceolata, Clark.

Pl. V. Figs. 42, 43, 44, 45, 46, 47.

C. cylindrica, Clark, Trans. Conn. Ac., 1876, III, p. 254.
C. urceolata, Clark, Proc. Phil. Ac. Sc., 1876, XXVIII, p. 215,
C. turgida, Clark, *ibid.*
C. reduplicata, Nutting, Proc. Wash. Ac., 1901, III, p. 172.
C. urceolata, Nutting, *ibid.*

Distribution. San Francisco, Tomales Bay, Pacific Grove, Cal., between tides. Yakutat, Al. (Nutting). Lituya Bay (9 fathoms) and Port Etches (12–18 fathoms), Al.; California (Clark).

The hydrothecae of this species are quite variable, the gonothecae somewhat less so. On the stolon (Fig. 42) two hydrothecae, one typical of *C. urceolata*, the other of *C. reduplicata*, may be borne side by side. These are the extremes. There are various gradations between them, corresponding to the typical hydrothecae of *C. cylindrica* and *C. turgida* as figured and described by Clark ('76). The gonothecae may be sessile or elevated on a pedicel of a few rings; always with small circular orifices. The walls are smooth or slightly wrinkled. There are numerous gonophores in each gonotheca.

A fact of some interest is the beautiful spiral annulation which appears on the hydrorhiza whenever it happens to grow for a space without touching the substratum. The hydrorhiza is smooth when in contact with the substratum (*Sertularia anguina* in the case of the San Francisco specimens). It is throughout its length twice the diameter of the stem. In one instance its free end had narrowed abruptly into a hydrotheca stalk with a hydrotheca at its extremity (Fig. 47). It seems clear that this striking heteromorphosis, and the change of form of the perisarc of the stolon are causally related to the presence or absence of a contact stimulus.

Campanularia volubilis (Linn.),

Pl. V. Fig. 48.

Sertularia volubilis, Linnaeus, Syst. Nat., XII ed., p. 1311.
Campanularia volubilis, Alder, Tr. Tynes. F. C., 1857, III, p. 125. Hincks, Brit. Hydr. Zoöph., 1868, p. 160. Hartlaub, Zoöl. Jahrb. Abth. Syst., Geogr. and Biol., 1901, XIV, p. 349. Nutting, Bull. U. S. F. C., 1901, XIX, p. 345.

Distribution. San Pedro and Tomales Bay, Cal. Bare I., near Vancouver, B. C. (Hartlaub). Gulf of St. Lawrence, 20–30 fathoms, (Packard). Massachusetts (Agassiz). "Off Reikiavik, Iceland, in 100 fathoms, amongst icebergs, on *Sertularia*" (Hincks). Norway (Sars). Mingan Is. (Hincks).

Dredged near San Pedro, Cal., from a sandy bottom covered with small stones and some kelp roots, in 9 fathoms. A single gonotheca, lost before it could be drawn, was much compressed. The margin of the hydrotheca is furnished with nine teeth and is frequently reduplicated. The colonies from Tomales Bay grew between the tides.

Gonothyraea clarki, nom. nov.

Gonothyraea hyalina, S. F. Clark, Proc. Phil. Ac., 1776, XXVIII, p. 215.

Distribution. Oakland, Cal. Alaska, 13–30 fathoms (Clark). Shetland (Hincks).

The form from Oakland Harbor agrees in all respects with Clark's description, save that the extracapsular medusoids are more nearly spherical than those of Clark's material. Male and female medusoids are of the same size and shape, the tentacles of the female being possibly a little longer. A feature which distinguishes this species from *G. loveni* is the absence of radial canals, though an endodermal lamella is present. The skeletal characters of the two are indistinguishable (Nutting). Hincks's *G. hyalina* was in all probability a form of *G. loveni*.

The ectoderm of the manubrium is very thin and may lie close to the subumbrella ectoderm so that the bell, lacking mesenchyme entirely, often appears in section to be composed of four extremely attenuated closely applied cell layers. The endoderm of the manubrium is a conspicuous layer of darkly staining columnar cells, showing signs of glandular activity and without doubt furnishing with yolk the ova which are pressed against it.

I have never seen a medusoid leave the gonotheca and do not know whether it actively aids itself or not. Certainly it does not move, so far as I have observed, after leaving the gonotheca. The blastostyle thins out as the medusoids leave, as though under a tension. But this tension could hardly be exerted by

the medusoids, which are motionless on the free ends of narrow blastostylar processes with no perisarcal covering.

I have seen neither tentacles on, nor fertilized ova in, intracapsular medusoids, though a great many observations have been made. In rare instances, an extracapsular medusoid is found with unfertilized ova. On one occasion a dancing mass of sperm was crowded around the bell mouth of an extracapsular medusoid, apparently attracted to that spot. It is here that the sperm probably penetrate, after the medusoid has left the gonotheca.

There may be four embryos in each female medusoid, which are retained until the planula stage.

There are usually four medusoids to the blastostyle in female, and five to seven in male colonies. Occasionally blastostyles with sterile medusoids are met with, such as those described by Weismann ('83). The cause of this sterility has not been determined, so far as I know. It is the more obscure because a whole colony is not always affected, but only here and there a blastostyle. The general external conditions of temperature, oxygen, light, food, etc., would seem to be the same for all parts of the colony; so that the cause is probably local, possibly malnutrition from some mechanical defect in the circulatory canals. Colonies in the University of California collection with medusoids taken in January, March, April, May, September.

Obelia.

Trophosome. All known species branched; otherwise as in Campanularia.

Gonosome. Blastostyles in axils of branches, giving rise to free disk-shaped medusae with four radial and a ring canal, eight lithocysts and more than eight tentacles; mouth without tentacles.

Obelia commissuralis, McCr.

Obelia commissuralis, McCrady, Gymno. Charls. Harbor, p. 95.
Agassiz, Contr. N. H. U. S., 1862, IV, p. 315.

Distribution. San Francisco Bay, Cal., between tides. Eastern U. S. (Agassiz).

This species has not been recorded previously for the Pacific Coast. The San Francisco specimens are identical with Agassiz's description of the Eastern form.

It is not an unusual thing to see the branches of *O. commissuralis*—and the associated *C. pacifica* and *G. clarki*—grown out into tendril-like processes. These appear so constantly in colonies confined in aquaria, or growing in dirty water or under other unfavorable circumstances, that there can be no doubt of a causal relation between their appearance and external conditions, though the definite cause is as yet obscure. The processes are usually attenuated, with very thin perisarc, and grow rapidly: 2 to 3.5 mm. in 24 hours. They may be ringed at intervals or smooth, and may be terminated by hydranths of proportionate size. They often behave like stolons. When one comes in contact with a solid substratum, it may cling to it. So long as it is in contact with the substratum it does not develop rings or end in a hydranth. The stimulus of contact, however, is not necessary to the transformation of these processes. While free they may not only remain smooth but give rise to buds at right angles to their own axes, just as attached stolons do. The growing point of each develops rapidly, while the hydrocaulus behind thins out and may degenerate completely. In this way a given area may be quickly occupied by colonies which have arisen non-sexually from a single one sexually produced. Here is a function of possibly adaptive value, its activity dependent, however, on appropriate external conditions.

It is apparent that the attenuated branches of these species have no phylogenetic significance, being explicable on physiological grounds. I have little doubt that the "long filiform tendrils" described by Calkins in *O. surcularis*, which bear "in some cases, one or two hydrothecae" are in the same category and have no value as specific characters.

Obelia dichotoma (Linn.).

Sertularia dichotoma, Linnaeus, Syst. Nat., 1756, X ed, p. 812.
Obelia dichotoma, Schulze, Nordsee Exp., Hydr., 1872, p. 129. Calkins, Proc. Bost. Soc. N. H., 1899, XXVIII, p. 356.

Distribution. San Pedro to Coronados Is., Cal. Puget Sound (Calkins). Sitka, Berg Inlet and Orca, Al. (Nutting). British coasts (Hincks). Heligoland (Schulze). Eastern U. S. (Nutting).

Colonies in San Pedro Harbor liberated medusae in December, 1901. The medusae possessed from 20–24 tentacles, this variation correlated with a variation in the number of tentacles in the several quadrants, and the spacing of the lithocysts. This is the only departure from the type described by Hincks.

All the colonies were growing on kelp when collected, save those in San Pedro Harbor, where they were fastened to the float at the ferry landing. In all cases they were near the surface except at the Coronados Is., where they came up in a haul at 18–24 fathoms.

Obelia geniculata (Linn.).

Sertularia geniculata, Linnaeus, Syst. Nat.
Eucope diaphana, Agassiz, Contr. N. H. U. S., 1862, IV, p. 322.
Obelia geniculata, Allman, Ann. Nat. Hist., 1864.

Distribution. San Francisco, Cal., between tides; Catalina I., Cal., in 42 fathoms. New Zealand (Hartlaub). Eastern U. S. (Agassiz). Europe (Hincks).

The length of internodes and the thickening of perisarc below the shoulder processes vary widely in the same stem. Near the bases of some stems there are no thickenings below the shoulders at all; they appear only near the tips.

The Catalina colonies were growing on a frond of *Macrocystis;* the gonothecae were loaded with medusae (June 28, 1901). The San Francisco colonies were found on boulders in the breakers at the entrance of the Bay, also with medusae in the gonothecae (Dec. 14, 1895).

Clytia.

Trophosome. Colony not regularly branched. Hydrothecae with long pedicels.

Gonosome. Gonophores liberated as medusae, with four tentacles.

Clytia compressa (Clark).

Pl. VI. Fig. 49.

Campanularia compressa, Clark, Proc. Ac. N. Sc. Phil., 1876, XXVIII, p. 214.
Clytia compressa, Nutting, Proc. Wash. Ac. Sc., 1901, III, p. 170.

Distribution. San Diego (5 fathoms) and San Pedro (3 fathoms), Cal. Orca, Al. (Nutting). Shumagin Islands (Clark), 6–20 fathoms, on Laminaria.

Colonies growing on seaweed. Trophosome resembles that of *C. everta*. The hydrothecae vary greatly. The margin is usually wavy, a character which is not mentioned in the original description. Gonosome present May 23 and July 13, 1901.

Calycella (Hincks).

Trophosome. Hydrotheca tubular, on short annulated pedicel from a creeping stolon; operculum of several triangular tooth-like pieces.

Gonosome. Gonothecae on stolon; with aerocysts at maturity.

Calycella syringa (Linn.).

Pl. VI. Fig. 50.

Sertularia syringa, Linnaeus, Syst. Nat., XII ed., 1767, I, p. 1311.

Calycella syringa, Hincks, Ann. Nat. Hist., (3), 1861–2, VIII, p. 293. Calkins, Proc. Bost. Soc. N. H., 1899, XXVIII, p. 358. Nutting, Proc. U. S. Nat. Mus., 1899, XXI, p. 741; Proc. Wash. Ac. Sc., 1901, III, p. 176. Clark, Proc. Ac. Nat. Sc. Phil., 1876, XXVIII, p. 217.

Distribution. Mouth of San Diego Bay, Cal., 1–5 fathoms. Puget Sound; Berg Inlet and Kadiak, Al. (Nutting). Coal Harbor and Shumagin Is., Al. (Clark). Beach, Kara Sea (Bergh). British coasts (Hincks). Iceland, 100 fathoms (Hincks). Greenland (Levinsen).

Fam. Lafoeidae.

Trophosome. "Hydrothecae tubular, margins without teeth or opercula, the hydrotheeal cavity not divided from the stem cavity by a partial septum.

Gonosome. "Gonangia forming a 'Coppinia' mass." (Nutting, '01).

Lafoea.

Trophosome. "Colony with a fascicled stem, and with hydrothecae either free or partially immersed in the stem, the distal portion not being abruptly turned upward.

Gonosome. "A 'Coppinia' mass." (Nutting, '01.)

Lafoea dumosa (Fleming).

Sertularia dumosa, Fleming, Edin. Phil. Jour., 1828, II, p. 83.

Lafoea dumosa, Sars, Bidrag til Kundskaben om Norges Hydroider, 1873, p. 45. Clark, Proc. Ac. N. Sc. Phil., 1876, XXVIII, p. 216. Nutting, Proc. U. S. Nat. Mus., 1899, XXI, p. 741; Proc. Wash. Ac. Sc., 1901, III, p. 177.

Distribution. Port Orchard, Puget Sound. California coast (Clark). Port Etches, Al., 12–18 fathoms, clayey mud (Clark).

Dutch Harbor, Al. (Nutting). New England coast (Verrill). West Indies, 450 fathoms (Allman). British Coast (Hincks). North Cape, Norway (Sars). Spitzbergen (Mark.-T.).

Lafoea gracillima (Alder).

Campanularia gracillima, Alder, Tr. Tynes, N. F. C., 1857, p. 39.
Lafoea gracillima, Clark, Proc. Ac. N. Sc. Phil., 1876, p. 216. Nutting, Proc. U. S. Nat. Mus., 1899, XXI, p. 741; Proc. Wash. Ac. Sc., 1901, III, p. 177.

Distribution. San Pedro, Cal. Puget Sound; Juneau, Berg Inlet, Orca, Al. (Nutting). Shumagin Is., beach, and Sitka, Al., 15 fathoms, gravel and mud (Clark). New England coast (Verrill). British coast (Alder). Spitzbergen (Mark.-Turn.).

No gonosome. August 1, 1901.

Fam. Sertularidae.

Trophosome. Hydrothecae sessile, more or less adnate to stem, in two or more series, separated from stem by basal septum. Hydranth with a conical proboscis.

Gonosome. Gonothecae with fixed gonophores.

Owing to our insufficient knowledge of the natural affinities of the members of this family, I have adopted as a temporary method of classification the system of groups proposed by Schneider ('97). With very few exceptions the original generic names have been retained.

Sertularella group.

Hydrothecae alternate, one to each internode.

Sertularella conica Allman.

Sertularella conica, Allman, Mem. Harv. Mus. Comp. Zoöl., 1877, V, p. 21.

Distribution. San Pedro, Cal., S. W. of Tortugas, 60 fathoms (Allman).

The specimens at hand agree perfectly with Allman's figures and description, though the latter does not indicate the range of variation. The habit is nearly simple and the hydrothecae are always wrinkled transversely, though they may approximate in general form the hydrothecae of *S. polyzonias*. The internodes of the stem vary also, in length and thickness. There is one character, however, which seems to separate this species defi-

nitely from *S. polyzonias:* there are without exception three teeth and three pieces to the operculum on each hydrotheca.

The gonosome still remains unknown. (August 1, 1901.)

Sertularella dentifera, sp. nov.

Pl. VI. Figs. 51, 52.

Trophosome. Stems slender, flexuous, branched. Branches arising within or in place of hydrothecae; similar to stem. Hydrothecae free for three-quarters of their length, tubular, slightly enlarged at base; margin reduplicated, furnished with three moderate teeth forming a triangle with apex nearest stem.

Gonosome not present.

Distribution. San Pedro, Cal.

In size and habit this species resembles *S. conica* Allman, and was brought up in the same haul with specimens of the latter. It is represented in the collection by a single stem, with portions of two branches. The mode of origin of its branches—within hydrothecae—places it in Allman's genus *Thecocladium*. That genus, however, seems to me quite as unnecessary as *Synthecium*, whose validity is discussed below (p. 62.)

Sertularella fusiformis, Hincks.

Pl. VI. Figs. 53, 54.

Sertularia fusiformis, Hincks, Ann. N. H., 1861–2, (3), VIII, p. 253.
Sertularella fusiformis, Hincks, Brit. Hydr. Zoöph., 1868, p. 243.

Distribution. San Francisco, Cal., between tides. Great Britain, between tides (Hincks). New Zealand (var. *nana*, Hartlaub).

Female gonothecae with acrocysts, January 22, 1902.

Sertularella halecina, sp. nov.

Pl. VI. Fig. 55. Pl. VII. Fig. 56.

Trophosome. Stems rising from a creeping stolon, about an inch in length and may branch once or twice. Branches similar to the stem, with two or three annulae at the base of each, and a hydrotheca in the axil. Stem and branches divided by faint oblique nodes, which may often be wanting, into equal internodes. Hydrothecae alternate, one to each internode, adnate at base only; cylindrical, with a slight swelling on the lower side at base and a wide aperture with a smooth everted rim, which may be reduplicated; without operculum.

Gonosome. Gonothecae (male) arise from within hydrothecae; long,

tubular, somewhat broader than hydrothecae and five to six times as long as broad. A single tubular gonophore.

Distribution. San Diego Bay, Cal., 5–12 fathoms.

The everted margin, with its frequent reduplication in old hydrothecae, suggests the Haleciidae. The remarkable position of the gonophores is characteristic of Allman's genus *Synthecium*. This genus is to my mind untenable, since it wrenches from their nearest allies such diverse species as *Sertularella alternans* and *Sertularia campylocarpum* and unites them on the basis of a feature which is chiefly interesting to the physiologist. It has doubtless arisen independently in several species, and cannot at most have more than specific value. It is significant that the species just named were taken in the same haul of the dredge and were thus presumably surrounded by similar conditions. To make manifest the importance of a physiological point of view in this connection, the fact might be recalled that in the genus *Obelia* an axillary bud may grow into either a blastostyle or a hydranth, the function being determined by physiological conditions operating *after* the bud has begun to grow.

The male gonosome develops, briefly, as follows: A hydranth degenerates. From its more or less disorganized tissue at the base of the theca a bud springs, with no sign of definitive sex cells in or near it. When this bud attains about twice the length of the hydrotheca, sex cells appear between the ectoderm and endoderm, in a region varying in length, extending from near the tip over the distal half of the bud. There is no sign of orifice in the covering of perisarc which has been secreted over the growing bud. The bud stalk does not behave as a blastostyle, since no secondary buds are produced; it alone functions as the gonophore. Full maturity has not been reached by any of these structures in the scant material at hand, but at this stage they bear a striking resemblance to the sporosacs among the Gymnoblastea. They may arise from any hydrotheca. The maturest may be distal or proximal to the others; the usual order of succession from base to tip of the colony is not observed.

The cause which determines the formation of a gonophore out of the substance of a degenerated hydranth in *S. halecina* is as mysterious as that which determines whether a certain bud in an

Obelia colony is to become a hydranth or a blastostyle. Hickson ('91) has described in *Millepora murrayi* the transformation of zooids into male medusae, brought about by the immigration of sex cells from the coenosarcal canals. This case differs from that of *S. halecina* in that in the latter no direct transformation of well formed hydranths into gonophores can be said to take place, much less through the agency of sex cells. Yet the two cases resemble each other in the substitution of one sort of individual for another. In *S. halecina* the degeneration of the hydranth does not appear to be due to the same cause which initiates a gonophore. It is possible, however, that the conditions which favor the degeneration of the one may determine the growth of the other. But the solution rests with the experimenter.

The following hydroids form a suggestive series with reference to the origin of the gonosome:

1. *Obelia*—in which the blastostyle is not preceded by any degeneration, does not take the place of another sort of individual, and is not determined by the presence of sex cells.

2. *Campanularia*—in which the blastostyle originates as in Obelia, accompanied, however, by sex cells which appear in the endoderm of the bud.

3. *Sertularella halecina*—in which the formation of the gonophore is preceded by the degeneration of a hydranth, though no causal nexus is apparent, and sex cells seem to be absent.

4. *Millepora murrayi*—in which the formation of the gonophore is preceded by the degeneration of a zooid, both being due to the same cause—the presence of sex cells in the wall of the zooid.

In each case the function of the buds which may form blastostyles or gonophores is determined by internal or external conditions. The problem is essentially physiological, and needs experimental analysis.

Sertularella hesperia, sp. nov.

Pl. VII. Figs. 57, 58.

Trophosome. Stems with a few branches and a rambling habit, rising from a creeping stolon to the height of 30 mm.; divided obliquely into

internodes which vary in length in different branches. Hydrothecae alternate, one to each internode; immersed for about half its length; distal half bent away from the stem, usually narrowing slightly to the orifice, which is furnished with three moderate sub-equal teeth.

Gonosome absent.

Distribution. Mouth of San Diego Harbor, Cal., 1–9 fathoms.

This species grows commonly int angles of other hydroids and bryozoa, which may account for the variation in internodes and hydrothecae.

Clark found in his Alaska collection what he considered to be a robust variety of *S. tricuspidata* Alder. The San Diego species corresponds well to his figures, differing, however, in the greater immersion of the hydrothecae. The aspect of the colony is quite unlike Hincks' figures of *S. tricuspidata.* So I have thought it best, in the absence of any knowledge of the gonosome, to consider it a distinct species.

Sertularella tenella, Alder.

Sertularella tenella, Alder, Trans. Tynes. Nat. F. C., 1857, III, p. 113. Hincks, Brit. Hydr. Zoöph., 1868, p. 242. Hartlaub, Zoöl. Jahrb., Abth. Syst. Geogr. u. Biol., 1901, XIV, p, 349.

Distribution. San Diego, Cal., 9 fathoms. Bare I. (Hartlaub). Great Britain, between tides to deep water (Hincks). New Zealand (Hartlaub).

Gonosome absent, July 16, 1901. Creeping in profusion over Fucus. Immediately below each opercular piece is a short longitudinal ridge projecting into the cavity of the hydrotheca. Longest stem, 4 mm. long; length of hydrotheca, .4–.5 mm.; breadth, .25 mm.

Sertularella turgida (Trask).

Pl. VII, Figs. 59–62. Pl. VIII, Figs. 63–69.

Sertularia turgida, Trask, Proc. Cal. Ac. Sc., 1854, I, p. 113.
Sertularella turgida, Clark, Trans. Conn. Ac., 1876, III, p. 259.
Sertularella conica, Calkins, Proc. Bost. Soc. N. H., 1899, XXVIII, p. 359.
Sertularella nodulosa, Calkins, *ibid,* p. 360.
Sertularella turgida, Hartlaub, Zoöl. Jahrb., Abth. Syst. etc., 1901, XIV, p. 349.

Distribution. San Diego, 5 fathoms; Catalina I., 42 fathoms; San Pedro, 9 fathoms; Pacific Grove, and San Francisco, Cal.,

between tides. Monterey, San Francisco, and Tomales Pt. (Trask). San Diego, Santa Cruz, Cal., and Vancouver I (Clark). Bare I. (Hartlaub). Townsend Harbor, 15–20 fathoms (*S. conica* and *S. nodulosa* Calkins.)

The figures on Pls. VII and VIII show at a glance the unusual variability of this species. Trask's type came from San Francisco Bay, and it is from colonies from San Francisco Entrance that Figs. 59, 60, and 61 have been drawn. Figs. 59 and 60 represent the two types of gonothecae described by Clark, the first approaching the gonotheca of *S. polyzonias*. Figs. 62 and 63 were drawn from the same colony from San Pedro, and mark stages in the transition from the unringed spiny type through a ringed spiny condition to the form typical of *S. polyzonias*, reached in colonies from San Diego (Fig. 68). As a rule the hydrothecae on colonies with annulated gonothecae are transversely ridged or annulated, and somewhat narrowed distally. The length and diameter of the internodes and the degree of immersion of the hydrothecae in the stem vary considerably.

In spite of the wide range of variation, there are always three teeth on the margin of each hydrotheca, the proportions are in general constant, and the stems are stiff, flexuous and sparely branched.

The causes of the variation are not clear. Trask's type grows on the shore rocks, between tides, from Tomales Pt. to Pacific Grove. The synonymous *S. nodulosa* Calkins, dredged at 15–20 fathoms in Townsend Harbor, Wash., is also found in 9 fathoms near San Pedro, Cal. Only the dredged forms seem to be transeversely wrinkled. It is impossible to estimate the value of these and similar facts, however, without the aid of experimentation.

Dynamena group.

Hydrothecae opposite, a joint between each pair.

Sertularia desmoidis, sp. nov.

Pl. VIII. Figs. 70, 71, 72.

Trophosome. Stems rising from a creeping stolon to the height of one to two inches, branching sparely and irregularly, forming at times a matted tangle with bryozoa. Internodes vary somewhat in length; the portion distal to the hydrothecae is never longer than the rest of the internode. On the

proximal portion of each internode is a pair of hydrothecae opposite and contiguous for half their length on one side of the stem. Each hydrotheca is well immersed, bending outward rather sharply in its distal half and narrowing slightly to a more or less bilabiate operculate aperture.

Gonosome. Gonothecae borne on stem; sessile, ovate, with a wavy outline and broad round aperture; half as broad as long. Single gonophore centrally placed, with coenosarcal processes connecting it on all sides with gonothecal wall.

Distribution. San Diego, (1–25 fathoms), San Clemente I., (42 fathoms), San Pedro, Cal., (13 fathoms); rocky and sandy bottom; growing usually on seaweed.

The portion of each internode distal to the hydrothecae is subject to considerable variation in length, so that the stems may have a rather stringy or a robust habit. The aperture of the hydrotheca is never conspicuously bilabiate; the greater diameter is transverse.

Sertularia furcata Trask.

Pl. VIII. Figs. 73, 74, 75.

Sertularia furcata, Trask, Proc. Cal. Ac., 1854, I, p. 112. Clark, Trans. Conn. Ac., 1876, III, p. 258.

Distribution. Near San Pedro, Cal., 9 fathoms; Coronados Is., 18–24 fathoms; San Diego, 5 fathoms; San Francisco, shore rocks. Farallone Is., Cal., (Trask). Santa Barbara and Santa Cruz, Cal., (Clark).

Gonothecae, hitherto unknown, were present in San Francisco (Nov. 24, 1897) and San Diego (July, 1901) colonies. Gonotheca broadly ovate, compressed, with moderate terminal aperture; blastostyle connected with gonothecal wall by numerous branching coenosarcal processes; two elongate ovate gonophores.

The San Francisco colonies were growing on erect stalks of *Phyllospadix*. The stems are short and project from all sides of the eel grass. Each stem leaves the eel grass at an angle of about thirty degrees, then bends quickly away so that for the most part it makes an angle of seventy degrees with the stalk. The hydrothecae of the first, and often of the second pair as well, are not in contact. Those of succeeding distal pairs are not only in contact for half their length but tend much more strongly toward the upper side of the stem than do the proximal hydrothecae. This would seem to be an instance of the effect of gravity

upon the direction of hydranth buds. The farther the stems diverge from the vertical, the more closely do the hydrothecae of each pair crowd each other on the upper side of the stem.

These facts, together with those which relate to the habit of *S. argentea* (p. 68), render it probable that geotropism is to some extent an efficient cause of the habits of various *desmoscyphus* forms. It is possible that the same explanation may be applicable to the habits of other colonial coelenterata, especially those cords in which the mouth axis of each polyp lies in a plane passing through the axis of the colony.

Thuiaria group.

Hydrothecae more or less alternating, in two rows, closely placed, and many to an internode.

Sertularia argentea E. & S.

Pl. VIII. Figs. 76, 77. Pl. IX. Figs. 78, 79.

Sertularia argentea, Ellis and Solander, Nat. Hist. curious and uncommon Zoöph., etc., 1786, p. 38. Clark, Trans. Conn. Ac., 1876, III, p. 257.

Thuiaria argentea, Nutting, Proc. Wash. Ac. Sc., 1901, III, p. 184.

Distribution. San Francisco, Tomales Bay and Patrick's Point, Cal., shore rocks. Santa Barbara, Cal. (Clark). Puget Sound, Wash., and Yakutat, Al. (Nutting). "Ostend (Van Ben.); mouth of the Elbe (Kirchenpauer); Greenland (Fabr. and Morch); North Cape, in 30–50 fath. (Sars); Southern Labrador, Caribou Island, in 8 fath., not common (A. S. Packard, Jr.); Nova Scotia (Dawson): Grand Manan, common in 4–6 fathoms, attached to stones (Stimpson); Massachusetts Bay (Agassiz); South Africa (Busk)." (Hincks, '68.) Greenland (Levinsen).

All the colonies in the collection are of the small variety mentioned by Hincks as occurring between tides. The tallest stem is 35 mm. long. The hydrothecae vary in shape and position on the branches; the two teeth are usually of equal length. Gonothecae are present on some of the San Francisco colonies, several with acrocysts (Jan. 22, 1902). The dimensions of the gonothecae as well as the length of their horns, vary considerably. The acrocysts are borne by broad gonothecae with long horns. All gonothecae are compressed.

The habit of the San Francisco colonies of *S. argentea* seems to be controlled in an interesting fashion by gravity. The branches are borne on all sides of the stems, which were fastened by their bases to the perpendicular side of a shore boulder. Each stem had curved upward, so that while the basal portion was nearly horizontal, the terminal fourth or fifth was approximately vertical. In this terminal vertical portion the branches and the hydrothecae on them were arranged symmetrically with respect to the axis of the colony; and in this region the axis of the colony and the lines of force of gravity were parallel. At the base, where they were not parallel, branches and hydrothecae were oriented with respect to the force of gravity alone. Both hydranth and branch buds, as well as the stem, thus appear to be more or less negatively geotropic, the hydranths always being borne on the upper sides of the branches; the latter grow obliquely away from the centre of the earth but never become parallel to the main stem.

Sertularia filicula E. & S.

Pl. IX. Fig. 80.

Sertularia filicula, Ellis and Solander, Zoöph., p. 57. Hincks, Brit. Hydr. Zoöph., 1868, p. 264.
Sertularia anguina, Trask, Proc. Cal. Ac., 1854, I, p. 112.
filicula, Clark, Proc. Ac. N. Sc. Phil., 1876, XXVIII, p. 219.
anguina, Clark, Trans. Conn. Ac., III, p. 255.
var. *robusta*, Clark, *ibid.*, p. 256.
inconstans, Clark, Proc. Ac. N. Sc. Phil., 1876, p. 222.

Distribution. San Diego (15–25 fath.), San Pedro, San Francisco (shore rocks), Cal. Monterey to Pt. Reyes, Cal. (Trask). Vancouver I. (Dawson). Nunivak I. to Shumagin Is., Al. (10 fath.); San Miguel I., Cal. (Clark). Grand Manan, 20 fath. (Stimpson). Labrador (Packard). British shores (Hincks).

Gonothecae are present on colonies from San Francisco Bay, and leave no doubt of the identity of *S. anguina* and *S. filicula*. It is probable, as Clark suggests, that the robust variety may prove to be identical with the European *S. abietina*, in which case the species will take the latter name. I do not agree, however, that the habit of *S. inconstans* is sufficiently distinct from that of *S. filicula* to cause a separation of the species.

Sertularia greenei Murray.

Sertularia tricuspidata, Murray, Ann. N. H., 1860, p. 250.
Sertularia greenei, Murray, *ibid*, p. 504.
Cotulina greenei, A. Agassiz, Ill. Cat., 1865, p. 147.
Sertularia greenei, Clark, Trans. Conn. Ac., 1876, III, p. 257.

Distribution. Navarro, Cal. Vancouver I. to Santa Barbara, Cal. (Clark). San Francisco, Cal. (Agassiz).

Sertularia incongrua, sp. nov.

Pl. IX. Figs. 81, 82.

Trophosome. Stems long, sub-cylindrical. Branches pinnately arranged, alternate, longest less than 15 mm. in length. Both stem and branches without nodal septa. Hydrothecae on stem in two rows, completely immersed, alternate, three or five intervening between contiguous branches, one being axillary; margin entire. Hydrothecae on branches similar to those on stem, in two rows proximally, usually in three rows on distal half of each branch, spirally arranged.

Gonosome absent.

Distribution. San Pedro, Cal.

The stem is slender, with heavy, brown perisarc. The collection contains fragments only, the longest of these being 130 mm. in length. The branches are colorless, the perisarc being inconspicuous. The coenosarc is in poor condition, so that no data concerning the hydranth can be given.

The branches exhibit a transition from the *Thuiaria* to the *Selaginopsis* type. I have thought it convenient to consider it for the present a member of the former group.

Sertularia traski, sp. nov.

Pl. IX. Fig. 83.

Trophosome. Stems long, slender, divided transversely into internodes of variable length, branching dichotomously once at the distal end. Other branches pinnately arranged, alternate, three or five to each internode of the stem, without nodal septa; borne by a narrow base on a short shoulder process. Hydrothecae on stem well immersed, in two rows, alternate, three between contiguous branches, one of which is axillary. Hydrothecae on branches similar to those on stem, in two rows, alternate, the orifice of one reaching the level of the base of the next distal one. Orifice small, without teeth, semicircular, operculate.

Gonosome not present.

Distribution. San Pedro, Cal.

This species closely resembles *S. incongrua* in habit. It is distinguished from the latter by the shape and degree of immersion of the hydrothecae, the regularity of the interval between branches and the nodes on the stem. It is named in remembrance of that pioneer worker on Pacific Coast hydroids, Dr. J. B. Trask.

Selaginopsis group.

Hydrothecae in more than two rows; many to an internode.

Selaginopsis cylindrica (Clark).

Thuiaria cylindrica, Clark, Proc. Ac. Nat. Sc, Phil., 1876, XXVIII, p. 226.

Selaginopsis cylindrica, Mereschkowsky, Ann. N. H., 1878 (5) II, p. 445. Calkins, Proc. Bost. Soc. N. H., 1899, XXVIII, p. 362.

Distribution. Port Orchard, Puget Sd., Townsend Bay, dredged (Calkins). "Port Möller, Alaska Peninsula; 5–17 fathoms, sand, August. Hagmeister Island, Bering Sea; beach. Chirikoff Island; beach. Chiachi Islands; 8–15 fathoms, gravel" (Clark).

No gonosome. One colony.

Selaginopsis mirabilis (Verrill).

Diphasia mirabilis, Verrill, Am. Jour. Sc., 1873, (3), V, p. 9. Smith and Harger, Trans. Conn. Ac., 1875, p. 53. Clark, Proc. Ac. Nat. Sc. Phil., 1876, XXVIII, p. 219.

Selaginopsis mirabilis, Norman, Ann. N. H., 1878, (5), I, p. 192.

Polyserias hincksii, Mereschkowsky, Ann. N. H., 1877 (4) XX, p. 228.

Distribution. Port Orchard, Puget Sd. Hagmeister I., Al., beach; Shumagin Is., Al. (Clark). White Sea (Meresch.).

No gonosome. One colony.

Hydrallmania group.

Hydrothecae in one row, several to an internode.

Hydrallmania distans Nutting.

Hydrallmania distans, Nutting, Proc. U. S. Nat. Mus., 1899, XXI, p. 746.

Distribution. San Pedro, Cal. Puget Sound (Nutting).

Nutting does not mention the presence of hydrothecae in the

axils of the branches. Otherwise the fragment in the University of California collection agrees well with his description.

FAM. PLUMULARIIDAE L. Ag.

Trophosome. "Hydrotheeae cup-shaped, usually more or less adnate to the stem or branches, and always arranged on one side only of the hydrocladia or branches, on which they grow. Nematophores present.

Gonosome. "Reproduction by means of planulae. No medusae." (Nutting, '01.)

Aglaophenia.

Trophosome. Hydrothecal margin dentate; a posterior intrathecal ridge present and well marked; two supracalycine and one mesial nematophore attached to each hydrotheca.

Gonosome. "Gonangia inclosed in a true corbula formed of a modified pinna, its leaves without hydrothecae at their bases. The corbula may be either open or closed" (Nutting.).

Aglaophenia diegensis, sp. nov.

Pl. IX. Figs. 84, 85, 86.

Trophosome. Stems attaining a height of 150 mm., divided into short internodes. Hydrocladia alternating, one to an internode. They may be divided by very faint nodes into internodes of equal length, each bearing one hydrotheca, adnate for almost its entire length; the nodal constrictions are quite often wanting, however, or reduced to exceedingly faint grooves on the side opposite the thecae.

Hydrothecae one-fourth longer than the diameter of the mouth, laterally compressed but flaring distally so that the aperture is approximately circular. Rim ornamented with nine irregular teeth, the median tooth is sharp and recurved, though less abruptly than in *A. struthionides*. The teeth next the median one on either side are the longest and directed strongly forward and laterally. The next two on each side are curved upward and outward, sub-equal. The smallest teeth are those next the hydrocladium. The teeth in size and arrangement are more regular than in *A. struthionides*. There may be a faint intrathecal ridge near the bottom of the theca, running obliquely upward.

Mesial nematophore reaches level of hydrothecal mouth; tapers slightly to tip after leaving wall of hydrotheca. Supracalycine nematophores reach rim of theca; curve upward, forward and outward, narrowing slightly to the orifice.

Septal ridge just below supracalycine nematophores and one just above bottom of hydrotheca. Cauline nemataphores as in *A. struthionides:* one triangular, in axil of hydrocladium; another tubular, on base of shoulder supporting hydrocladium; and a third, larger, tubular, just proximal to latter.

Gonosome. Corbulae substituted for the usual hydrocladia. Each corbula is three times as long as broad, formed of eight pairs of alternating leaflets,

each leaflet, save first and last, carrying on its anterior edge eight nematophores. There is one hydrotheca (exceptionally two) between corbula and stem. Gonophores in two rows, about twelve in number; oval statoblasts.

Color. Stem dark horn; hydrocladia light brown.

Distribution. San Diego, Cal., on piles of wharf, and at mouth of harbor in 3–7 fathoms, July, 1901.

This species differs from *A. pluma*, which it closely resembles, in the possession of a recurved median tooth and much longer stems and hydrocladia.

Aglaophenia inconspicua, sp. nov.

Pl. IX. Figs. 87, 88, 89.

Trophosome. Stems in clusters, stout, 35-40 mm. high; divided by antero-posteriorly oblique nodes into internodes as broad as long. Hydrocladia borne on same side of stem, alternate, one from each internode, 3-4 mm. long; divided transversely into internodes of equal length. A nematophore in the axil of each hydrocladium and two at its base, in line with its axis. Hydrothecae deep, slightly compressed, free for not more than one-fourth their length; median tooth recurved, the next one on either side longest. Intrathecal ridge extending obliquely upward from near base of theca. Two ridges on each internode.

Mesial nematophore reaching nearly or quite to the mouth of theca. Supracalycine nematophore divergent, not reaching level of mouth of theca.

Gonosome. Corbulae in place of hydrocladia, not more than twice as long as deep, arched, slightly compressed; form of four to six leaflets the longest with ten nematophores on distal edge and occasionally one or two at tip of proximal edge. One well formed hydrotheca on distinct internode at base. Gonophores sporosacs, six to twelve in number.

Dimensions. Hydrotheca: length, .29 mm.; width, .155 mm. Hydrocladial internode, .24–.28 mm.; cauline internode, .18–.20 mm. Corbulae, 2 mm. long; greatest diameter, 1.1 mm.

Distribution. San Diego, Cal., 5 fathoms. July, 1901.

Several shoots were growing in a cluster of *A. struthionides*, and so closely resembled the smaller shoots of the latter in color and habit that at first I overlooked them. distinguishing them finally by the shape of the corbulae and the much smaller hydrothecae with nine instead of eleven marginal teeth.

A. inconspicua approaches the European *A. pluma*, from which it differs in the recurved form of the median tooth, the shape of the corbula and the stiff, ungraceful habit.

Aglaophenia pluma (Linn.).

Pl. X. Figs. 90, 91.

Sertularia pluma, Linn., Syst. Nat.
Aglaophenia pluma, Lamx., Hist. Pol. Flex., 1816.
Aglaophenia pluma, Hincks, Brit. Hydr. Zoöph., 1868, p. 286.

Distribution. Off Coronado, Cal., on kelp. South Africa. Belgium. Naples. Messina (30–40 fathoms). Gt. Britain (Hincks).

A. pluma has not been reported previously from North America, I believe. It is readily distinguished from the other species of *Aglaophenia* on the Pacific Coast by its non-recurved median tooth and the contrast of colors, first, between the dark brown stem and light brown hydrocladia; second, in the arched corbulae, which are light brown, with dark brown stripes along the ribs. Three or four stems arise from the same spot on the kelp, to the height of 25–35 mm. Spread of hydrocladia 8–10 mm.

Aglaophenia struthionides (Murray).

Plumularia struthionides, Murray, Ann. N. H., (3), V, 1860, p. 251.
Aglaophenia franciscana, A. Ag., Ill. Cat. N. A. Acal., 1865, p. 140.
Aglaophenia arborea, Verrill, Rep. Comm. Fish and Fisheries, 1871–72, p. 730.
Aglaophenia struthionides, Clark, Trans. Conn. Ac., III, 1876, p. 272.

Distribution. Puget Sound to San Diego, 1–32 fathoms.

This species was obtained in almost every haul of the dredge off the Southern California coast. It is quite variable, especially in the length of the hydrocladia, the character of the teeth on the hydrothecae and the length of the mesial nemetophores. There are often two hydrothecae at the base of each corbula, instead of three. Branches are frequently present, though not commonly numerous. Corbulae present in January, June, July (University of California Collection).

Antenella Allman.

Trophosome. "Colony consisting of hydrocladia springing directly from the hydrorhiza without the intervention of stems or branches; hydrocladial internodes and hydrothecae as in the *catharina* group of the genus Plumularia." (Nutting, '00.)

Gonosome. Gonothecae ovate, unprotected.

Antenella avalonia, sp. nov.

Pl. X. Figs. 92, 93, 94.

Trophosome. Stems rooted by creeping stolon, unbranched; longest 7 mm. high, with five hydrothecae. Each stem divided by alternately oblique and transverse nodes, which are always weak, into alternating thecate and intermediate internodes. Hydrothecae as deep as broad, free for half their length, with slightly everted circular margin. Mesial nematophores borne on small processes of the stem. Intermediate internodes with one or two nematophores, never three.

Gonosome. Gonothecae broadly ovate, with short, slightly ringed peduncles, borne in pairs on the thecate internodes, one on each side of the mesial nematophore. Pair of nematophores at the base of each.

Distribution. Avalon, Catalina I., Cal.

This species differs from *Monostaechas quadridens* McCrady only in size, absence of hydrocladia and the occurrence of the gonothecae in pairs. It is possible that the first two differences may be due to immaturity; yet on no stem was there a remote sign of a branch. On one stem 5 mm. long there were three pairs of male gonothecae, decreasing in size distally, none quite mature, though suggesting the maturity of the colony.

The branching form is probably to be derived from the unbranched form, the first branch arising from the base of the proximal hydrotheca and remaining non-thecate in its proximal portion; the second branch would arise at the base of the proximal hydrotheca of this first branch, and possess a distal thecate and proximal non-thecate region; the third branch would develop in a similar way on the second, and so on. Two branches may arise at the same point, producing a false dichotomy, as in *M. quadridens.*

Cat. No. 689a., University of California Collection. Type.

Halicornaria, Busk.

Trophosome. "Stem not fascicled, no posterior intrathecal ridge; an anterior intrathecal ridge usually present; hydrocladia not branched; hydrocladial internodes without septal ridges.

Gonosome. "Gonangia borne on the stem or on the bases of the hydrocladia not taking the place of hydrothecae, and not protected by corbulae or phylactocarps of any description." (Nutting, '00.)

Halicornaria producta (Bale).

Pl. X. Fig. 95.

Azygloplon productum, Bale, Linn. Soc. N. S. W., 1888, (2), III, Pt. I, p. 774.

Kircheupaneria producta, Bale, Proc. Roy. Soc. Viet, VI, p. 111.

Trophosome. Colony with simple stem, divided obliquely into internodes which vary in length according to age; those on the same stem are equal. Hydrocladia alternate, each from a shoulder projecting from the middle region of each internode. Each hydrocladium divided more or less obliquely into equal hydrothecate internodes. Hydrothecae somewhat compressed, with a broadly oval, smooth orifice which may be roughened by wear; about as deep as long; free for one third its length. Strong intrathecal septum about two-thirds the length of the hydrotheca from bottom, and reaching about one-third across theca at widest point.

No cauline nematophores. Mesial thecate nematophore very short, not reaching the base of the theca, expanding into the form of a sickle-shaped segment of a saucer, with a diameter two-thirds that of theca and embracing the internode for half its circumference. Pair of supracalycine nematophores, seldom reaching higher than two-thirds the height of the theca, never reaching the rim.

Height of longest stem 10 mm. Hydrothecae .2 mm. broad and long. Internodes of stem .3 to .4 mm. in length, in breadth varying from .2 in older to .12 mm. in younger colonies. Internodes of pinnae about the same length, but somewhat slenderer than younger stems.

Gonosome absent.

Distribution. San Diego, Cal., along shore of Ballast Point; growing on seaweed. Australia (Bale.)

The trophosome agrees so well with Bale's description that I do not hesitate to indentify my material with his species, even though the gonosome is lacking.

Plumularia.

Trophosome. Coenosarc of stem not canaliculated. hydrocladia unbranched, pinnately disposed, alternate or opposite. Hydrothecae with smooth margins; all nematophores movable.

Gonosome. Gonothecae borne on hydrocaulus or hydrocladia, without corbulae or protective structures of any kind. (Nutting's definition, slightly modified.)

Plumularia alicia, sp. nov.

Pl. X. Figs. 96, 97.

Trophosome. The colony is composed of a cluster of slender, loosely branching stems rising from a creeping hydrorhiza to a height of three to five inches. Each stem is divided transversely by inconspicuous nodes into short internodes of equal length. Hydrocladia are borne alternately on either

side of the stem, one from the distal end of each internode. There are four to seven hydrothecae in each hydrocladium. Thecate alternate with non-thecate internodes, the basal internodes being non-thecate. The nodal joints are alternately transverse and oblique, beginning with the basal joint. The thecate are less than twice the length of the non-thecate internodes.

Each hydrotheca rests on a swelling of the proximal portion of the internode. In profile the outer edge is straight, forming an angle of forty-five degrees with the axis of the hydrocladium. The inner edge is free for a distance equalling more than half the length of the outer edge, and while approximately parallel to the latter, flares slightly near the theca-mouth. It reaches the level of the distal extremity of the internode.

The hydrotheca is laterally compressed, the sides straight and diverging slightly from a narrow base to the mouth, which is broadly oval with smooth margin.

Each internode has a septal ridge near each end: the distal ridge on the hydrothecate internode is less conspicuous than the others, which are moderate.

A single nematophore is borne on each internode of the stem on the side opposite the origin of the hydrocladium. Two nematophores occur in each axil. Each hydrocladial non-thecate internode bears a single mesial nematophore; each thecate internode bears one mesial nematophore just below the point at which the hydrotheca becomes free from the hydrocladium.

The perisarc of the stem is thick and brown; that of the hydrocladia is delicate and colorless.

Gonosome. Male gonophores small, ovate, attached by very short peduncles between the nematophores in the axils of the stem or branches, one to an axil. Chitinous investment very thin.

Distribution. San Diego (15–25 fathoms) and Long Beach (5–13 fathoms), Cal., on rocky and sandy bottoms. June and July, 1901.

Plumularia goodei Nutting.

Pl. X. Figs. 98. Pl. XI. Figs, 99, 100.

Plumularia goodei, Nutting, Am. Hydr., Pt. I., Special Bull. U. S. Nat. Mus., 1900, p. 64.

Distribution. Pacific Grove, Cal., shore. Santa Barbara Cal., outside reefs (Nutting).

The gonosome is present (July 25, 1899), and is remarkable for the fact that the gonothecae take the places of hydrothecae. They are borne near the base of the stem or on the hydrorhiza. There are no traces of regeneration. Apparently a bud which would ordinarily become a hydrocladium may change its function under the influence of appropriate stimuli.

There are not always two hydrocladia to an internode of the

stem, as stated by Nutting with reference to the specimens from Santa Barbara. On the same stem there may be one, two or three to an internode, according as none, one or two nodes respectively have been suppressed. The tentacles number 17–22. In other respects, the Pacific Grove specimens agree with Nutting's description.

Plumularia lagenifera Allman.

Plumularia lagenifera, Allman, Jour. Linn. Soc. Lond., Zoöl., 1885, XIX, p. 157.

Plumularia californica, Marktanner-Turneretscher, Ann. desk. k. nat. Hofmus., 1890, V, No. 2, p. 255.

Plumularia lagenifera, Nutting, Am. Hydr., Pt. I. The Plumularidae, 1900, p. 65.

Distribution. Off San Pedro and Santa Cruz, Cal. Berg Inlet, Al. Puget Sound (Nutting).

The single specimen from San Pedro is a slender stem 200 mm. long, of uniform thickness and almost denuded of hydrocladia. Here and there, however, are hydrocladia with one or two hydrothecae. There are from one to four non-thecate internodes at the base of each hydrocladium, one to three between hydrothecae, varying in length. The thecate internodes have the characteristic shape, septa and hydrothecae of *P. lagenifera*.

Gonosome absent (August, 1901).

The Santa Cruz material consists of several stems growing on *Styela montereyensis* attached to wharf piling. Their great variability gives them a position intermediate between the typical *P. lagenifera* and the variety *septifera* which at first I took to be a distinct species. One or several internodes may intervene between hydrothecae. They may each have one or two septal ridges. The supracalycine nematophores may originate below the margin of the hydrothecae. Some cauline internodes are furnished not only with proximal and distal septal ridges but with one between these and one on the shoulder supporting the hydrocladium.

The stems reach a height of 20–25 mm. There is no gonosome (December, 1895).

Plumularia lagenifera, var. septifera.

Pl. XI. Figs. 101, 102.

Trophosome. Stems 10–15 mm. high, from creeping stolon, in loose clusters. Divided by transverse septa into equal internodes with a conspicuous septum at each end and on the shoulder which carries hydrocladium. Nematophores in axils of hydrocladia and one on each internode on side opposite branch and immediately distal to proximal septum.

One hydrocladium from the distal portion of each internode; branches alternate, all in one plane; divided transversely into unequal internodes, the intermediate usually less than half as long as the thecate, with one strong septum near the proximal end and one nematophore immediately distal to it. Thecate internodes alternate with intermediate; hydrothecae near middle of each internode, slightly broader than deep. Three septa, all heavy, on distal side of branch; one at proximal end on a slight swelling of internode, one at distal end, one opposite hydrothecal septum, and sometimes a fourth between the latter and the distal septum. Mesial nematophore attached immediately above proximal septum; supracalycine nematophores attached below the mouth of hydrothecae. Hydranth with fifteen tentacles.

Gonosome. Gonothecae borne in pairs, one on each side of the shoulder processes of the stem internodes; broadly ovate, compressed, with narrow neck terminated by small circular orifice. Gonophores in the form of sporosacs, numerous, packed together without apparent order.

Stem and branches light brown to colorless.

Distribution. Catalina I., Cal. Growing on seaweed frond. July, 1901.

This variety closely resembles the typical *P. lagenifera* Allman, from which it may be distinguished by its unusually heavy septal ridges. It is more constant than the latter in certain characters; there is never more than one internode between thecate internodes, and no intermediate internode has more than one septal ridge, which is always very heavy.

Plumularia plumularoides Clark.

Pl. XI. Figs. 103, 104.

Halecium plumularoides, Clark, Proc. Ac. Nat. Sc. Phil., 1876, XXVII, p. 217.

Plumularia plumularoides, Nutting, Am. Hydr. Pt. I. The Plumularidae, 1901, p. 62.

Distribution. San Diego, Cal., dredged from a bottom of cobbles and sand, 15–25 fathoms. Cape Etolin, Nunivak I., Al., 8–10 fathoms (Clark).

There are but two small fragments in the collection. The coenosare is lacking in many places, but the perisarc is in good condition, The internodes of the stem are of constant length, separated by well marked nodes and each bearing distally one hydrocladium. Each hydrocladial internode possesses mesial and supracalycine nematophores, all monothalamic, as in *P. goodei*.*

The internodes of both stem and hydrocladia are much longer than those of the latter species, and the hydrocladia are not so strongly arched. The hydrothecae are similar in shape. In the hydrothecae of *P. plumularoides* are series of bosses similar to those found in *Halecium*.

Three empty gonothecae are present, borne singly on the cauline processes supporting the hydrocladia. All are evidently immature, having no external aperture. They are widest distally, tapering abruptly from the truncated end to the base. The wall is more or less irregularly wrinkled.

Plumularia setacea (Ellis).

Pl. XI. Fig. 105.

Sertularia setacea, Ellis, Nat. Hist. Zoöph., 1786, p. 47.

Plumularia setacea, Lamarck, Anim. sans Vert., 1st ed., 1815, p. 129. Calkins, Proc. Bost. Soc. N. H., XXVIII, 1899, p. 362. Nutting, Am. Hydr. Pt. I. The Plumularidae, 1900, p. 56.

Plumularia palmeri, Nutting, *ibid*, p. 65.

Distribution. San Diego (1–25 fathoms), Avalon, San Pedro, and San Francisco, Cal. Victoria, B. C. and San Diego (Nutting).

In a careful examination of numerous colonies of *P. palmeri* from Monterey, San Pedro and San Diego, I was unable to find any constant characters distinguishing it from *P. setacea*. The colonies range in height from 5 mm. to 100 mm. The longest have the stoutest, darkest stems, and the most conspicuous septal ridges. In the smallest colony the various ridges are present or absent, usually weak when present, and the stem is colorless, slightly sinuous toward the tip. The larger stems are

*In both species the nematophores are delicate, with narrow bases, and are frequently wanting, while their sarcostyles may remain. I have not seen more than one supracalycine nematophore or sarcostyle to each hydrotheca. Clark, who described *P. plumularoides*, saw nothing of either.

sparsely and irregularly branched. Gonosome absent in colonies collected in San Pedro Harbor, December 30, 1901. Male gonothecae are present in colonies from San Diego (July) and Monterey (December). They may be borne in pairs on the stem, one on each side of the shoulder that supports each hydrocladium. The members of each pair are not of the same age, one being mature before the other is half grown. Mature male gonophores are elongated and compressed, the proportions of length, breadth, and thickness being as 10:4:2. The neck is moderate, with a small circular terminal aperture.

Large colonies dredged off San Diego in 1–25 fathoms, on sandy and rocky bottom; also on float in San Pedro Harbor, and outside the harbor in several fathoms, on sandy bottom covered with loose masses of *Nitrophyllum*. Small colonies on kelp and eel grass, Avalon, Catalina I.

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For fuller bibliographies see Allman ('71), Calkins ('99), Marktanner-Turneretscher ('90), and Nutting ('00).

PLATE I.

Fig. 1.—**Bimeria annulata.** Perisarc surrounding hydranth, the latter having been removed by caustic potash. x 30.

Fig. 2.—Same species. Hydranth, showing continuation of perisarc upon tentacles. x 30.

Fig. 3.—Same species. Gonophore, with original perisarcal investment partially retracted. x 30.

Fig. 4.—**Bimeria franciscana.** Portion of a main branch. x

Fig. 5.—**Bimeria robusta.** Hydranth. x 40.

Fig. 6 —Same species. Young hydranth; perisarc extending over bases of tentacles. x 40.

Fig. 7.—Same species. Semi-diagramatic view of a developing hydranth from above, to show the order of appearance and arrangement of the tentacles. x 40.

Fig. 8.—**Clava leptostyla.** Heteromorphic regeneration of a piece of stem; a set of tentacles at each end.

Fig. 9.—Same stem, two days later.

Fig. 10.—**C. leptostyla.** Regeneration of a hydranth; stage with four tentacles.

Fig. 11.—Same individual, twenty-four hours later; second quartette of tentacles appearing.

Fig. 12.—Same; third quartette appearing.

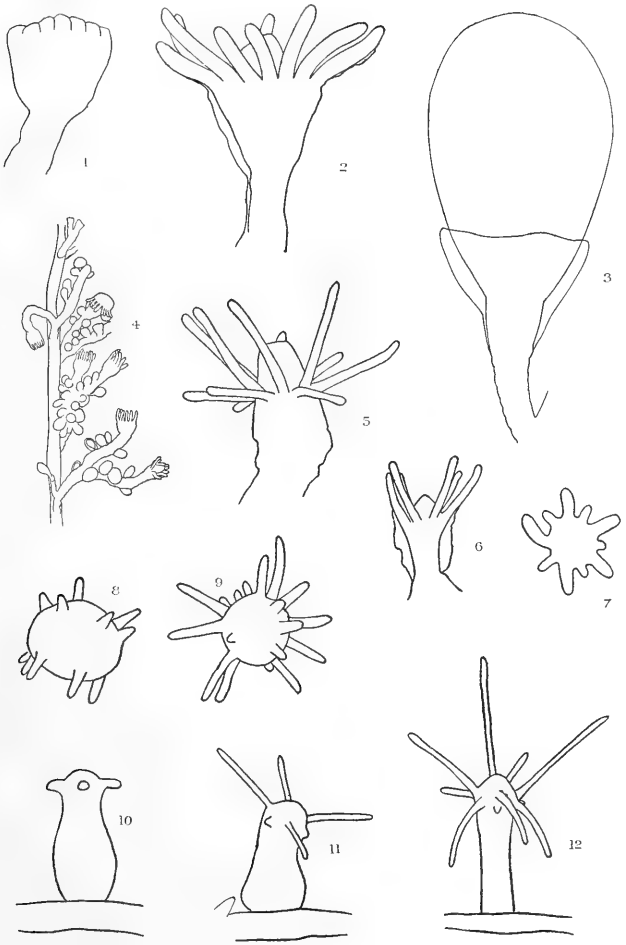


Photo-Lith. Britton & Rey, S. F.

PLATE II.

Fig. 13.—**Eudendrium californicum.** Blastostyle, with young hydranth fastened to its stalk.

Fig. 14.—Same species. Young blastostyle.

Figs. 15-20.—**Hydractinia milleri.**

Fig. 15.—Sterile hydranths. x 27.

Fig. 16.—Distal portion of fertile hydranth with six tentacles. x 90.

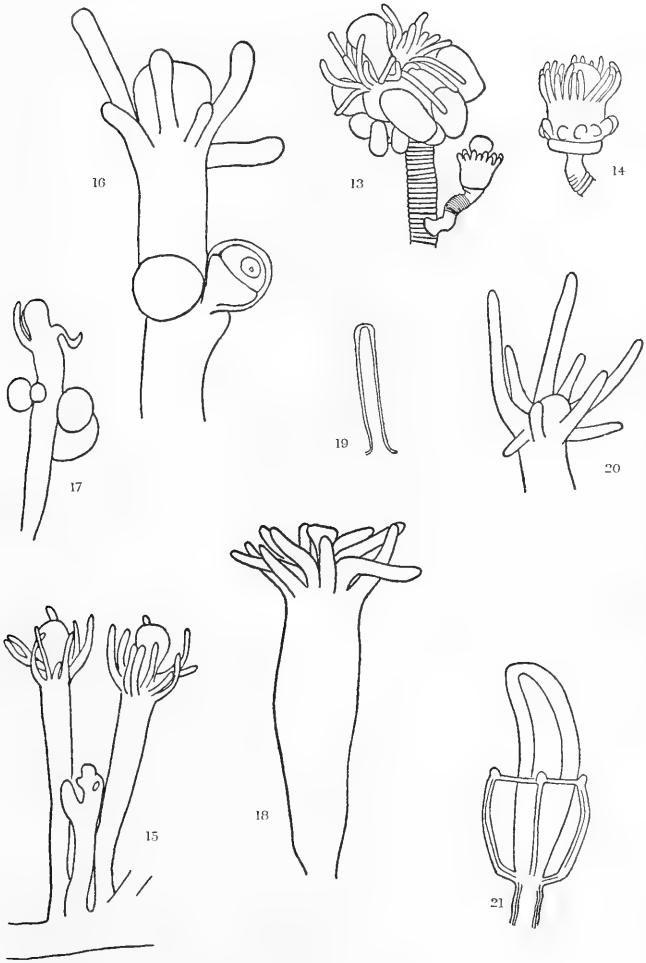
Fig. 17.—Fertile hydranths with three tentacles. x 27.

Fig. 18.—Large sterile hydranth; proboscis contracted, club-shaped. x 27.

Fig. 19.—Spine. x 30.

Fig. 20.—Sterile hydranth, showing arrangement of tentacles in quartettes.

Fig. 21.—**Corymorpha palma.** Gonophore.



H. B. T. Del.

Photo-Lith. Britton & Rey, S.F.

PLATE III.

Fig. 22.—**Tubularia crocea.** Male gonophore.

Fig. 23.—Same species. Female gonophore with ova.

Fig. 24.—**Tubularia marina.** Male gonophores.

Fig. 25.—Same species. Female gonophores.

Fig. 26–29.—**Campalecium medusiferum.**

Fig. 26.—Hydrotheca. x 45.

Fig. 27.—Hydranth. x 45.

Fig. 28.—Gonotheca with four gonophores. x 45.

Fig. 29.—Gonophore. t_1 t_1, first pair of tentacles; t_2, one of the second pair, much smaller; *ec*, ectoderm of umbrella, subumbrella and manubrium. The specimen from which this figure was drawn showed no canals in the endoderm of the bell.

Fig. 30.—**Halecium annulatum.** Portion of branch. x 30.

Fig. 32.—Same species. Female gonotheca and gonophore. x 30.

Fig. 32.—**Halecium kofoidi.** Portion of trophosome. x 40.

Fig. 33.—Same species. Gonotheca, arising from base of hydrotheca.

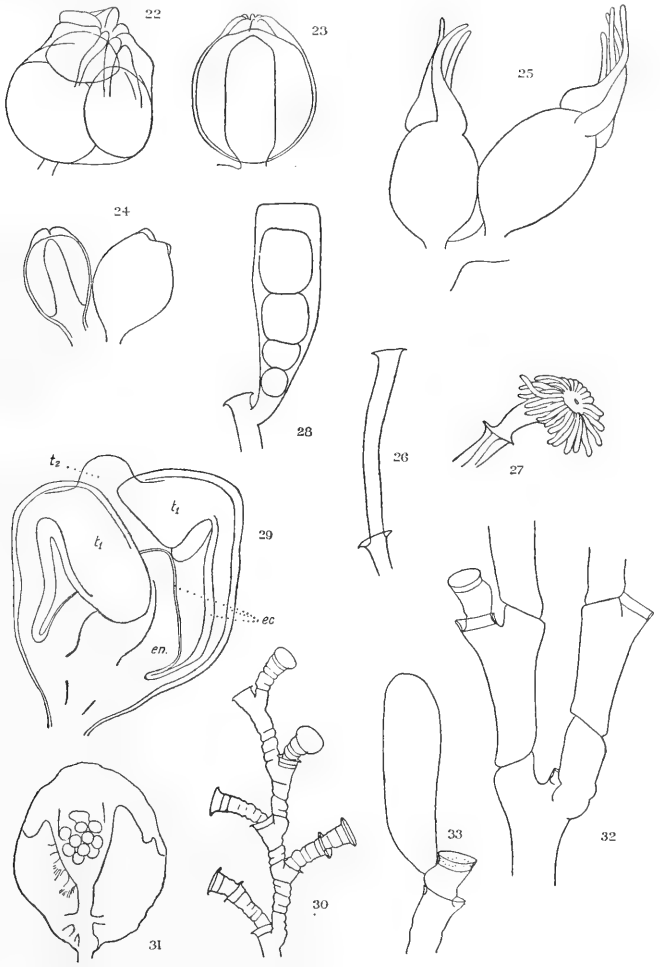


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PLATE IV.

Fig. 34.—**Campanularia denticulata.** Hydrotheca and pedicel, showing "knee." x 40.

Fig. 35.—*a*, *b*. **Campanularia everta.** Types of hydrothecae, in optical sections. x 45.

Fig. 36.—*a*, *b*. Same species. Two views of male gonotheca. x 45.

Fig. 37.—*a*, *b*. Same species. Two views of female gonotheca, with aerocyst, gonophore and embryos. x 45.

Fig. 38.—**Campanularia fascia.** Hydrotheca. x 40.

Fig. 39.—**Campanularia pacifica.** Two hydrothecae, from slightly different points of view. x 45.

Fig. 40.—Same species. Female gonangium. x 45.

Fig. 41.—Same species. Male gonangium. x 45.

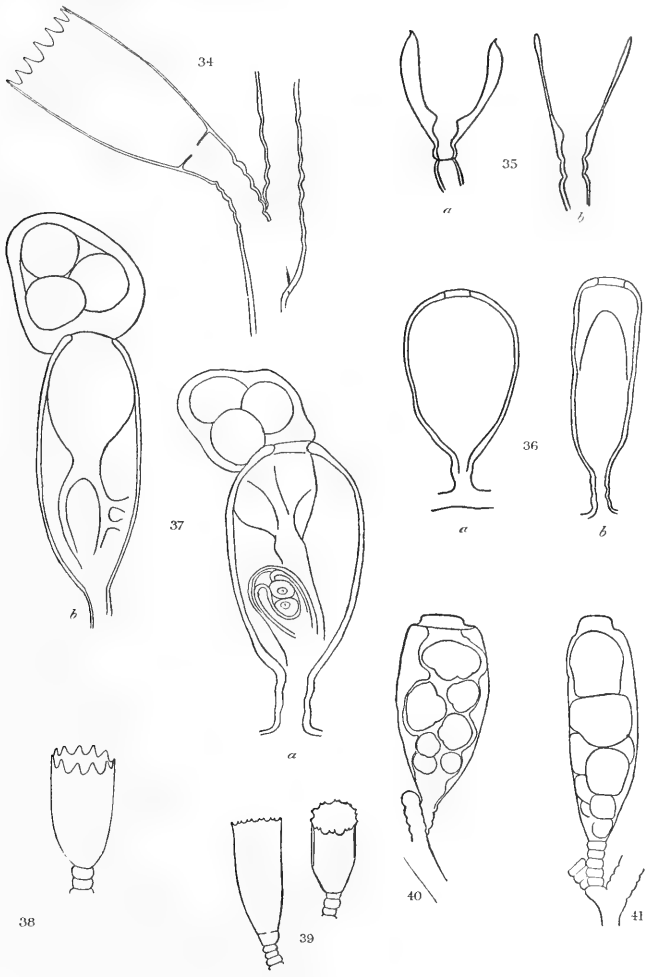

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PLATE V.

Figs. 42–47.—Campanularia urceolata.

Fig. 42.—Hydrothecae from same colony. *a*. Typical *C. urceolata* Clark (x 45); *b*. Typical *C. reduplicata* Nutting (x 45); *c*. Portion of colony showing position of *a* and *b* on stolon. From Yakutat, Alaska.

Fig. 43.—*a*, *b*, *c*. Hydrothecae showing variations in form. From Pacific Grove, Cal. x 45.

Fig. 44.—*a*, *b*, *c*, *d*. Hydrothecae (x 45). *e*. Gonotheca (x 30). From San Francisco, Cal.

Fig. 45.—Gonothecae (x 27). From Yakutat, Alaska.

Fig. 46.—Gonotheca (x 45). From Pacific Grove, Cal.

Fig. 47.—Hydrotheca and pedicel terminating a free stolon. x 45.

Fig. 48.—Campanularia volubilis.—*a*, *b*, *c*. Types of hydrothecae, same colony. x 45.

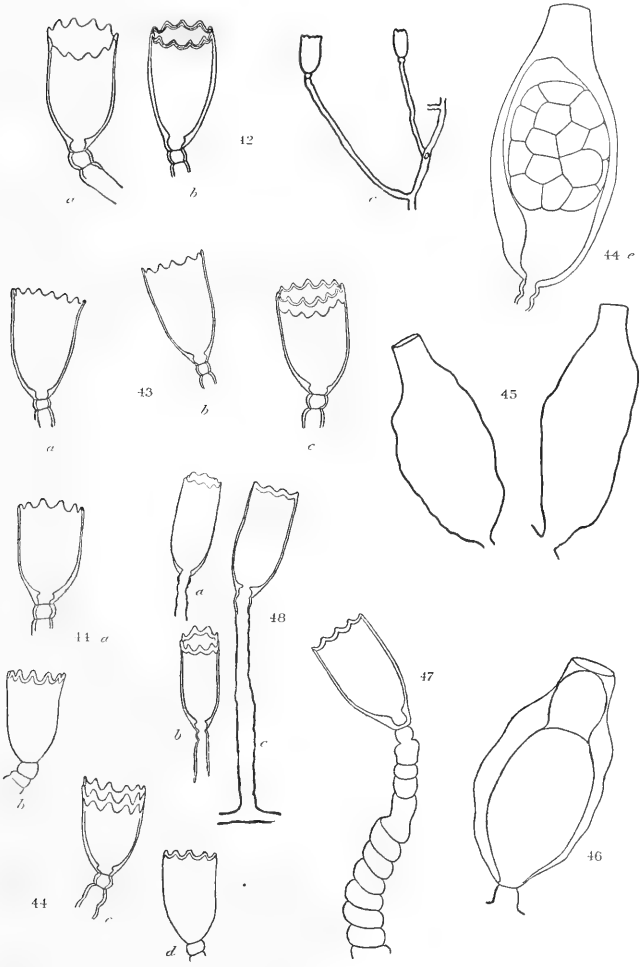

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PLATE VI.

Fig. 49.—Clytia compressa. *a*, *b*, *c*. Types of hydrothecae. *d*. Medusa about to leave gonotheca. Immature gonophore near base of latter. x 60.

Fig. 50.—Calycella syringa. Hydrotheca; gonothecae, each with a single ovum.

Fig. 51.—Sertularella dentifera. Portion of stem, with two hydrothecae. x 30.

Fig. 52.—Same species. Portion of stem, with bases of two branches arising from hydrothecae. One hydrotheca slightly ruptured. x 27.

Fig. 53.—Sertularella fusiformis. Portion of stem. x 30.

Fig. 54.—Same species. *a*. Female gonotheca. x 30. *b*. Female gonotheca with aerocyst; ova within gonotheca. x 30.

Fig. 55.—Sertularella halecina. Hydrothecae. x 30.

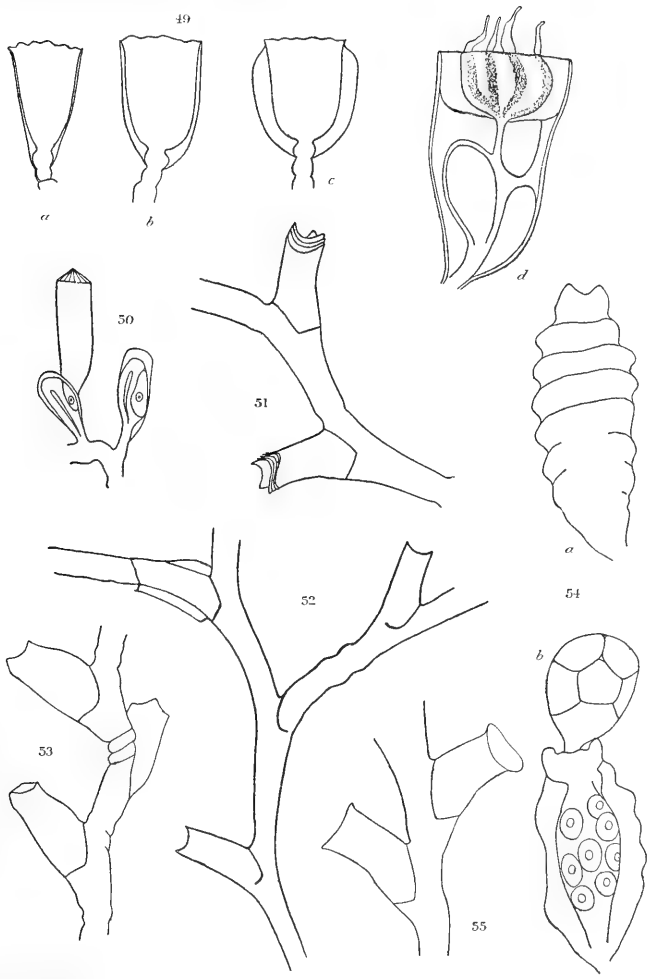

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PLATE VII.

Fig. 56.—Same species. *a*. Gonophore arising from hydrotheca. x 30. *b*. Gonotheca somewhat collapsed; gonophore indicated. Re duplicated hydrotheca. x 30.

Fig. 57.—Sertularella hesperia. *a*, *b*, *c*, *d*. Types of hydrothecae. x 45.

Fig. 58.—Same species. Stem. x 45.

Figs. 59–69.—Sertularella turgida.

Fig. 59.—Gonotheca. From San Francisco. x 22.

Fig. 60.—Gonotheca. From San Francisco. x 22.

Fig. 61.—Hydrothecae. From San Francisco. x 22.

Fig. 62.—Gonotheca. From San Pedro. x 22.

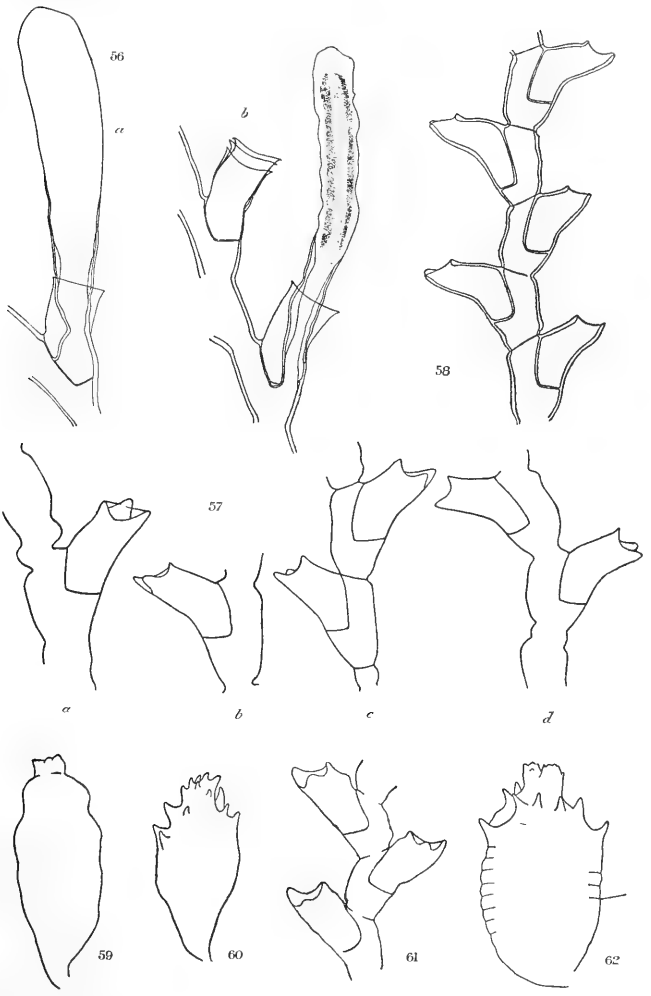

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PLATE VIII.

Fig. 63.—Sertularella turgida. Gonotheca. From San Pedro. x 22.

Figs. 64, 65.—Hydrothecae. From San Pedro. x 22.

Fig. 66.—Portion of stem. From San Pedro. x 22.

Fig. 67.—Gonotheca. From San Pedro. x 22.

Fig. 68.—Gonotheca. From San Diego. x 22.

Fig. 69.—Hydrothecae. From San Diego. x 22.

Fig. 70.—Sertularia desmoidis.—*a*, face; *b*, reverse. x 22.

Fig. 71.—Same species. Hydrothecae, face view. x 22.

Fig. 72.—Same species. Gonangium. x 27.

Fig. 73.—Sertularia furcata. Hydrothecae. *a*, face; *b*, reverse. Extreme type. x 30.

Fig. 74.—Same species. Hydrothecae from proximal portion of stem. Face view. x 30.

Fig. 75.—Same species. Gonangium, showing a large and a small gonophore, and coenosareal processes. x 30.

Figs. 76–79.—Sertularia argentea.

Fig. 76.—Young hydrothecae. x 30.

Fig. 77.—Young gonotheca. x 30.

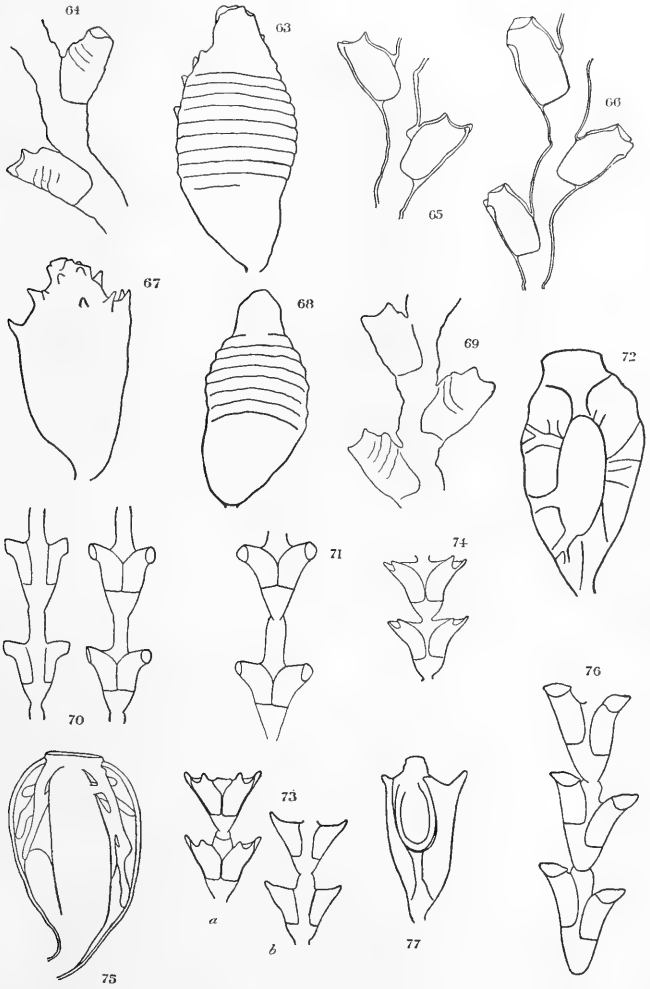

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PLATE IX.

Fig. 78.—**Sertularia argentea.** Gonotheca with aerocyst, showing horns, and maximum breadth. x 30.

Fig. 79.—Gonotheca with aerocyst, from the side. Horns not shown. x 30.

Fig. 80.—**Sertularia filicula.** Gonothecae.

Fig. 81.—**Sertularia incongrua.** Near distal end of branch; three rows of hydrothecae. x 30.

Fig. 82.—Same species. Proximal portion of branch; two rows of hydrotheca. x 30.

Fig. 83.—**Sertularia traski.** Stem with proximal portion of one branch and origin of another. x 30.

Fig. 84.—**Aglaophenia diegensis.** Hydrothecae, lateral view. x 52.

Fig. 85.—Same species. Hydrotheca, front view. x 52.

Fig. 86.—Same species. Corbula. x 18.

Fig. 87.—**Aglaophenia inconspicua.** Hydrothecae, lateral view. x 45.

Fig. 88.—Same species. Hydrothecae, front view. x 45.

Fig. 89.—Same species. Corbula. x 18.

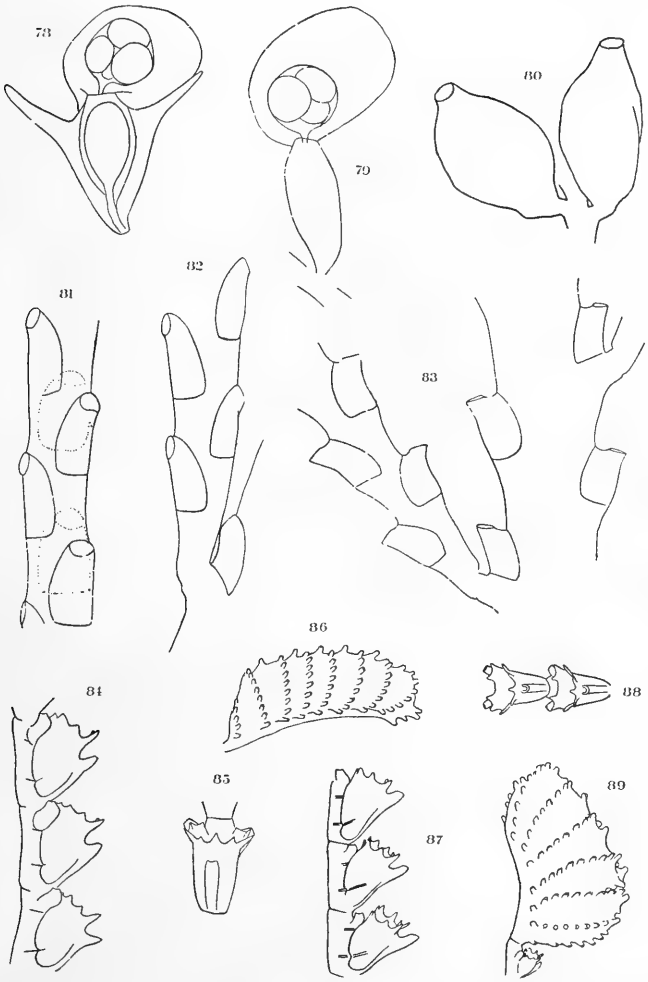

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PLATE X.

Fig. 90.—**Aglaophenia pluma.** Hydrothecae. x 45.

Fig. 91.—Same species. Corbula. x 14.

Fig. 92.—**Antenella avalonia.** Stem. x 45.

Fig. 93.—Same species. Showing a pair of gonophores arising from the base of a hydrotheca. x 45.

Fig. 94.—Same species. Gonotheca, one with two basal nematophores.

Fig. 95.—**Halicornaria producta.** Hydrothecae. x 60.

Fig. 96.—**Plumularia alicia.** Portion of hydrocladium. x 40.

Fig. 97.—Same species. Portion of stem, with gonophores. x 30.

Fig. 98.—**Plumularia goodei.** x 45.

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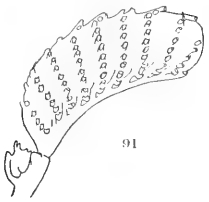
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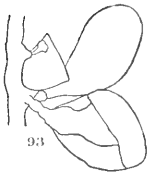
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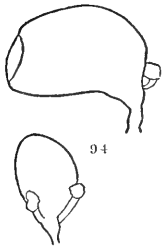
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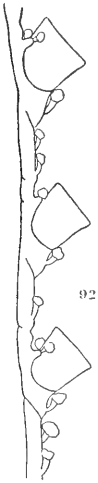
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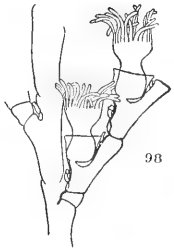
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PLATE XI.

Fig. 99.—**Plumularia goodei.** Gonotheca on hydrohiza. x 27.

Fig. 100.—Same species. Female gonangia taking the place of hydrocladia. x 27.

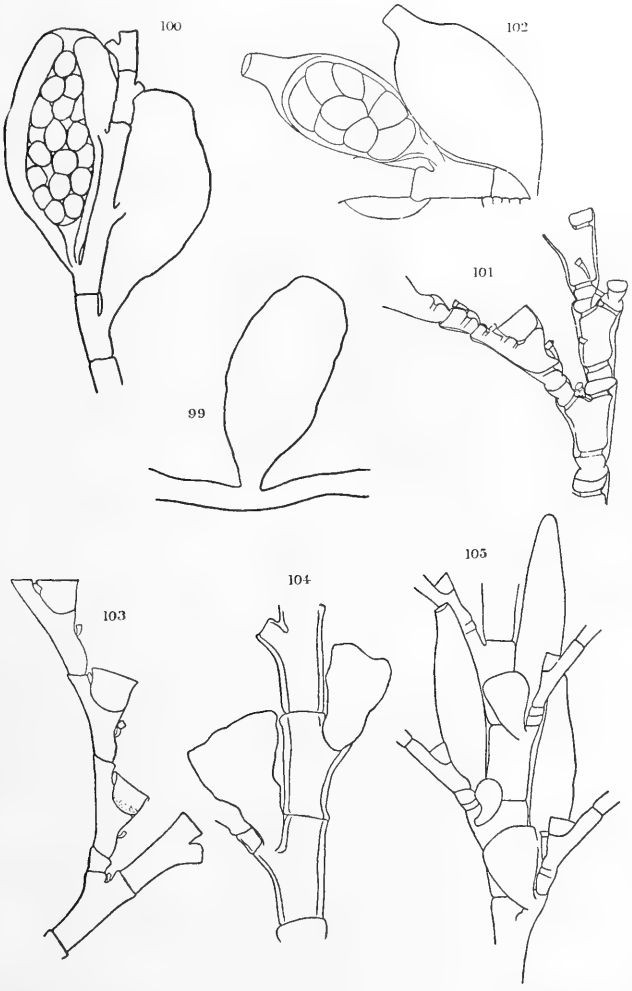
Fig. 101.—**Plumularia lagenifera,** var. **septifera.** Portion of stem and hydrocladium. x 40.

Fig. 102.—Same species. Gonangia. x 40.

Fig. 103.—**Plumularia plumularoides.** Portion of stem and hydrocladium. x 45.

Fig. 104.—Same species. Stem with immature gonothecae. x 45.

Fig. 105.—**Plumularia setacea.** Stem with gonothecae in pairs. x 45.



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INTRODUCTION.

It is well known that, while in most animals the heart beats continuously in one direction only, in the Ascidians its contractions normally reverse their direction at fairly regular intervals. The earlier investigators, who studied the heart reversal chiefly in the intact animal, mostly concluded either that the cause of the reversal is the "necessity of the distribution of the arterial blood to all the organs" (Roule, 1884, p. 151), or that it is the increasing pressure that the heart has to labor against in forcing the blood through vessels that cannot easily accommodate it (Lahille, 1890, p. 292; Ritter, 1893, p. 75).

Recently the problem of the reversal has been attacked from a physiological point of view by Lingle (Loeb, 1900, pp. 28–29). Professor Loeb has informed us orally that the species used in these investigations was *Molgula* (*Bostrichiobranchus*) *manhattensis*. Lingle found that if the heart be divided at the center each half beats continuously from the end towards the cut; and also that the automatic activity was confined to two small regions near the ends, so that after these had been cut away they continued beating, while the long part between them no longer contracted in sea water. Professor Loeb has told us that the central piece did not contract in a solution of pure sodium

OCT

chloride. In commenting upon these results Loeb (1900, p. 29) says that they prove that the reversal is "determined by each of the two ends getting the upper hand alternately, and forcing the other to act in its rhythm for a while." This explanation was tested by the members of Professor Loeb's class in physiology at Wood's Hole, who found that towards the end of a series of contractions passing from one end, *a*, the beats become slower, or stop altogether. During this pause the other end, *b*, "succeeds in sending out a wave of contraction which reaches *a* before it has a chance to send out a wave of its own." Occasionally both ends contract at the same time, but the one which is about to stop delays in sending out its next contraction, and thus the beat from the end just beginning to contract can traverse the whole heart. Schultze (1901) in his study of the heart of Salpa came to the same conclusion as Loeb concerning the cause of the reversal, and confirmed most of the results of Lingle and Loeb's students. He found, in addition, that even when one end of the heart had been cut away, the rest of it which continued beating in one direction, regularly gave rise to alternating series of slower and faster contractions.* The slow series, he thought, corresponded to the time when, in the intact heart, the contractions would have been coming from the end which had been removed. He also discovered that a constant direction of contraction could be maintained by electrical stimulation of either end of the heart. This stimulus so increased the rate of contraction that the unstimulated end could not get control of the heart. In both Salpa and Ciona Schultze found that isolated pieces from the center of the heart would contract in sea water if they were left there long enough.

Neither Schultze nor any of the previous investigators of the subject have found ganglion cells in the Tunicate heart. Hunter (1902), however, has found in *Molgula manhattensis* a small collection of ganglion cells at both ends of the heart, where the contractions originate, and in a later paper (1903) has given

*We observed the same phenomenon in Ciona hearts from which one end had been removed. In such hearts series of normal and much slower contractions alternated. In some cases the heart would contract normally for a while, then stop entirely for a time that about corresponded to the duration of the series of slow contractions, and then beat normally again.

evidence for the conclusion that these ganglia are connected with the brain.

EXPERIMENTS.

The experiments here described were carried on at the San Pedro laboratory of the University of California during the summers of 1901 and 1902. They were almost entirely the work of the junior author, and were concerned, almost exclusively, especially in the second summer's work, with the problem of the physiological polarization of the Ciona heart, and not with the general question of the Tunicate heart-beat. For very kindly assistance and advice in connection with preparing the results for publication we wish to express our thanks to Professor Loeb.

Ciona intestinalis was the only species used; the heart being examined in sea water unless the contrary is stated. Pieces of the heart were separated from one another principally by cutting. When tied they gave in general the same results; but although no case of contractions passing a ligature was observed, isolation by tying was avoided on account of the possibility of such a passage.

Ordinarily (in 148 out of 253 pieces) we found that pieces of the heart not connected with either end contracted spontaneously, and frequently these contractions began immediately after isolation. In other cases it was found that they began only after a variable quiescent interval. When pieces isolated in this way failed to contract automatically, contractions could almost invariably be started by immersion in a one per cent. sodium chloride solution. Equimolecular solutions of potassium chloride and calcium chloride had no such effect. Comparing these results with those of Lingle and Schultze on the automaticity of pieces of the heart, it will be seen that different species, and even the same species at different places, may differ in this respect. This difference need not surprise us when we remember the variability of living beings in general. It may be due to the presence of ganglion cells in the central part of the heart in some species, or to some other characteristic of the tissues which would make them less sensitive to the action of the constituents of the sea water that tend to inhibit automatic contractions.

We have seen that Lingle and Schultze agree that if a part of a tunicate heart be physiologically connected with but one of its ends, the contractions continue uninterruptedly from that end. This result we obtained in most cases, though occasional exceptions were encountered. Now the fact that we wish particularly to emphasize, and to the consideration of which this paper is devoted, is that *not only does the direction of the contractions remain fixed while a part of the heart is connected with only one of its ends,** *but that in some way a change is effected in the heart tissue so that the direction of the contractions still remains fixed after the part has been isolated from the end which was instrumental in producing the fixation.* That is, we may say that the heart tissue has become physiologically polarized by being left in contact for a while with only one end of the heart.

Experiments directed merely to determining whether such a polarization is a fact consisted first in leaving a part of the heart connected with only one of the ends for a while. It was then isolated from this end, the direction of the contractions noted, and finally frequently divided into still smaller pieces, and the direction of the contraction in each recorded. The character of the evidence is best made clear by reference to a typical experiment:

Experiment 39a.—

10:37—Visceral† end of heart removed. The contractions are ab-branchial.†

10:44—Pulsations have continued in the same direction. Branchial† end removed. Pulsations in the long central loop of the heart are still ab-branchial.

10:54—Visceral side of the loop cut in half.

10:58—Pulsations in both the pieces thus formed are ab-branchial.

* It should be stated that in all of these experiments the two ends behaved the same. We could not see that it made any difference which end was cut away first.

† In Ciona one end, which is attached to the viscera, is called the visceral, and the other, which connects with the branchial sac, is called the branchial end. Contractions passing in the direction from the branchial towards the visceral end are called ab-branchial, those passing in the opposite direction ab-visceral. This nomenclature is that of Schultze slightly modified.

11:07—Cut branchial side loop in half. Small central loop is contracting, but the direction cannot be made out. The other two pieces are contracting ab-branchially.

11:14—All three pieces are now clearly contracting in the original ab-branchial direction.

1:46—All contractions have stopped.

In some cases the pieces failed to contract and immersion in the sodium chloride solution was necessary before the direction of the heart-beat could be recorded. Contractions were obtained from insolated pieces of 51 hearts experimented upon in this way; and in 41 (or 80 per cent.) of them all the isolated pieces that contracted at all did so in the direction they had before being isolated. From some of these hearts as many as four or five pieces all contracting in the fixed direction* and unconnected with either end were obtained. From the ten hearts that did not behave normally many isolated pieces that contracted in the direction of fixation were also obtained. But as in all of these hearts at least one piece did not follow the normal law they were considered as furnishing evidence against polarization. However, in spite of this method of estimating the evidence which is decidedly unfavorable to our theory, still the preponderance of evidence in favor of polarization is too large to have been due to accident.

It seemed possible, however, that the persistence of the fixed direction after isolation of the pieces might not be due to a change in the heart tissues, but that the result might have been caused by a tendency for the pieces always to beat in the direction *away* from the most recent cut, which could then be considered as the stimulus controlling the direction of the contractions.

The most convincing type of experiment bearing on this question consisted in first removing one end of the heart to allow the direction of the contractions to become fixed. Then the second end was also removed, and a long loop connected with neither end and pulsating in the direction of fixation was obtained. Five or six small pieces were now cut from the end of the loop

* By contraction in the fixed direction or the direction of fixation we mean the direction of the contractions when the part of the heart in question was connected with only one of the ends of the heart

toward which the contractions were travelling; but the result of these experiments was always negative. The cuts did not change the direction of the contractions. Finally, to make the consideration of the evidence complete, all the cuts made were considered from this point of view, and it was found that in the great majority of cases the direction of the contractions did not change after the cut. In a few cases it did change, but the character of the change was not a constant one, for after the change the direction of the contraction was *toward* the most recent cut, exactly as frequently as it was away from it. *It is very clear then, that the stimulus due to isolating the pieces cannot account for the persistence of the fixed direction of contraction.*

Another possible explanation of the phenomenon is that it may be caused by the refractory qualities of the Ciona heart during and immediately following each contraction. Schultze (1901) found that the Salpa heart has a refractory period, similar to that found in Vertebrates, during which no stimulus could provoke an extra contraction. Now if a piece of beating Ciona heart be isolated, one end of it will have finished contracting before the other, and might consequently be in a better position to originate spontaneous contractions than the other. The contractions would consequently start at the end of the isolated piece which formerly contracted first. That is, they would continue in their original direction.

This possibility was tested in two ways:

In the first place, if this explanation is correct, then the direction of contractions *immediately* preceding isolation is the important thing, and it should not matter whether the piece was isolated during a normal series, or after the direction of the contractions had been rigidly fixed by first removing one end. Accordingly pieces of the heart were isolated during the normal series, and it was found that in 13 hearts out of 21 (or 62 per cent.) the pieces did not change their direction after isolation. These results seem to indicate that there is a tendency for pieces of the heart isolated during the normal series to maintain the original direction of contraction after isolation; but this tendency is much weaker than in those cases where the direction was fixed before isolation.

Secondly, if the direction, in which an isolated piece of the heart beats, depends upon the fact that previous to isolation one end had contracted before the other and consequently had recovered its excitability more completely; then, if the heart could be made to stop beating for a short time, the excitability of the two ends would soon become equalized, and there should be no relation between the direction of contraction before and after isolation. Accordingly, to test this explanation, our records of experiments in which pieces stopped after isolation and then started again when brought into the sodium chloride solution were gone over. They showed that after a quiescent period of from 3 to 90 minutes, 13 of the 14 pieces experimented upon contracted in the direction they had before immersion in the salt solution. Since the quiescent interval in these experiments was very much longer than the normal interval between contractions, the results, in spite of their small number, make it very improbable that the differential recovery of the two ends of the pieces from the lowered excitability following each contraction is the cause of the fixed direction of the contractions in isolated pieces of the Ciona heart.

As neither of the two possibilities considered accounts for the phenomena, we are forced to conclude that connection with only one end of the heart brings about a change of some kind in the tissues as the piece so connected continues after isolation to beat in the previous direction. This change may be termed a physiological polarization, but whether it is caused by the long continued constant direction of the contractions or the connection with one end only, apart from the direction of the contractions, we cannot say. So far as we know similar cases of polarization have not been described.

DEVIATIONS FROM NORMAL BEHAVIOR.

Occasionally the normal behavior of the heart, which presented strong evidence in favor of polarization, was replaced by contractions of the most varied kind, which will be briefly described.

Pulsations from both ends at the same time, which have been seen by both Loeb and Schultze, were observed in two of seven Cionas, in which puncturing the body wall had exposed the

heart without in any way injuring it. These contractions do not appear to have been ante-mortem phenomena like those observed by Schultze, but rather an exaggeration of the similar contractions described by Loeb at the time of reversal, for at first they alternated with the normal series of contractions, and were finally entirely replaced by the normal series.

Pulsations from the center of the heart were observed:

1. In 2 cases out of the 7 described above in which the heart was isolated without injury.

2. In two cases out of 63 in which one end of the heart had been isolated from the remainder.

3. In 8 out of 28 half hearts obtained by tying the heart across its center.

4. Occasionally in still smaller pieces.

In some of these cases the contractions came steadily from the center, while in others the direction was sometimes reversed.

Reversals in pieces of the heart subjected to no external influences, except the sea water in which they were immersed, were noted:

1. In 2 hearts from which only one end had been removed. Series of pulsations from the center alternated with series from the intact end.

2. In 3 of the 28 half hearts: Series from the center alternating with series from the end.

3. In 4 out of 82 still smaller pieces one end of which was an intact end of the heart.

4. In 3 out of 158 pieces which were not connected with an end of the heart. In one of these, series from the center alternated with series from one of the cut ends, in the others the contractions began at the cut ends.

These observations on contractions from the center and the reversal of small pieces of the heart show that the heart of Ciona as obtained at San Pedro is of a more uniform character throughout its whole extent than had been formerly supposed. The tissues at the end are of such a character that ordinarily the contractions start there. But the center resembles them so closely that even in the intact heart contractions may originate in that place. In fact, all parts of the heart are so remarkably similar

that the slight changes accompanying metabolism, together with immersion in sea water are sufficient to so raise the excitability in some parts of the heart that the contractions originate from them instead of from the usual places.

University of California,

March, 1903.

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EMBRYOLOGY AND EMBRYONIC FISSION IN THE GENUS CRISIA

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EMBRYOLOGY AND EMBRYONIC FISSION IN THE GENUS CRISIA.*

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INTRODUCTION.

The processes of embryonic fission in the Cyclostomata were first made known a few years ago by Dr. Sidney F. Harmer. That investigator found that this unique process of reproduction of the embryo occurs in several somewhat distantly related genera of the subclass, viz., in *Crisia*, in *Lichenopora*, and in *Tubulipora*. The facts disclosed were so interesting and remarkable, that further study of the phenomena was deemed desirable, both for the corroboration of the results, and for the purpose of completing more of the details. The investigation reported in the following pages has been made upon *Crisia* only, several species of which occur abundantly in the vicinity of San Francisco Bay. The chief results of Dr. Harmer's investigations, that is, the discovery of the occurrence in this genus of a budding of the embryo, the separation of the buds from the mother embryo, and their ultimate transformation into free swimming larvæ, have been fully confirmed. Besides as thorough a study as possible has been made of the origin of the genital products, both male and female. Some unique features have been found in the origin and development of these elements, all of which may be interpreted as secondary modifications due to the high degree of colonial specialization to which these bryozoa have attained.

* Dissertation presented to the Faculty of the College of Natural Sciences of the University of California in partial fulfillment of the requirement for the Degree of Doctor of Philosophy.

Technique.—For this investigation, material has been collected each month, and twice in the month during the spring, when the tides were favorable. Although specimens have been secured from various localities, they have been regularly obtained from a locality known as Lands End, near the entrance of the Golden Gate, California. The results most relied upon have been obtained then, from material killed and fixed under the most favorable circumstances, *i.e.*, very soon after collection. The relatively thick calcareous ectocyst of *Crisia* makes it difficult to fix the tissues rapidly enough to prevent their shrinkage and consequent distortion. The most successful results were obtained by the use of a solution of hot corrosive sublimate. In most cases a solution of this with glacial acetic was used, in other cases, the hot corrosive sublimate alone. The specimens were allowed to remain in the fixing fluid only long enough to become penetrated, when they were washed in 50% alcohol containing iodine. After this, they were carried through the various grades of alcohol and finally preserved in 85% alcohol. The process of killing and fixing did not include decalcification. Such portions only as were required for mounting, were afterward completely decalcified. In the process of decalcification, much trouble is frequently experienced by the formation of bubbles of gas. It was found easy to avoid these, however, and the consequent tearing of the tissues, by decalcifying small pieces in a high grade of alcohol made weakly acid. The stains used were Delafield's and Ehrlich's hæmatoxylin with eosin; Benda's iron hæmatoxylin alone, and with eosin and fuchsin; and Auerbach's mixture of methyl green and fuchsin. Many other stains were experimented with, but these gave the most satisfactory results.

Four species of *Crisia* are more or less abundant in this region, viz., *Crisia eburnea*, *Crisia geniculata*, *Crisia cornuta*, and a new species, *Crisia occidentalis*. A full description of this last species will follow in a later paper. Special reference is made in this paper to *Crisia eburnea*, although all the species have been studied more or less in regard to their method of reproduction. *Crisia eburnea* is certainly dioecious, the two kinds of genital products never being found in the same colony. This is thought to be true also of *Crisia occidentalis*, although the evi-

dence is less conclusive for this species. The other two, *Crisia geniculata* and *Crisia cornuta* are probably monœcious.

REPRODUCTIVE PROCESSES.

SEXUAL ELEMENTS.

1. *Origin of the Male Genital Products.—Crisia*, and perhaps other genera of the Cyclostomata, differ from the rest of the bryozoa in the production of the sexual elements. In young and growing colonies of this genus these products originate and are differentiated as such, *at the tips of the branches.* This can best be seen in the spring when the colonies are growing actively, and when the germinal tissue is in the healthiest condition. During the fall and winter months the tissue is thin even at the growing points, stains badly, and is in a degenerated state. In the latter part of February and throughout March, April, and May, however, both sorts of germinal cells are abundant, and form very conspicuous objects in all the young tips. The tissue at the growing points at this time forms a thick layer of "embryonic" cells closely packed together and staining deeply in hæmatoxylin. It is here differentiated into two layers which form the body wall, or lining of the zoœcia. Pl. XII, Fig. 1, represents the tip of a branch of *Crisia eburnea*, which has been decalcified, stained and mounted in toto. It consists of two series of zoœcia (z^1 and z^2) lying side by side. At the growing point (*gr. tis.*) the zoœcia are cut off alternately from the outer edges, the bases (*b.*) or proximal extremities of each pair being in contact, while their distal portions are separated by the bases of the next succeeding pair. The branch is thus somewhat flattened, having a dorsal (*d.*) and a ventral side (*v.*), and a right (*r.*) and a left (*l.*) edge. The growing point includes that portion which is anterior to the youngest pair of zoœcia and consists of two parts, (*a*) the layers of deeply staining cells (*gr. tis.*), and (*b*), the budding region. This latter is represented in Fig. 1 by young polypides (*pd. bd.*) in various stages of advancement. These portions are again shown in Pl. XIII, Fig. 18, which represents the tip of an actively growing branch containing, besides a developing ovicell (*ovl.*), a number of young polypides (*pd.*).

The cell layers which make up the body wall of a colony may be distinctly seen in section. Pl. XII, Fig. 2, represents a section from a growing tip of a male colony, in which the outer, or ectodermal layer consists of small rounded cells (*ec. cls.*), while the inner or mesodermal layer consists of much larger cells possessing a distinct large nucleus (*mes. cls.*). It is part of this inner layer which becomes modified into a germinal epithelium, (*ger. cls.*), and from which both ova and spermatozoa originate. Pl. XII, Fig. 3, is a section from the same series representing much the same characters. If these two sections be compared, the mesodermal cells in each (*mes. cls.*) are seen to be of various sizes. Many are of normal size (*mes. cls.*), while others are much larger, and constitute the cells of the male germinal epithelium (*ger. cls.*). In the germ cells, the nucleus and nucleolus have increased in size, and are surrounded by a layer of finely granular cytoplasm. The mesodermal cells which go to form the parietal layer are of various sizes and shapes, but of similar appearance. The ectodermal cells are either rounded or elongated, depending upon the portion of the tip in which they are. Near the edges, right and left, they are round, while near the middle they become much elongated and less numerous, (Pl. XII, Figs. 10 and 11, *ec. cls.*).

The relation between the polypide buds and the germinal tissue is shown in Fig. 4, a section from a male colony which represents several stages in the development of the polypides. At the anterior edge, in the angle toward the left (*l.*) the germinal cells may be seen (*ger. cls.*). Proximal to this point, a mass of cells represents the youngest polypide bud (*pd. bd. 2*), and below this there is an older bud (*pd. bd.* 1) in which the cavity of the stomach is formed (*st.*). As the distal portion of the branch continues to grow, the fully formed germinal cells are left behind at or near a point where a polypide bud forms, and in a male colony a few of these cells become attached to each bud constituting the testis of the developing polypides. In Pl. XII, Fig. 4, a number of large cells closely resembling the cells of the germinal tissue in size and appearance of the nucleus, are attached to the stomach of the older polypide bud (*pd. bd*

1., *tes.*). Below the stomach of the polypide (*pd.*) is a similar but larger mass of cells constituting the testis of that animal (*tes.*). If more of the branch of which Fig. 4 is a section could be shown, each succeeding polypide would be found to possess a corresponding structure. Examination of a series of polypides shows that the development of the testis proceeds with that of the polypide, the lower and hence the older polypides possessing the larger testis.

The spermatozoa, two of which are shown in Fig. 5, may be found clustered about large cells which are more or less abundant throughout the testis, or may be seen passing in a stream through the testis toward its distal portion, to a point at the base of the tentacles. Their actual egress was not detected, so that it is not known whether it occurs through a definite opening or only after the degeneration of the polypide, as is the case in most bryozoa. Harmer ('93) mentions the escape of the spermatoza of *Crisia cornuta* through the aperture of the zoœcium, but fails to state whether or not the polypide had degenerated. Hincks ('80) observed them passing in a stream through the intertentacular organ. The ectoprocts are not thought to have a sperm duct, the sperm escaping presumably through the orifice of a zoœcium after the polypide has degenerated. Since in most cases ova and spermatozoa are produced in the same zoœcium, either simultaneously or in succession, the necessity for a means of egress so that the one may reach the other is not so important. It is possible that in *Crisia* they may escape before the death of the polypide, and what evidence I have would indicate that those that mature do so while the polypide is still intact. In examining a quantity of material, however, the scarcity of ripe spermatozoa is very noticeable. In the spring, at least, the male genital products can be obtained in abundance and in various stages of development, but one searches almost in vain for spermatozoa. In a collection of preparations representing a hundred or more polypides, and made from material obtained during the season when the sexual elements are most abundant, in only *one instance* was ripe sperm found. Fig. 7 represents a section of living testis in a somewhat advanced stage of development, showing a typical arrangement and appearance of the

cells. These are in groups of darkly staining nuclei, sometimes arranged in large numbers around a central mass of cytoplasm, very frequently in groups of four nuclei imbedded in a mass of cytoplasm. (Pl. XII, Fig. 7, *tet*, and Fig. 7A.) The individual members of these tetrads consist sometimes of solid masses of chromatin, sometimes of an outer layer of chromatin surrounding a vacuole. Whether vacuolated or not, these probably represent stages in the development of spermatozoa—a development which apparently proceeds no further. Without making an exhaustive study of the spermatogenesis, it is, of course, impossible to state positively that degeneration of the testis occurs at this stage in the development of the sperm cells, and such a study has not been made; but in view of the evidence adduced, the suggestion that the testis does thus degenerate is worth consideration.

In examining branches of male colonies in which regeneration is taking place, the quantity of degenerated material in each zoœcium is unusually large as compared with that found in other bryozoa. Such a mass of material is shown in Fig. 6, which represents a section of a zoœcium containing a small regenerating polypide (*re. pd.*) and the remains of a degenerated polypide, the former occupant of the zoœcium (*b. b.*). In this "brown body" two portions can be distinguished, a round, somewhat homogeneous mass representing the tentacles and alimentary canal of the degenerated polypide (*de. pd.*), and a long, tapering mass extending almost to the base of the zoœcium representing, perhaps, the degenerated testis (*de. tes.*). This latter occupies the position of the testis and closely resembles it in appearance, both of the whole mass and of the individual groups of cells, among which the tetrads, both vacuolated and non-vacuolated, can be detected.

Comparing the early regenerating stages of male and female colonies, the quantity of material in the "brown bodies" in the latter is smaller than that in the male, and represents the degenerated polypides only. Each is at first a homogeneous mass which later disintegrates more or less, and falls into the base of the zoœcium. In the later stages, when the regenerated polypide has attained its full growth, the difference in appearance of the

"brown bodies" of the sexes is not so apparent. In both the residue becomes pushed into the extreme base of the zoœcium and is packed into smaller space.

The evidence for degeneration which is afforded by the scarcity of spermatozoa, and by the resemblance between the "brown body" of the male colonies and the testis, is strengthened by its probable correlation with what occurs in the female colonies. Here, as will be shown, large numbers of ova are produced, but on account of the reproduction peculiar to *Crisia*, relatively few give rise to larvæ, hence a relatively small number of sperm are functionally necessary. Degeneration of the male genital product, if it occur, is to be regarded, then, as a secondary modification correlated with the fact that every egg that contributes to the perpetuation of the species produces, through embryonic fission, not one, but a great many colonies.

2. *Origin of the Female Genital Products.*—In the female colonies of *Crisia eburnea* the ova arise as do the male germ cells, from the mesoderm of the growing tip of the branches. They are *differentiated at the tip of the branches, and in no other part of the colony.* Pl. XII, Fig. 8, represents a section from the ventral side of a female colony, in which the two layers of the body wall are distinctly shown. Close to the anterior edge is a row of small round ectodermal cells (*ec. cls.*), forming the outer layer, while inside of this is a layer of larger cells possessing very large distinct nuclei, and constituting the mesodermal layer (*mes. cls.*). The cells of this layer perform various rôles in the economy of the colony, some giving rise to part of the parietal lining of the zoœcia, some being transformed into the mesenchymatous tissue of the branches (*mes. tis.*), and the remainder producing the germinal epithelium. If a comparison be made between Fig. 8 of a female colony, and Fig. 2 and 3 of a male colony, no difference will be recognized in the cells of this tissue. In both, the germinal cells are of the same size, and bear identical relations to the growing points. It was shown for the male colonies that the germinal cells are more numerous in the angles, right and left, of the tip. This is true also of the female colonies, as may be seen in Pl. XII,

Figs. 9 and 10, which represent serial sections from the growing tip of a female colony, each of which shows the accumulations of modified mesodermal cells in the angles of the branch (*ger. cls.*). They are found, too, at a time earlier than that at which the polypide bud appears. This is especially clear in Pl. XII, Fig. 11, representing a section of the bud-forming region of a female colony. At the anterior edge of the tip are the germ cells (*ger. cls.*), while proximal to these is a series of polypide buds in various stages of development. In the oldest bud (*pd. bd. 1*) the cavity of the stomach is visible (*st.*). No ova have united with any of these buds, and an examination of older portions of the branch does not reveal their existence in the older zoœcia. On the other hand, numberless sections prove that not only are single, detached *ova* produced at the anterior extremities of the branch, but it is in these places that the *ovaries* are located. Evidence of this is given in Pl. XII, Fig. 12, and Pl. XIII, Figs. 13 and 14, consecutive sections taken somewhat obliquely through the germinal region of the tip of a colony. The line of cells (*sep.*) in the three sections, represents different parts of the same septum. Fig. 12, the first section of the series, is composed mainly of cells forming the ventral wall, the heap of cells lying near the septum (*pd. bd. 2*) representing the outer layer of a polypide bud. Fig. 13 represents the same polypide bud (*pd. bd. 2*), while proximal to it is another (*pd. bd. 1*). Distal to the anterior bud (*pd. bd. 2*) in this section, five cells of an ovary are shown, one of which (*ov.*) has advanced considerably in development. Fig. 14 shows an ovum (*ov.*) from the same ovary, which lies in close proximity to a polypide bud (*pd. bd. 1*). From this point forward there extends to the tip of the branch, an almost unbroken line of ova, constituting an ovary. A similar condition is represented in Pl. XIII, Fig. 15, a section from another colony, where several ova lie close to the septum (*sep.*), within the cavity of the branch. These are in close proximity to a mass of small cells (*pd. bd. 2*), and constitute the older portion of an ovary (*ovy.*), which as succeeding sections show, extends forward to the anterior edge of the branch. Examination of a great number of series reveals the same condition, *i.e.*, the formation of groups of ova, or ovaries at the tips

of the branches. Such a precocious appearance of ova is reported in a few instances among the Cheilostomata (Calvet '00), but as far as I am aware no other case is known in which the *ovary itself* is thus precociously formed. The early appearance of the germ cells in *Crisia* is somewhat comparable to what takes place in the *Hydromedusae* ('90). In both classes of animals it is a secondary condition correlated with the subordination of the sexual individuals, and the assumption by the colony of the reproductive function.

Throughout the bryozoa the sexual elements are produced, as a rule, in the zoœcia and in connection with the polypides. Thus, Nitsche ('69) found that in *Bugula* the ova arise from the inner surface of the endocyst of the younger zoœcia. In the older zoœcia he found the spermatozoa and in still older ones, the fertilized ova. Vigelius ('84) reports that in *Flustra membranacea-truncata* the genital products, both male and female, also arise from the endocyst of the zoœcium, and Prouho ('92) in a series of observations upon the Ctenostomes, found essentially the same condition as far as the time and place of origin of the sexual elements are concerned.

More recently, Calvet ('00) has reported a series of observations upon no less than forty-four species of marine bryozoa. These studies have reference mainly to the Cheilostomata and the Ctenostomata, his study of the Cyclostomata having been very restricted. In one species of the Cyclostomata, viz., *Crisia denticulata*, he made some observations on the reproductive processes, corroborating the researches of Harmer on the fission of the embryo. In the list of species whose spermatogenesis he studied, he mentions two Cyclostomes: *C. denticulata* and *Tubulipora flabellaris*. In his discussion he makes no particular mention of them, however, merely including them in the list with others, in which he says the primitive sperm cells originate as in *Bugula sabatieri*, *i.e.*, in the vicinity of the funicular cord in the lower portion of the zoœcium. One can only infer that he made no investigation of the growing tips of these two species, and the study of the adult animals alone would certainly mislead one as to the time and place of origin of the spermatoblasts.

Calvet's study of ovogenesis in *Bugula sabatieri* reveals an

interesting similarity between the origin of the ova in that species and in *Crisia*. Thus, in the young tips, he finds large cells which he considers to be "éléments ovulaires." Furthermore, he finds these cells in a cavity of a branch, distal to the region where the polypide buds are found. He says: "Dans les blastozoïdes jeunes, soit par l'observation directe sur le vivant, soit par l'examen comparatif des coupes histologiques, on peut suivre pas à pas la genèse des différentes parties constitutives de l'ovaire adulte. Il n'est pas rare de rencontrer, parmi les éléments libres de la cavité d'un blastozoïde terminal renfermant un polypide à l'état de rudiment massif, un certain nombre de cellules qui, par leurs grandes dimensions et leurs caractères histologiques, se désignent déjà comme éléments ovulaires (Pl. V, fig. 7et9, *ovu*)." His description of these cells leaves no doubt that they are eggs, and his figures show the close resemblance between them and the ova found at the growing points of a colony of *Crisia* (Pl. XII, Figs. 13, 14, and 15). This writer regards the ova which he finds at the growing points of *Bugula* as exceptional, and not as showing the ordinary method of their development. When so found they constitute merely the "anlage" of the future ovary, and in no case does he find the mature ovary outside of a zoœcium containing a polypide. In this respect then, *Bugula* differs materially from *Crisia*, since in the latter genus the ova which appear among the free elements of the tips of the branches, constitute the ovaries, and it is here that the ovum matures, is fertilized, and unites with a young bud to form an ovicell.

There is much in confirmation of these observations on the early development of the genital products, and of their independence in their earliest stages, to be obtained from Harmer's investigations. That writer reports the finding of egg-like cells in the growing tips of *Crisia*, and says, "The fact that these eggs are commonly found in the growing points, leads me to suppose that several are produced in each fertile internode; apparently by a modification of the funicular tissue, and that their further development depends upon their entering into definite relation with a polypide bud." In *Tubulipora* ('98), he finds that eggs are abundant in the young lobes. He found them in many of the zoœcia in connection with polypides and polypide

buds of every stage of growth. In *Lichenopora* ('97), he found but one egg, as a rule, in each colony, and always in the second or third zoœcium, and when the polypide was very young. In all these cases he regards the egg as "probably differentiated *in situ* from the outer layer of a young polypide bud," or, "The eggs appear as part of the polypide bud." Or again, "The eggs (of *Tubulipora*) are developed at a very early stage by the polypide buds, as in *Lichenopora* and *Crisia*." Furthermore, he found an egg-like cell 9.6 μ in diameter at the growing margin of a colony of *Lichenopora*. He did not feel sure that this was normal, although as he says, it recalls the condition in *Crisia*. In his study of embryonic fission this observer made no special study of the origin of the sexual elements. He explains the occurrence of ova at the growing margin as due either to the productiveness of the young buds, or as an unusual, perhaps abnormal phenomenon.

In *Crisia* one fails even in the height of the breeding season to find even a rudimentary ovary within the individual zoœcia, or elsewhere. What becomes of the relatively large number of ova? Do they all reach maturity? If not, what is their fate? In answer to these questions it is to be said that all ova do not produce embryos. According to their fate they fall into three classes. The first (*a*), comprises the relatively small number that produce embryos within an ovicell. The second (*b*), includes the small number which reach a *partial development* within the zoœcia, and the third (*c*), includes the remainder which *fail* of development entirely.

It has already been shown in the case of the male colony that proximal to the region where the germ cells are formed is the budding region, and further that in order that the male germinal cells may complete their development, they must become united with a polypide bud. (Pl. XII, Fig. 4, *pd. bd. 1.*) In a similar manner, in order that an *ovum* may reach maturity, it is necessary that a union should be effected with a polypide bud. In his account of the reproductive processes in the Cyclostomata, Harmer ('93) has shown that a peculiar relation must exist between a bud and an ovum, in order that an ovicell should be formed. He says: "One of these (egg-cells) acquires a close

relation to the potential alimentary canal of the ovicell polypide," that is, to a bud which without the intervention of an ovum would have developed in the ordinary fashion. And further, "This potential alimentary canal grows round the ovum, losing its previous form and becoming a compact multinucleated follicle surrounding the egg . . . " The study of a series of sections from an ovicell-bearing colony, shows that the relations entered into by the bud and ovum are of two sorts, each producing opposite results. In the first the *ovum* develops, while the bud is aborted. This includes all the cases of the first class (*a*) as given above, and represents the only relation recognized by previous observers. In the other, the *polypide* grows to maturity while the ovum is aborted, and includes the second class (*b*) above. To distinguish between the earliest stages of these two possible relations is extremely difficult, if not impossible, since before the cells of the bud become somewhat differentiated, there is no criterion by which it can be certainly known whether or not an ovicell will result. Thus, in Pl. XIII, Fig. 14, an ovum (*ov.*) is shown in close proximity to a bud (*pd. bd. 1*), but the outcome of this relation cannot be predicted. Again in Fig. 15 several ova are seen in close connection with a group of small cells (*pd. bd. 2*), but whether or not there is here an incipient ovicell, cannot be asserted. Can the union indicated by the proximal polypide bud of this figure (Fig. 15, *pd. bd. 1*) be interpreted as the beginning of an ovicell? This bud consists of a long column of cells having a somewhat definite arrangement, and caught at its proximal extremity is a large ovum. This, for a time, was thought to represent an incipient ovicell, but the conditions shown in Fig. 16 reveal its true meaning. But one bud (*pd. bd.*) is represented in this figure, and this has reached a stage of development similar to that shown for the proximal bud of the preceding figure (Fig. 15, *pd. bd. 1*). If we compare the arrangement of the cells of the bud in these two cases, with buds which represent early stages of undoubted polypide formation, the resemblance is strong, and there can be no doubt that these are stages in polypide development. Thus in Pl. XII, Fig. 11, are shown several instances of the earlier stages in the development of a polypide. The cells in the upper portion of the bud

arrange themselves in parallel lines forming the incipient tentacles (*pd. bd. 1* and *3 in. tent.*), while those in the lower portion form into a hollow sphere to produce the cavity of the stomach (*st.*). The proximal bud of Pl. XIII, fig. 15 (*pd. bd. 1*), and the anterior bud of Fig. 16 (*pd. bd.*), represent a stage in the development of polypides identical with those in Fig. 11. The significance of the union of ovum and polypide in these two cases is further revealed by the polypide just proximal to the young bud (Pl. XIII, Fig. 16, *pd. 2*). Here attached to the cæcal end of the stomach of an adult polypide, is a veritable embryo (*emb.*) consisting of at least three cells. That these are blastomeres of an embryo, and not merely a bunch of ova, is shown by the condition of the nuclei. The two upper cells have apparently just completed their mitosis, and the nuclei are relatively small. The nucleus of the lower cell has lost its nuclear wall, and the cell is preparing for division. This case affords an explanation of those instances where an ovum is held by a delicate membrane at the proximal end of a column of cells, and represents a kind of union that may occur between a bud and an egg, but one in which *no ovicell results*. The next older polypide (*pd. 1*) possesses neither ovum nor embryo. Young embryos of two or three cells are not uncommon upon buds or young polypides near the growing points, although single ova attached to young buds and to adult polypides are of more frequent occurrence. This figure (Fig. 16) represents a typical section through the growing tip of a young colony. In the growing tissue, right and left, ova are more or less numerous. Proximal to this, the youngest bud frequently possesses an ovum, and below this, one or two polypides may carry a single ovum each, or a young embryo. The coexistence of polypide and embryo or ovum has not been previously noted in this subclass of bryozoa, and while it is probably an abnormal condition for *Crisia*, it is, perhaps, indicative of a more primitive method of reproduction. I have never observed this except at the height of the breeding season, when ova are being rapidly produced. In the older portions of the colony neither eggs nor embryos have been found, nor have larvæ been obtained, in any of the older zoœcia. These embryos, apparently, never attain complete development, but are absorbed.

This kind of union was not recognized by Harmer, and as a consequence the instances which he offers as probable early stages of an ovicell are somewhat doubtful ('93, Pl. 22, Figs. 1 and 2). This is especially true of Fig. 1, which is probably an instance of this second relation.

The partial development of an embryo in connection with a polypide is interesting for two reasons. In the first place, it probably points to a more primitive method of reproduction, and in the second place, it is important for the light it throws on the time and place of fertilization.

In regard to the indications of more primitive conditions, it is clear, aside from the question of the origin of the ova, that in *Tubulipora* (Harmer, '98) ova occur in many of the zoœcia. Moreover, in this genus any zoœcium may become an ovicell, and usually several zoœcia of a colony become thus transformed. In the constant occurrence of eggs in the individual zoœcia, and in the direct transformation of the latter into ovicells, *Tubulipora* shows the least specialized condition of any Cyclostome whose history is known. In *Lichenopora* an ovum is found only in that young zoœcium which becomes the ovicell of the colony, and which Harmer designates as the fertile zoœcium. In this case specialization may be considered to have gone a step further in setting off a certain zoœcium to perform the function of an ovicell, and perhaps to produce the single egg which comes to maturity. In *Crisia* specialization has proceeded so far that the ovicell is at no time a zoœcium, although from its position in the internode it must be considered homologous with one. While the ova in this genus are a colonial production and always originate at the anterior edge of the branch, they are occasionally found in the individual zoœcia. Such instances may be regarded as representing an early tubuliporidan stage, or possibly a more primitive stage in which each zoœcium brought at least one ovum to maturity.

In regard to the time and place of fertilization, it may be said that since *Crisia* is dioecious the question arises as to the time when, and the manner in which the spermatozoa reach the ova. According to Harmer, fertilization probably takes place after the egg has been inclosed by its follicle and after the ovicell

has been started. He considers that the very thin wall of the anterior end of the ovicell is not impenetrable to the spermatozoa. If, indeed, the spermatozoa reach the ova at all, they must penetrate the tissues of the colony at some point. Whitman ('90) has shown that a method of impregnation somewhat similar to this is not uncommon in several groups of animals. In most of the cases he mentions the spermatozoa are forcibly injected through the cuticle, and wandering through the tissues, some succeed in reaching the ova. *Crisia* is covered with a calcareous layer which is pierced at intervals by pores that extend through the chitinous ectocyst beneath it. The epithelial cells of the body wall pass through these pores and spread out over the surface, forming a very thin layer upon it. These pores afford innumerable points where spermatozoa could effect an entrance. Moreover, near the growing tip the outer covering becomes thinner and the deposition of calcareous material does not keep pace with the growth of the branches, so that the growing points are covered with an extremely delicate chitinous layer only. Since, as has been shown, the ovaries are situated at the growing tips, it is practicable for fertilization to take place before, or at the time that the ovum becomes associated with the bud. The occasional occurrence of embryos in a zoœcium, as for example in the case shown in Pl. XIII, Fig. 16 (*emb.*), where cleavage has occurred, indicates fertilization thus early, as does also the early cleavage in an undoubted ovicell shown in Pl. XIII, Figs. 19 and 20. One of the blastomeres resulting from the first cleavage is shown in each of these figures (*bl.*). They are not surrounded by the cells of the polypide bud (*pd. bd.*), and yet the first division has taken place, so that cleavage occurs, apparently, at or before the time that the ovum is surrounded by the cells of the bud, and before the ovicell is formed.

The view that Harmer advances in regard to the time of fertilization is based upon his belief that the ovum is the product of the polypide bud ('97). He considers that only certain buds in each internode produce eggs, that these are equivalent to fertile polypides, and that they give rise to ovicells. The evidence from my own observations, however, proves that eggs are produced in every terminal internode, independently of either buds or poly-

pides, and that they become only secondarily united with buds. Moreover, it seems probable that *any* bud may form a union with an ovum, but that all such unions are not fertile, *i.e.*, do not produce embryos that give rise to larvæ. The view that fertilization may take place at a time earlier than that at which the ovicell is formed, and before the egg is surrounded by its follicle, is supported by the facts given above.

This brings us to the consideration of another possibility which correlates the probable degeneration of the male cells with a possible parthenogenetic development of the ovum. A most careful and thorough search has been made through both young and old portions of ovicell-bearing colonies for spermatozoa. None whatever were found, although their size is not so minute that they should be imperceptible with the high power of magnification used. The possibility of parthenogenesis has already been suggested by Smitt ('63), who, according to Claparède ('70) had observed the asexual development of the egg in the ovicells of *Crisia eburnea* and *C. aculeata*. Smitt's reason for supposing that the ova of several species of bryozoa develop parthenogenetically is mainly the failure to find spermatozoa. On this point Claparède remarks that from Smitt's account it seems probable either that the forms he reported upon are diœcious, or that parthenogenesis may occur in the bryozoa under certain circumstances. Of course, mere failure to find spermatozoa is insufficient ground upon which to base a belief in parthenogenetic development, and as a matter of fact, one of the species Smitt mentions, viz., *C. eburnea*, is diœcious. At the same time the evidence here given of degeneration of the testis adds weight to this suggestion, and the small number of spermatozoa compared with the vigorous growth of testis is not only remarkable, but may be correlated with the small number of ova that reach maturity either partial or complete. It is possible that this degeneration may be carried so far as to produce no mature spermatozoa whatever, or so few that their rôle in the economy of reproduction is reduced to the lowest degree.

Instances of the third class of ova (*c*), *i.e.*, those that fail of development, may be found in sections of the extremity of a branch where ova are frequently found in various positions,

sometimes upon the tentacle sheath of a developing polypide, sometimes lower down upon a septum, and sometimes free in the mesenchyme which fills the interior of the tip. In this last situation they frequently possess long processes which suggest that they have an amœboid motion. Their position, however, is to be attributed not so much to their own movement as to the fact that the tip has grown away from them, and has left them suspended in the network of interior cells. Pl. XIII, Fig. 17, represents a section in which two such ova have been thus left behind (*ov.*) and which, like those embryos which reach only a partial development, are absorbed. Measurement shows that the ova decrease in size as their distance from the growing point increases, and in the lower zoœcia no eggs are found, they having gradually disappeared.

A number of measurements of ova in various positions, *e. g.*, those in the ovaries, those on young buds or polypides, and those free in the different portions of the internode, shows that much variation in size occurs, but that these variations follow a regular law. Thus a gradual growth can be traced from the very small ova at the anterior edge of the tip, 5.4 μ in diameter, to older ones measuring 10.8 μ, 14.4 μ, and 18 μ. A parallel growth of the nucleus also occurs, those ova whose diameter is 10.8 μ possessing a nucleus of 7.2 μ, while those whose diameter is 14.4 μ and 18 μ have a nucleus measuring 10.8 μ.

The eggs attached to buds or polypides are, as a rule, larger upon the younger buds, and gradually diminish with the development of the bud. Instances are found where the ovum attached to the bud measures 21.6 μ with a nucleus 10.8 μ in diameter. A frequent size upon young buds is 18 μ, while upon older buds and polypides it diminishes to 11.7 μ and 10.8 μ, with nuclei varying in size from 9 μ to 7.2 μ. If the ovum develops even partially (Fig. 16, *emb.*), the blastomeres of the embryo, while large apparently, are smaller than the larger ova. In the instance shown in Fig. 16, *pd. 2*, the boundaries of the blastomeres are somewhat indistinct. One of them, however, measures 14.4 μ, while its nucleus is only 3.6 μ. Here, although the size of the blastomere as a whole equals that of some of the ova, the nucleus is much smaller. The outlines of

the others are too indisitnct for measurement. As a whole they are smaller than the upper blastomere, their nuclei measuring about 5.4 μ. The ova which fail of development and are free in the various portions of the internode, vary in size from 10.8 μ to 7.2 μ. Of these the smallest are invariably found at the greatest distance from the tip.

It is thus seen that ova increase in size from their origin at the anterior edge of the tip to the proximal border of the ovary. If, at this point, they unite with a bud, they may continue to increase somewhat in size. If the bud develops into a polypide, the ovum either becomes an aborted embryo or is absorbed without further development. Those ova which form no union with a bud are frequently found in the lower portion of an internode, much diminished in size. Those which develop in ovicells will be discussed later.

The data afforded by the preceding observations show that the time at which the genital products appear, both male and female, is much earlier than that at which the buds arise. The place of origin of each has also been shown to be different, and that the close relation existing between bud and ovum at a later period is secondary. Furthermore, it is shown that any bud may form a union with an ovum, *i.e.*, the possibility of a union between genital product and bud is the same for both males and females. As a matter of fact, however, every bud in a female colony does not unite with an egg, nor conversely does every egg succeed in uniting with a bud, a large number of ova undergoing degeneration. Of those ova which effect a union with a bud only a relatively small number give rise to larvæ, *i.e.*, become inclosed in ovicells. It seems probable, then, that certain buds only possess the possibility of developing into ovicells, viz., those which arise at that point in the internode where the ovicell is found. Any or every internode then has the possibility of being a fertile one. The questions are, Why does not every internode possess an ovicell? And why do some unions result in only a partial development of an embryo and no ovicell? What the determining factor is, is not known. A struggle seems to ensue between the two elements, bud and ovum, the one obtaining ascendency over the other. The result

may be due in part to the *time* at which the union is effected, *i.e.*, if the bud has already got started toward the formation of a polypide, the momentum of growth may be so great that the development of the egg has no power to change or hinder it. Whereas if the union takes place early enough, before bud differentiation has begun, the embryo gains the ascendency, and an ovicell results.

DEVELOPMENT OF THE PRIMARY EMBRYO.

The Ovicell.—Development of the embryo in *Crisia* takes place within a special structure, the ovicell. Smitt ('65) first called attention to the fact that the ovicell of *Crisia* develops according to the same laws as zoœcia, and Harmer has shown that in several genera of the Cyclostomata it is homologous with a zoœcium. The reasons for these conclusions are first, in *Crisia* the ovicell occupies a position in the internode similar to that of a zoœcium. In *C. eburnea* there are ordinarily seven zoœcia in an internode, so that ovicell-bearing internodes consist of six zoœcia and an ovicell, the latter taking the place of the second or third zoœcium.* Second, within the ovicell is found a bud which is equivalent to that found in a zoœcium. In the latter this develops into a tentacle sheath and the alimentary canal of a polypide, in the ovicell, into a tentacle sheath and the follicle inclosing the embryo. Third, in *Lichenopora* and *Tubulipora* the ovicell originates in an actual zoœcium. In the former it is the second or third zoœcium of the colony and functions as a brood pouch only after the degeneration of the first polypide; in the latter, any zoœcium may become an ovicell, and after it has already had one or two occupants.

Pl. XIII, Fig. 18, represents in optical section a decalcified tip containing a young ovicell (*ovl.*) in the so-called "funnel stage", in which is a very young embryo (*emb.*), and the beginning of the tentacle sheath (*tent.*). Starting with the chitinous articulation (*art.*) at the base of the internode, the ovicell is found in this instance to occupy the place of the third zoœcium.

* This statement may seem inconsistent with that made on p. 134 relative to the difficulty in locating early ovicell stages, but determinateness in the position of the ovicell is not accompanied by constancy in its occurrence, relatively few internodes possessing ovicells.

In the rear of the ovicell the continuation of the internode appears in the form of young buds. These would have eventually grown beyond the ovicell and have constituted the remaining zoœcia of that internode. Just what stage of development this embryo has attained, it is difficult to say, but judging from others of similar size and appearance it probably consists of three or four blastomeres.

Early Cleavage Stages.—It was remarked above that the earliest stages of ovicells are difficult to distinguish. In the sectioned material, no instance has occurred in which a single ovum is contained within an undoubted ovicell. There are many cases of juxtaposition of ovum and group of cells, but as has been shown the interpretation of this relation is not always possible. It is true that at an early stage an ovicell can be detected by its size, but on sectioning material that could be thus distinguished, cell division has always been found to have occurred. Since in *Crisia eburnea* the ovicell occurs in the proximal portion of the internode, usually in the place of the second or third zoœcium, it would seem relatively easy to secure the early stages by preparing in large numbers the young tips of colonies in active reproduction. This method was adopted, but without success in obtaining an undoubted ovicell containing an ovum previous to cleavage. In all of the earliest stages secured, the first cleavage at least had occurred, and there are reasons for supposing that cleavage usually occurs before the ovicell is definitely set off. Pl. XIII, Figs. 19 and 20, are consecutive sections of one of the three youngest ovicells obtained. The embryo consists of two blastomeres, one being represented in each figure (*bl.*). These latter are large ovum-like bodies imbedded in cells and lying distal to a mass of elongated cells which represent the polypide bud of an ordinary zoœcium (*pd. bd.*), and which seem to be arranging themselves around the embryo to inclose it. The cells of the embryo possess a large vesicular nucleus, and in size and appearance bear so close a resemblance to ova, that the question arises whether they may not be such. The strongest evidence that they are the result of cleavage is found in the relative size of nucleus and cell. Measurements of a large number of ova show that the ratio of the size of the

whole cell to that of the nucleus is 2:1.5 or less, whereas in the blastomeres it is 2:1 or more. This latter rule holds in the present case. Thus in Fig. 19, although the blastomere is as large as many ova, *i.e.*, 14.4 μ in diameter, its nucleus is only 7.2 μ, while in Fig. 20 the blastomere measures 9 μ with a nucleus of 3.6 μ. In the first the ratio is just 2:1, in the second it is slightly greater. Additional evidence that these bodies are not ova is afforded by the difference in their rate of growth since cleavage. In a second instance an ovicell in the same stage contained an embryo of two blastomeres still adhering to each other as if division had but recently occurred. The cells of this embryo are relatively very small, the two measuring 14.2 μ, about as much as a single ovum. The cells of the bud have much the same appearance and bear the same relation to the embryo as those shown in the bud of Figs. 19 and 20. That the latter represent an early stage in the development of the embryo is further shown by the fact that the blastomeres are not yet surrounded by the cells of the bud (*pd. bd.*). Nevertheless that some time has elapsed since cleavage occurred is shown again by the presence of the small cells between the blastomeres. Furthermore, the separation of the blastomeres shows that cell division takes place some time previous to or following very close upon the formation of the ovicell. In this ovicell there is yet no appearance of the tentacle sheath, the two lines of cells extending downward from the anterior border being those that form the vestibule (*vest.*).

A somewhat later stage of embryonic development is represented in Pl. XIV, Fig. 21. Here the embryo (*emb.*) contains at least three blastomeres which are not only surrounded by the follicle but are pushed apart and separated by the interior cells. The beginning of the tentacle sheath is shown in the layer of cells separating from the distal surface of the bud, the cavity formed between the outer surface of the bud and this layer (*tent.*) being the cavity of the tentacle sheath (*tent. cav.*). Here again the blastomeres have the same ovum-like appearance as in the two-cell stage, but they are smaller, the larger of them being 10.8 μ in diameter, and the other two about 7.2 μ. In this stage the cells between the blastomeres are smaller than those in

a similar position in the two-cell stage. The separation of the blastomeres and the interpolation of small cells is a characteristic of the early stages of *Crisia*, and in most older stages than the two-cell stage the blastomeres divide quite independently of one another. Pl. XIV, Fig. 22, represents a four-cell stage in which again are shown the separation of the blastomeres and the interpolation of the follicle cells (*sm. fl. cls.*). This ovicell is further interesting as showing the characteristics of the follicle cells. These now surround the embryo so that it lies in the center of a sphere consisting of a number of concentric layers composed of cells which form a net-work by the union of their protoplasmic processes (*fl. cls.*). In the interior of the spherical follicle the four blastomeres of the embryo may be distinguished by their larger size (*bl.*). The other cells of the interior (*sm. fl. cls.*) are of various sizes, those nearest the embryo being the smaller, those nearest the inner layer of the follicle, the larger. An examination of a large number of specimens shows that the multiplication of the small cells is accompanied by a diminution in number of the cells of the concentric layers. The former seem without doubt to be derived from the latter and to represent a stage in their absorption. Pl. XIV, Fig. 23, represents an embryo in the eight-cell stage, only four blastomeres being visible in this section. The separation of the cells of the embryo is clearly brought out, the blastomeres being perfectly distinguishable by their larger size and their different staining capacity. The increase in the number of small interior cells is noticeable as is also the decrease in the follicle inclosing the embryo.

This separation of the blastomeres continues to be a striking feature of the embryonic development of *Crisia* until about the twenty or twenty-four cell stage when the blastomeres unite to form a more or less compact ball. Harmer ('93, '97 and '98) has shown that it is characteristic of this and also of other genera of the Cyclostomata viz., *Lichenopora* and *Tubulipora*. In a recent paper, Braem reports a somewhat similar method of cleavage for *Plumatella*. According to this writer the egg of *Plumatella* consists of two quite distinct parts, an outer granular zone, and an inner zone containing the nucleus.

It is the latter only which takes part in cleavage and from which the blastomeres are formed. At the first cleavage the plane of division does not pass entirely through the egg, even of that part out of which the embryo is formed, and as a consequence the first two blastomeres, while being connected at one pole, fall asunder at the other. The undivided portion, called the middle piece (mittelstück), remains intact through the two, four, and eight-cell stages, while the blastomeres are widely separated at the animal pole. In the meantime the granular zone disintegrates more or less, its granules become larger, and nuclei appear between the free ends of the blastomeres. It is in the sixteen-cell stage that the resemblance between the embryos of *Plumatella* and *Crisia* is closest. At this time the middle piece disappears and the blastomeres being set free completely separate from each other. They continue to increase in number, although not regularly, while in the spaces between them are numbers of small cells. With further increase in the number of blastomeres, the small cells gradually decrease in number until, in the twenty-four cell stage the blastomeres having united into a ball, the small interpolated cells disappear almost entirely. From this point development proceeds in the regular manner. A comparison of the series of figures I to V in Fig. 104, Pl. IV, of Braem's paper, with Figs. 22, 23, and 24 of this paper will show the similarity of the cleavage in the two cases. The resemblance consists not only in the separation of the blastomeres but in the appearance between them, as if shoving them apart, of numerous small cells resembling those similarly situated in the embryo of *Crisia*. The function of these cells in both cases is probably identical, *i.e.*, they serve as nourishment for the embryo. As in *Crisia* the interpolated cells gradually disappear and the blastomeres unite at about the twenty or twenty-four cell stage into a solid ball.

The Ball Stage.—From the twenty-cell stage onward the embryo of *Crisia* forms, as has been said, a more or less compact ball. Pl. XIV, Fig. 24, represents an embryo measuring 43 μ in diameter and containing from sixty to seventy blastomeres which have united into a ball, although still surrounded

by the original follicle (*f.*). In this case the small follicle cells have not disappeared but may be seen packed together in the space around the embryo in the cavity of the follicle (*sm. fl. cls.*). Numbers of mesenchymatous cells forming a net work are present in the cavity of the tentacle sheath.

Pl. XIV, Fig. 25, represents a much older stage. This embryo is a compact ball with a well differentiated outer layer. Its greatest length is 150 μ, while the size of the separate cells varies from 5.4 μ to about 8 μ or 9 μ. At higher magnification these larger cells are shown to be in division, but mitosis does not seem to occur more actively in one part of the embryo than another. The absence of the follicle is very noticeable at this stage, but that its loss is probably more gradual than has so far been indicated, is shown by Pl. XIV, Fig. 26. This is a section of an ovicell of *Crisia occidentalis*, in which the embryo has attained about the development of that in Fig. 25. Here a portion of the original follicle remains in the chain of cells lying below the embryo (*fl. cls.*). These cells occupy the position and have the appearance of the follicle cells of other embryos, possessing the enlarged nuclei with scattered chromatin granules. In this ovicell a number of other cells are present below the embryo which represent a possible source of a second follicle (*sec. fl. cls.*). These latter are most numerous in connection with a chitinous tube (*chi. t.*) which extends from a septum (*sep.*) below the embryo to the base of the ovicell. In development this tube begins as a layer of chitin below the young embryo then consisting of only a few cells. Later the chitinous layer becomes more extensive and assumes a cone shape, the apex of which, with the continued growth of the ovicell, extends to the proximal extremity of the ovicell. Meantime a chitinous ring forms immediately below the embryo (*chi. r.*), dividing the ovicell into two parts. The tissue lining the ovicell is continued over the septum into the tube, and throughout its extent and in close connection with it there appears numerous large cells often possessing two or three nuclei, resembling the giant cells (*gi. cls.*) found in the ovicell of *C. ramosa*. The interior of the tube is filled with a net-work of deeply staining cells that extends above the septum and around the embryo. The chitinous ring or

septum,* (*chi. r.*) probably serves as a supporting structure to keep the embryo from passing downward into the narrow portion of the ovicell, but the whole tube seems to be related to the great development of the second follicle in this species. In *C. eburnea* the follicle of the adult ovicell consists of a relatively small number of cells scattered among its contents (Pl. XV, Fig. 28). In *C. occidentalis*, however, the second follicle is a mass of cells in which the embryos and larvæ are imbedded (Pl. XV, Fig. 29). With the disappearance of the spherical follicle and the appearance of a second follicle, the embryo attains a relatively enormous size before budding begins.

The Secondary Embryos.—An early budding stage is shown in Pl. XIV, Fig. 27. This is drawn to the same scale as Figs. 25 and 26, and a comparison with these two figures will give an idea of the great size which the embryo attains, this one being 200 μ. in its longest diameter. As the embryo increases in size it comes to occupy a higher position in the ovicell, moving upward apparently to the point where the walls are more widely expanded. This is especially noticeable in *Crisia cornuta* where the ovicell is widest at the distal end. The embryo is not anchored in any way in *C. eburnea*, and is often found at the top of the ovicell close against the valvular closure (Pl. XV, Fig. 28, *prim. ebm.*) Buds are formed at various places on the body of the embryo. In the case represented in Fig. 27, two somewhat irregular processes project distally, from the extremities of which small portions are constricted (*sec. emb.*). These are not the only budding regions, however, for on other parts of the surface outgrowths occur which as other sections reveal, are incipient buds (*in. bd.*) At the proximal extremity there are a few cells which the examination of preceding sections shows belong to another bud (*sec. emb.*). There are instances also where the first buds are constricted from the extremities of long arms extending proximally through the whole length of the ovicell. The primary embryo frequently possesses a somewhat rounded triangular form, and the buds are

* The septum found in the base of the ovicell of *C. occidentalis* is probably homologous with the chitinous articulation occurring on each zoœcium of this and the related species, *C. geniculata* and *C. cornuta*. Evidence for this homology will be given in a later paper.

given off at the apices. This is contrary to the observations of Harmer who finds that the primary embryo of *Crisia ramosa* buds only at the distal extremity. Calvet ('00) also represents the same condition for *Crisia denticulata*.

The buds of the primary embryo, from whatever portions of the body they arise, constitute the secondary embryos and from them the free swimming larvæ develop. When first set free the secondary embryos of *Crisia eburnea* consist of a small number of cells united into a solid ball, and varying in size from 25 μ to 35 μ in diameter, containing approximately from 55 to 65 cells. Redivision of the secondary embryos has not been observed in this species. In *Crisia occidentalis*, however, there occurs not only the formation of secondary embryos by budding, characteristic of *C. eburnea*, but also, in some cases, a redivision of these to form tertiary embryos. In these cases the primary embryo breaks up into large masses of cells, the secondary embryos, which in turn, become budding centres, from which tertiary embryos arise, these ultimately becoming the ciliated larvæ. This is illustrated in Pl. XV, Fig. 29, which represents a section of an almost adult ovicell of *C. occidentalis*. On examination of the series of sections to which this figure belongs, it is seen that the ovicell contains a few fully developed larvæ (*lar.*). The presence of these indicates that the primary embryo had budded off a few secondary embryos at an early period, and that, later, it divided almost simultaneously into a number of embryos. Some of these may have undergone no further division, while others notably the masses *a* and *b*, divided into tertiary embryos. The method of division in these cases is different from that which takes place in *C. eburnea*, although the result is the same. At the point where the division is about to occur, the nuclei arrange themselves into two linear series parallel to each other, or almost so. In this way two or more masses are formed which round up, separate from each other, and become the tertiary embryos. Many instances of this method of division are shown in the series of which Fig. 29 is a section. In the mass of cells, *x*, such a process is taking place. Pl. XV, Fig. 30 represents an embryonic mass, taken from another ovicell, showing two tertiary embryos (*ter. emb.*) which are forming from a large secondary

embryo. In *C. eburnea*, neither in the primary embryo nor in the buds when first set free, is there any differentiation into cell layers. As the primary embryo increases in size, the cells upon the surface become more compactly arranged, the inner cells forming a loose, spongy mass. The secondary embryos of *Crisia denticulata*, according to Calvet, possess two distinct layers, an outer containing large nuclei, and an inner containing much smaller nuclei surrounding a central cavity. This is true even before the buds are detached from the parent. This central cavity persists and forms part, at least, of the general cavity of the first individual of the new colony. When the secondary embryos of *Crisia eburnea* are first set free they do not differ histologically from the primary embryo. No cavity is present, the cells being heaped together in a somewhat irregular way. When a cavity appears it is not at first lined by a distinct layer of cells as is the case in *C. denticulata*. By the time the ovicell has completed its growth it is filled with larvæ of various sizes and in various stages of advancement. Fig. 28 is a section through an ovicell which is almost mature, *i.e.*, one in which the larvæ outnumber the embryos and will soon be set free. In this instance many of the larvæ have attained their full development and are confined in their narrow quarters only until the valvular membrane can be perforated. The larger larvæ possess long cilia, which fact suggests that either they move bodily through the ovicell, or that the vibrations of their cilia set up currents which carry the smaller bodies about. It is not uncommon to find the secondary embryos remote the length of the ovicell from the primary embryo, showing that the contents of the ovicell must have been in motion during life. The size of the larvæ seems to be pretty constant, at least in a given species. Those of *C. eburnea* measure about 86 μ in diameter, while those of *C. occidentalis* are somewhat larger, measuring 107 μ. The opacity of the living ovicell prevents any study of the living contents while the ovicell is intact. But if a living ovicell be crushed in a drop of sea water, a very interesting scene is presented. The larvæ dart away and swim about with great activity. Smaller ciliated balls move about in clusters. The color of the whole mass, larvæ, embryos, and cellular

tissue, is yellow. Perhaps the most interesting sight is the primary embryo which floats out with the rest of the material and frequently becomes isolated. It may easily be obtained by the dissection of a living ovicell, or from a stained decalcified ovicell dissected in a drop of oil. In the latter case the embryo is a more compact and clearly defined mass than in the former, but the characteristic features of both are the same. Projecting from the surface in various directions protuberances appear which are the buds of the secondary embryos.

Near the top of the ovicell represented in Fig. 28, the primary embryo appears much reduced in size, but still budding actively. As budding continues the primary embryo decreases in size, both as a whole, and in the size of its individual cells. This may be seen by comparing Figs. 27 and 31, the latter representing the primary embryo of Fig. 28 drawn to the same scale as that in Fig. 27. This, as has been said, measures 200 μ in length, while the older embryo (Fig. 31), measures but 71 μ in length. In the older embryo cell boundaries are less distinct, and the cells are more closely massed together. In examining a number of ovicells, primary embryos are frequently found much smaller than this, and much smaller than the contained larvæ. Thus in one instance the primary embryo measures 50 μ and the adult larvæ 86 μ. This ovicell contained a number of secondary embryos 25 μ in diameter. The secondary embryos in the older ovicells average slightly smaller than those in the younger. It seems extremely probable for several reasons that the primary embryo is completely used up in the process of budding. Evidence for this is found in the gradual decrease in size of the embryo resulting from its continued activity in budding. Again, the instance of *Crisia occidentalis* (Fig. 29) in which the primary embryo divides into a large number of secondary and tertiary embryos, so that no one of the masses present can be called the primary embryo, and in which each mass of cells is apparently either rediviling or is transforming into a larva, is strong evidence that no portion of the original embryo is left over. Further, complete series of sections of ovicells are obtained in which no primary embryo can be found, although larvæ and half grown, secondary embryos are abundant, and the aperture of the ovicell

is still unperforated. Finally, although empty ovicells are remarkably scarce, yet in one instance at least, a complete series was obtained which possessed neither larvæ, nor embryos, the interior containing nothing but a fine network and some degenerated cells. The evidence seems to be conclusive, then, that the whole of the primary embryo is converted into larvæ.

The number of larvæ to which a colony of *Crisia* gives rise is probably not less than is produced by other bryozoa although *Crisia* produces few mature eggs. As far as the evidence from my observations is concerned all the larvæ found in the ovicell, arise from one egg. Both Harmer and Calvet, however, believe they have evidence that more than one ovum may develop simultaneously within a single ovicell. Harmer ('97, Pl. 9, Fig. 25), represents two young embryos whose blastomeres are still separated, which he considers are the result of the development of two eggs. While this may be true, there is a possibility that the conditions presented may have resulted from the blastomeres of the two-cell stage of a single ovum having become so widely separated that each has gone on to develop into a separate embryo. The numerous recent experimental demonstrations of the power of independent development possessed by the blastomeres, and this too, in ova whose blastomeres normally retain their connection with one another, renders this hypothesis the more probable. Calvet figures a similar condition (Pl. 10, Fig. 15) which he considers affords undoubted evidence of the presence of two ova and of their simultaneous development within a single ovicell. Here again the facts may be differently interpreted. The two embryos may represent the individual development of two blastomeres which had become separated in the two-cell stage and had not reunited, or it may be an instance of a condition similar to what occurs in *Crisia occidentalis*. The two large masses, the two so-called primary embryos, may be two secondary embryos, and the smaller masses arising from these, may be tertiary embryos. The production of tertiary embryos is reported for *Lichenpora* and *Tubulipora*, but has not been previously found in *Crisia*. In the species in which it undoubtedly occurs, *Crisia occidentalis*, there is more or less variation, and it will not be surprising to find it in all species of the genus.

The protection and nourishment afforded the embryo of *Crisia* are typical of the Cyclostomata, and are paralleled to a certain extent among the Ctenostomata and the Phylactolæmata. According to Prouho, the Ctenostomes are, as a rule, viviparous, the different genera showing degrees of this condition varying from the primitive state exhibited by *Alcyonidium duplex*, where the young are sheltered during a portion of their development only, to that found in *Pherusa tubulosa*, for example, where several embryos develop in the tentacle sheath of a degenerated polypide. Joliet ('77), who studied the living animal, has given the most detailed account of the process. He shows that in *Valkeria cuscuta*, another Ctenostome, upon the degeneration of a polypide there appears in the zoœcium both an egg and a new bud. The latter grows into an immature polypide, but develops a tentacle sheath and the muscles belonging thereto. The small polypide soon degenerates while into the newly formed tentacle sheath the egg finds its way, and there develops into an embryo and ultimately into a larva. In both *Crisia* and *Valkeria* the development of the embryo is accompanied by the destruction of the polypide, and in both the embryo develops inside of the tentacle sheath newly produced to receive it, in the one case in a highly modified zoœcium, in the other, in an old unmodified one.

The developmental processes of the Phylactolæmata as exhibited by *Plumatella* show a closer resemblance in some respects to those of *Crisia*. According to Braem an ovary and a bud develop simultaneously on the body wall, the bud differing from an ordinary polypide bud in the possession of a high columnar layer and a flattened mesodermal layer. One of the cells of the ovary grows larger than the others, and partly by increase in its size, partly by pressure from behind, it approaches the side of the bud, pushes through it and becomes enveloped by it. This bud which according to Braem, Kraepelin ('93) and others is homologous with an ordinary polypide bud, now performs the function of a broodsac or oœcium, and shelters the embryo until it develops into a larva. The origin of the ovary of *Plumatella* appears to be similar to that in *Crisia* in its independence of a polypide. The suggestion of Braem, however, in regard to the relation sustained by the ovary of *Plumatella* and the bud which

forms the oœcium is probably true, viz., that ovary and bud together constitute the equivalent of a sexual animal, the nutritive portion of which, the polypide, has undergone a change of function. The complete envelopment of the egg by a polypide bud is similar in the two cases, but in *Plumatella* this bud is set off structurally at an early stage, whereas in *Crisia* any bud may be thus set apart, no structural difference between it and an ordinary bud being at first discernible.

In its main features, the processes of embryonic fission as described by Harmer for *Crisia ramosa* and other Cyclostomes have been confirmed by this investigation, while certain additional facts and individual variations have been noted. Observations have also been made on the origin of the sexual elements and their secondary union with the polypide buds. The results may be summarized as follows:

1.—In the genus *Crisia* the sexual elements are produced in both male and female colonies, at the edge of the growing tips of the colony. The germ cells arise from the mesodermal layer, and are differentiated at a point anterior to the budding zone, and at a time earlier than the origin of the buds.

2.—In the male colonies of *Crisia eburnea* a few of the primitive germ cells attach themselves to each bud as it arises, and these form the beginning of the testis. In a majority of cases degeneration of the testis probably occurs before the spermatozoa become mature.

3.—In the female colonies the ovaries are produced at the anterior edge of the young tips. As in the male colonies, in order that the germ cells may reach maturity, it is necessary that they unite with a polypide bud. In this case one of two results may follow:

a.—The ovum may develop into an embryo, while the polypide bud as such, becomes aborted.

b.—The polypide bud may develop, while the ovum either degenerates at once or soon after it has passed through the early cleavage stages.

Many ova are produced which never form a union with a polypide bud. These soon degenerate.

4.—From the time the ovum leaves the germinal epithelium there is a steady increase in its size until it reaches the boundary of the budding region. If here it forms a union with a polypide bud, the size increases somewhat until division occurs. If after this union is effected, the polypide bud develops, the ovum gradually grows smaller. Those ova which fail of development, decrease in size as they become more remote from the ovary.

5.—Fertilization, if it occurs, takes place before or near the time at which the union of bud and ovum is effected. In view of the probable degeneration of the testis the possibility of parthenogenetic development is suggested.

6.—During its development the embryo within an ovicell becomes gradually inclosed by the bud which forms into a spherical follicle consisting of several concentric layers of cells.

7.—A characteristic feature of the early cleavage of *Crisia* is the complete separation of the blastomeres. This continues up to the twenty or twenty-four cell stage when the blastomeres unite into a more or less compact ball.

8.—The separation of the blastomeres is accompanied by the penetration between them of numbers of small cells, and by the diminution of the concentric layers of the follicle. With the continued growth of the embryo, the follicle being absorbed by the embryo gradually disappears.

9.—The primary embryo attains a size many times that of the original ovum before it divides to form the secondary embryos. In *C. occidentalis*, the secondary embryos divide to form tertiary embryos which develop into ciliated larvæ. At the close of its proliferation the primary embryo itself becomes a larva.

University of California,
May, 1903.

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LIST OF ABBREVIATIONS USED IN THE PLATES.

art.—articulation.
b. b.—brown body.
b.—proximal extremity of a zoœcium.
ba. cls.—ball of cells.
bl.—blastomere.
chi. r.—chitinous ring.
chi. t.—chitinous tube.
d.—dorsal side of internode.
dc. cls.—degenerated cells.
dc. pd.—degenerated polypide.
ec. cls.—ectodermal cells.
emb.—embryo.
fl.—follicle.
fl. cls.—follicle cells.
ger cls.—germinal cells.
gi. cls.—giant cells.
gr. tis.—growing tissue.
in. bd.—incipient bud.
in. tent.—incipient tentacles.
l.—left side of the internode.
lar.—larva.
m.—membrane.
mes. cls.—mesodermal cells.
mes. tis.—mesodermal tissue.
ov.—ovum.
ovl.—ovicell.
ovy.—ovary.
pd.—polypide.
pd. bd.—polypide bud.
prim. emb.—primary embryo.
r.—right side of internode.
re. pd.—regenerating polypide.
sec. emb.—secondary embryo.
sep.—septum.
sm. fl. cls.—small follicle cells.
st.—stomach.
t. cls.—cells of the tube.
tent.—tentacle.
tent. cav.—cavity of the tentacle sheath.
ter. emb.—tertiary embryo.
tes.—testis.
tet.—tetrads.
v.—ventral side of the internode.
vest.—vestibule.
z.—zoœcium.

All drawings made with the aid of a camera lucida, and all figures except 1 and 18, by the use of Zeiss oculars and objectives.

PLATE XII.

Fig. 1.—Portion of a young decalcified internode of *Crisia eburnea* showshowing the growing tissue (*gr. tis.*), the budding region (*pd bd.*), and the alternate arrangement of the zoœcia (*z.*).

Fig. 2.—Section from the tip of a male colony, close to the edge, right or left, showing the character of the cell layers, the small round ectodermal cells (*ec. cls.*), the larger mesodermal cells (*mes. cls.*), and a few cells of the germinal epithelium (*ger. cls.*). × 600

Fig. 3.—Section from the same series as the preceding, showing practically the same cell layers at a point nearer the middle of the tip where the ectodermal cells are thinning out and are becoming elongated (*ec. cls.*). × 600

Fig. 4.—Section from a male colony through the budding region. In the angle toward the left edge of the branch, are a number of germinal cells (*ger. cls.*). Proximal to this is a young polypide bud (*pd. bd. 2*), still lower down is an immature polypide (*pd. bd. 1*) possessing a stomach (*st.*), and an incipient testis (*tes.*). × 600

Fig. 5.—Two spermatozoa from a ripe testis of *C. eburnea*. × 2500

Fig. 6.—Section of a zoœcium from a male colony showing a regenerating polypide (*re. pd.*), and below this a "brown body" (*b. b.*) extending to the base of the zoœcium. The brown body consists of a homogeneous mass of yellowish brown degenerated cells, the remains of the polypide (*de. pd.*) and the testis (*de. tes.*). 600

Fig. 7.—Section through a zoœcium containing a normal testis. Distally, the stomach (*st.*) of the polypide is shown, while extending into the base of the zoœcium is the testis (*tes.*) in which the cells are arranged in scattered groups of various sizes. Numerous groups of four nuclei (*tet.*) are visible. × 600

Fig. 7A.—Group of four nuclei (*tet.*) in a mass of cytoplasm. × 2500

Fig. 8.—Section from the growing tip of a female colony showing the two cell layers of the body wall, the outer or ectodermal layer (*ec. cls.*), consisting of small round cells, the inner or mesodermal layer (*mes.. cls.*) consisting of larger cells, part of which gives rise to the germinal epithelium (*ger. cls.*), part to the spindle-shaped mesenchymatous tissus (*mes. tis.*). × 600

Figs. 9 and 10.—Serial sections from the same tip as the preceding. The ova are accumulated in the corners (*ger. cls.*). × 600

PLATE XII.—*(Continued.)*

Fig. 11.—Section through the bud forming region of a female colony, showing the relation of the polypide buds and the germ cells. The latter (*ger. cls.*) are differentiated at a point anterior to that where the buds form. Four buds are shown, in the older of which (*pd. bd. 4*) the cavity of the stomach has formed (*st.*). The cells above the stomach are arranged in somewhat regular rows, and represent incipient tentacles (*in. ten.*). These are again shown in the third polypide bud (*pd. bd. 3*, *in. ten.*). × 600

Fig. 12.—Section from the ventral side of a female colony, showing the cells of the zoœcial wall, the outer layer of a polypide bud (*pd. bd.*) lying close to the septum (*sep.*) which separates two zoœcia. The germ cells (*ger. cls.*) are prominent in the germinal tissue (*ger. tis.*). × 600

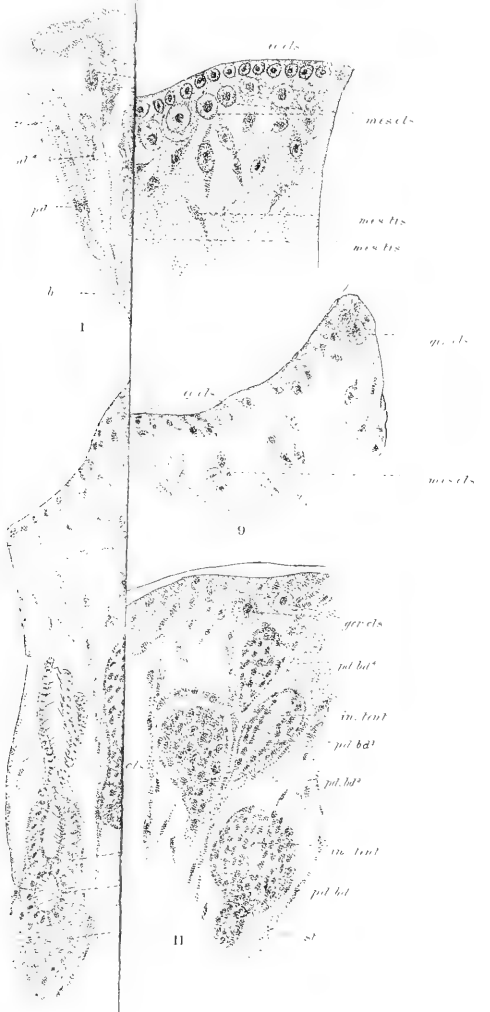

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PLATE XIII.

Fig. 13.—A section which follows the preceding in consecutive order, representing a portion of the same septum (*sep.*) and of the same polypide bud (*pd. bd. 2*). There are shown besides a portion of another bud (*pd. bd. 1*) and numerous large ova constituting an ovary (*ovy.*). × 600

Fig. 14.—A section following the preceding in consecutive order, showing a portion of the septum (*sep.*), and in the cavity of the branch a large ovum (*ov.*) in close proximity to a polypide bud (*pd. bd.*). × 600

Fig. 15.—Section through the tip of a female colony, representing a part of an ovary (*ovy.*), a few cells of a young bud (*pd. bd. 2*) and a portion of an older bud (*pd. bd. 1*) to the proximal extremity of which a large ovum is attached (*ov.*). × 600

Fig. 16—Section through the tip of another colony, showing two ova in the germinal epithelium of the anterior edge (*ov.*), a polypide bud (*pd. bd.*) with an ovum attached to its proximal extremity. In the next older zoœcium is an adult polypide (*pd. 2*) with a small embryo (*emb.*) attached to the cæcal end of the stomach, and in the succeeding zoœcium is a still older adult polypide (*pd. 1*). × 600

Fig. 17.—Section through the tip of a female colony showing two ova (*ov.*), which are attached by long processes to the interior the branch. These have formed no union with a bud and would have degenerated. × 600

Fig. 18.—Decalcified internode of *Crisia eburnea*, containing an ovicell (*ovl.*) in an early stage of development. At the proximal extremity is the articulation (*art.*), by which the internode is connected with the branch. Arising from the articulation are two zoœcia (*pd. 1* and *pd. 2*), while the ovicell takes the place of the third zoœcium. At the distal extremity of the branch, two or three buds are forming (*pd. bd.*). The ovicell contains a young embryo (*emb.*), and a tentacle sheath (*tent.*).

Fig. 19.—Section of a young ovicell, containing an embrye in the two-cell stage. This figure contains but one blastomere (*bl.*), not yet surrounded by the cells of the polypide bud (*pd. bd.*). × 600

Fig. 20.—Section immediately following Fig. 19, showing the second blastomere (*bl.*) of the embryo, a portion of the elongated cells of the polypide bud (*pd. bd.*), and the beginning of the vestibule (*vest.*) × 600

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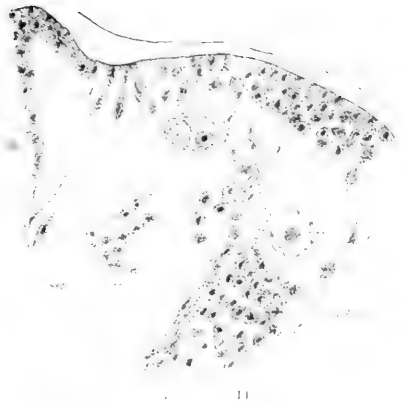

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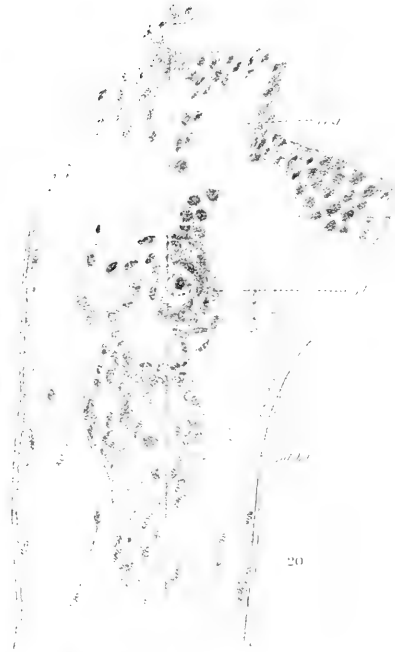

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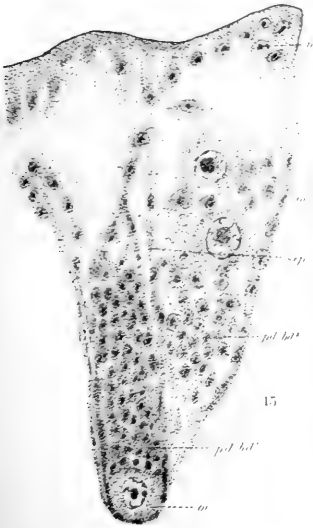

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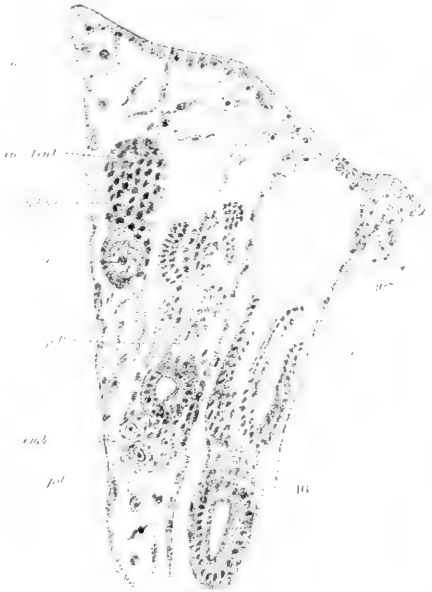

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PLATE XIV.

Fig. 21.—Section of an ovicell of *C. eburnea* containing an embryo in the three-cell stage. The outer layer of cells represents the tentacle sheath (*tent.*), and the cavity between it and the follicle (*fl.*) is the cavity of the tentacle sheath (*tent. cav.*). × 600

Fig. 22.—Another four-cell stage of *C. eburnea*, in which the blastomeres are separated (*bl.*) and between them are numerous small cells (*sm. fl. cls.*). The spherical follicle (*fl. cls.*) is diminished, the tentacle sheath is well developed (*tent.*), and below the embryo in the proximal portion of the ovicell are numbers of mesenchymatous cells (*mes. tis.*). × 600

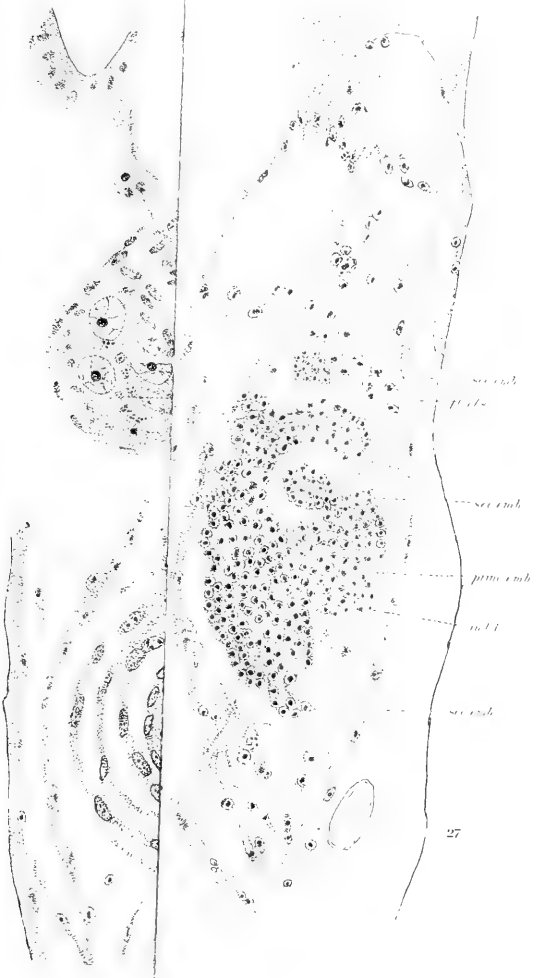
Fig. 23.—Section of an ovicell showing four blastomeres of an embryo in the eight-cell stage. The concentric layers of follicle have decreased (*fl. cls.*), while the small cells (*sm. fl. cls.*) interpolated between the blastomeres have greatly increased. × 600

Fig. 24.—Section of an ovicell containing an embryo whose blastomeres have united to form a ball (*emb.*) which is still surrounded by the follicle (*fl. cls.*). Close to the embryo are a number of the small follicle cells (*sm. fl. cls.*). × 600

Fig. 25.—An advanced stage in ovicell and embryo formation. The follicle cells have disappeared, and within the tentacle sheath above and below the embryo are a number of cells of the mesenchyme (*mes. tis.*). × 600

Fig. 26.—Section of a ball stage of *Crisia occidentalis* representing an embryo at about the same stage of advancement as that in the preceding (Fig. 25). A portion of the original spherical follicle yet remains (*fl. cls.*). Below the embryo is the chitinous septum (*chi. r.*), separating the ovicell into two parts. The chitinous tube (*chi. t.*) contains large numbers of cells forming a network. Among them are numbers of multinucleated or giant cells (*gi. cls.*). × 600

Fig. 27.—Section of an ovicell of *C. eburnea*, containing a budding embryo (*prim. emb.*), and a number of secondary embryos (*sec. emb.*). At various points on the surface of the primary embryo are a number of projections, indicating the formation of buds (*in. bd.*) or secondary embryos. The follicle is represented by a number of scattered cells (*fl. cls.*). The tentacle sheath is intact (*tent.*). × 300



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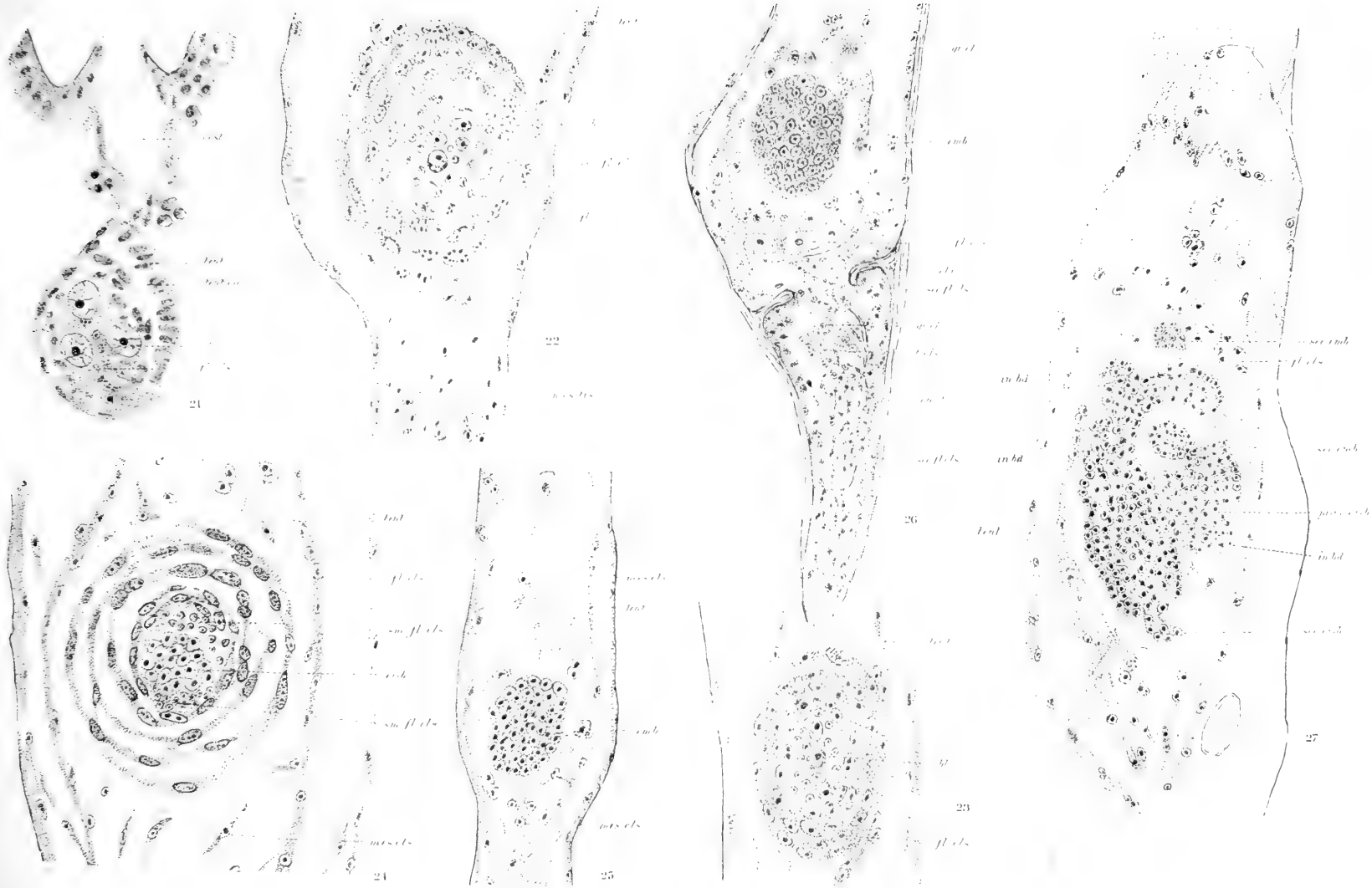

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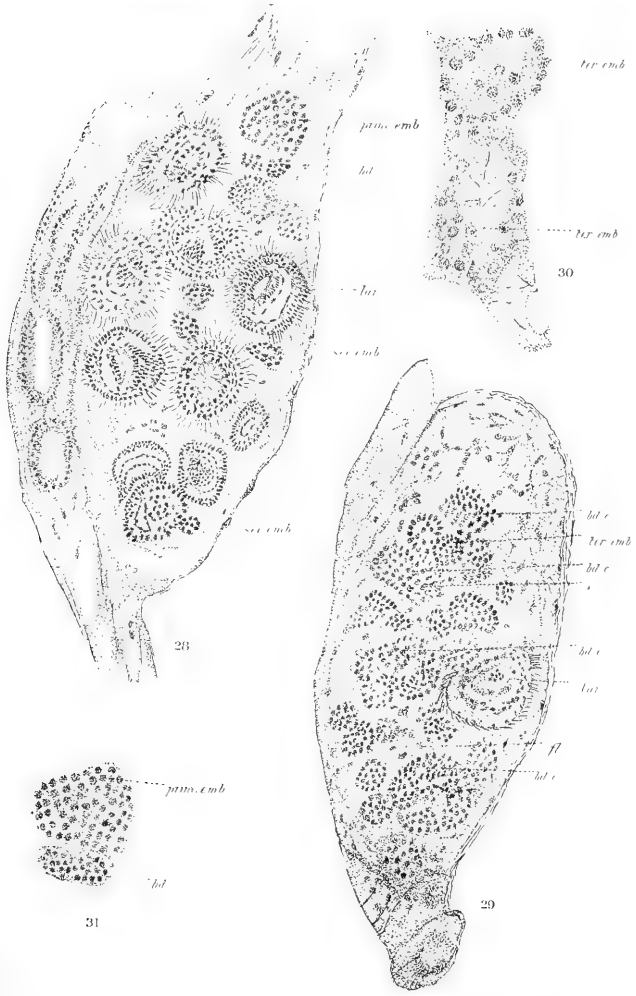
PLATE XV.

Fig. 28.—Section of a mature ovicell of *C. eburnea*, in which the larvæ outnumber the embryos. The primary embryo (*prim. emb.*) lies at the distal end of the ovicell, still giving off buds (*sec. emb.*). × 200

Fig. 29.—Section of an ovicell of *C. occidentalis*, showing the formation of tertiary embryos (*ter. emb.*), and the large amount of follicle (*fl.*). Tertiary embryos are forming from a number of budding centers (*bd. c.*), which are large secondary embryos. × 250

Fig. 30.—A single budding centre or secondary embryo from another ovicell of *C. occidentalis*, in which the two tertiary embryos (*ter. emb.*) are forming. × 2500

Fig. 31.—The primary embryo of Fig. 28 drawn to the same magnification as that of Fig. 27, to show the reduction in size of the former. × 300



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CORRELATED PROTECTIVE DEVICES IN SOME CALIFORNIA SALAMANDERS

BY

MARIAN E. HUBBARD

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MARIAN E. HUBBARD

The observations recorded in these notes were carried on in the laboratory of Zoology at the University of California. I am especially indebted to Professor Ritter for his kind and suggestive direction of the work. I wish also to express my thanks to Professor Charles A. Kofoid, to Dr. Harry B. Torrey and to Mr. Calvin Esterly of the Department of Zoology of the University, for kindly assistance; also, to Mr. Leverett Mills Loomis, Director of the Museum of the California Academy of Sciences, to Dr. John Van Denburgh, Curator of Herpetology, and to Miss Forbes, Assistant Librarian of the same institution, for the use of specimens and the library of the Academy. I am furthermore indebted to Dr. Lorenzo Yates, President of the Society of Natural History in Santa Barbara, for the use of specimens in the collection of that society.

Much has been written on the various skin glands of the Batrachia. Leydig, Engelmann, Wiedersheim, Zalesky, Schulz, Heidenhain, Eberth, Nicoglu, Capparelli and many others,* are among the investigators who have devoted more or less attention to the problems in this field, and Hoffmann, Nicoglu, Fatis, Wiedersheim and Boulenger in particular have given us valuable reviews of the literature and *résumés* of our knowledge.

* See bibliography at end of this paper for a somewhat more extended list of these investigators.

Beyond the questions of the structure and development of the glands, of their differentiation into such types as serous and mucous, of the chemical nature and physiological effects of the secretion, lies the fundemental problem of the *rôle* of the glands in the economy of the animals. This last problem has been much less studied than the others.

Some doubt is now being cast on the theories of protection in the animal kingdom that have been most in favor for half a century. Many structures and products of the organism hitherto regarded as sufficiently explained when they have been shown to be defensive are seen to owe their existence to more direct and simpler causes, as, for example, physiological activity, the effects of climate and other environmental influences, etc., and consequently if protective at all are often so only secondarily.

The study, the results of which are embodied in these notes, at first aimed merely at finding the nature of the enlarged condition of the tail in one species of salamander, *Plethodon oregonensis*. As the work advanced, however, its scope broadened until it touched upon the general problem of animal protection, the particular aspect of the problem chiefly involved being that of the correlation of protective devices.

The salamanders upon which observations have been made are *Plethodon oregonensis* Girard, *Diemyctylus torosus* Esch., and *Batrachoseps attenuatus* Esch. A fourth species, *Autodax lugubris* Hallow., occurs commonly at Berkeley, but does not enter into these notes because of the difficulty of obtaining specimens at the time the work was being done. Batrachoseps and Diemyctylus are very abundant, the former living under stones, old boards and rotting logs in damp, shady places, while the latter is found almost everywhere, but is especially given to congregating in the water of reservoirs and in quieter places in streams. Batrachoseps has a habit of burrowing in the soil, almost like an earthworm. Plethodon, though not so abundant as the other two species, is not uncommon. Like Batrachoseps it is found under rocks, logs and old boards, in moist, shady places. Neither of the last two species appears ever to enter the water.

Diemyctylus is diurnal in its habits, while Plethodon is nocturnal. I have never found a specimen of the latter abroad in

the daytime. Though conspicuous, it remains quiet when discovered under boards or rotting logs, not writhing or jumping about as Batrachoseps frequently does. Several times at night individuals in the terrarium were found alert and walking about, but the approach of the light soon sent them back to their hiding places beneath the bark and stones.

As stated before, this work began with the study of the tail of *Plethodon oregonensis*. This member in the great majority of cases is enlarged, the swelling being marked off from the rest of the body by a constriction just behind the anus. Out of sixteen individuals direct from the field fourteen were distinguished in this way, one of the exceptions being an immature individual, the other full grown. Of sixteen museum specimens fifteen showed the tail enlarged to a greater or less extent. The extreme of the swollen as compared with the unswollen condition is well shown in fig. 1, Pl. XVI. The tail segment in which the condition occurs is shorter than those immediately preceding and succeeding, as can be seen in figs. 1 and 2. This enlargement is independent of sex, for it is found in both male and female, in sexually immature specimens, and at any time of the year, regardless of the breeding season, which, as recorded by Dr. Van Denburgh, occurs in April. Thus I have noted it in specimens taken on the following dates. February 28, March 17, March 31 (sexually immature), April 17, August 20, October 1 and November 30, and its absence in two specimens taken March 17 and April 17.

At least some others of the urodela show a condition of the tail similar to that of Plethodon. In the collection at the California Academy of Sciences it was present in *Plethodon croceater* and in *Amblystoma opacum*. The former species occurs in California, the latter east of the Mississippi, from Massachusetts to Louisiana, so the peculiarity is not a matter of geographic range.

An examination of the tail, both macroscopic and microscopic, reveals the anatomical nature of the swelling. The dorsal half of the epidermis of this organ is covered with minute and thickly crowded pores which can be seen with the naked eye. These are present alike in tails enlarged and in those that are not, as shown in fig. 1. The skin of this region is enormously thickened.

Even in the unswollen tail it measures about one-sixth of the vertical diameter of the organ, but in the swollen ones it may reach one-fourth of this dimension, as in the one shown in fig. 4. The thickness decreases from a point just outside the median dorsal line, and becomes of ordinary depth at the meeting of the dark upper and light lower surfaces. From the caudal border of the anus to within nearly a millimeter of the tip this thickened skin sits like a saddle astride the tail's back.

A median dorsal groove occurs on the inner surface of this skin. The whole of the surface exhibits a marked granular appearance to the unaided eye, which is due, as can be seen with a hand lens, to the presence of distinct bodies so closely crowded together that they become five-, six- and seven-sided in outline. On cross section of the skin these bodies appear as columns about four times higher than wide, flattened at the inner ends, the spaces between the outer ends being filled with smaller cylindrical and spherical bodies, fig. 4, Pl. XVI. These structures prove to be greatly enlarged epidermal glands. Each one is made up of large granular cells, and opens to the exterior by a short duct. The smaller cylindrical and spherical bodies mentioned in the preceding paragraph are also glands. As will be seen in fig. 4, the large glands on the dorsal side of the tail grade into the small ones which occur on the ventral side of that organ, and, less thickly crowded on almost every other portion of the body of the animal. In the swollen tail they are closely set together and filled to the utmost with secretion, while in the unswollen one, as shown in fig. 5, they have discharged and new glands are forming.

In neither Diemyctylus nor Batrachoseps do we find any such development of tail glands. The skin everywhere of these species is richly provided with glands, and in Diemyctylus these are large and abundant in certain regions of the back, but they are not massed upon the tail.

It is evident from a comparison of the tail glands of Plethodon, both with those from other regions of the body of the same animal and with those of other species, that we are dealing here with structures widely distributed among the Batrachia. Numerous authors have described them in many species of both urodela and anura. Their massing along the ridge of the tail is not uncommon

in Amblystoma and Chondrotus, for Cope describes it in *A. punctatum*, *conspersum*, *opacum*, *talpoideum* and *copeanum*, *Chondrotus paroticus* and *decorticatus*, and at least in *A. opacum* the tail is swollen in consequence. Cope does not mention this condition in *Plethodon oregonensis* nor in *P. croceater*, though he does describe it in *P. glutinosus*.

The glands of Plethodon secrete a milky fluid which is poured out freely when the animal is stimulated by an induction current, either upon the back or upon the tail. In the same way they respond to the touch of a drop of acid, to irritation in the form of stroking with a knife blade, to a forcible holding of the tail either in the hand or in the jaws of a snake. That the secretion is acid is shown by its turning blue litmus paper red. It appears not to be mucus, for it is insoluble in water, or in water to which has been added ammonia or caustic potash or salt, whether the solutions are strong or dilute, cold or boiling hot. The glands upon the tail, as well as those from other regions of the body, likewise fail to respond to specific stains for mucus. Thionin, used by Nicoglu to discriminate glands of different character in various European Tritons, stains the sublingual of the cat, the oesophagus of Plethodon and the skin of the earthworm in three minutes, so that the mucus stands out in red violet upon the blue background of the rest of the cell. Mayer's mucicarmine also in fifteen minutes brings out the mucus in the cat's sublingual red against a pink background. None of the skin glands of Plethodon, when treated in these ways, give a mucus reaction. The secretion dissolves at once in a solution of hydrochloric acid. When exposed to the air it quickly hardens into a tough translucent mass. The least trace of it upon the tongue produces a drawing, drying sensation, with an astringent taste. In general the secretion seems to be similar to that of certain glands of other Batrachia, as of *Triton cristatus*, described by Capparelli.

Diemyctylus also, when stimulated electrically, yields a copious milky secretion, not merely upon the tail, but very generally over the whole dorsal surface. Batrachoseps, on the other hand, yielded very little.

Before we take up the question of the significance of these glands, we should consider another phenomenon of quite different

nature presented by two of the species under consideration, namely, the capacity for autotomy of the tail. Batrachoseps drops its tail very readily and on slight provocation, the break occurring at almost any point. It also regenerates this organ. Diemyctylus does not shed its tail. Plethodon stands between Batrachoseps and Diemyctylus in this respect, for though it can and does part with the member, it does this only under stress of the most untoward circumstances. Holding the animal by the tail, irritating it with acid or by an electric current produces no effect. It was not until individuals were put tail foremost, half way down the throat of a snake, that they finally parted with their caudal appendages, and it actually took four encounters with a ring-necked snake to bring off the tail in one specimen. Thus it would appear that Plethodon reserves this act of autotomy as a last resort, using it only when nothing else avails.

As has been said, the break in the tail of Batrachoseps occurs at any point. In Plethodon, on the other hand, so far as direct observation has gone, it comes only at the constriction behind the anus. Thus it took place here in three individuals which shed their tails in the terrarium, in two which were held in the throat of a snake, in one which was attacked by a snake, and it was seen in another which had been regurgitated. It occurred here in an individual which was placed in the killing fluid without a previous anaesthetic, and in numerous museum specimens, probably killed in the same way, the tail showed a weakness in this spot, breaking here very readily. Three specimens from the field were regenerating the organ from this point. In one case only did there seem to be an exception to this rule, and that was in an individual which was regenerating the tail at a point somewhat more than a centimeter from the anus, as shown in fig. 3, Pl. XVI. But this exception is of doubtful significance, for the tail may have suffered some accident or been bitten off, though it seems somewhat inconsistent with the general conclusion to suppose that the animal would permit this loss in preference to parting with the whole organ.

Dissection shows that the division occurs simply by an unlocking of the vertebræ, not by a break in the centrum, as in the case of self-amputation of the lizard's tail.

As might be expected, Plethodon has the power to regenerate the tail. Three specimens found in the field had tails about a centimeter long, white, somewhat translucent and pointed. When autotomy occurs naturally bleeding does not take place. In regenerating, the stump first rounds out with translucent tissue, and then there grows from the middle point a small bud, at first blunt and of uniform diameter afterwards pointed, as shown in fig. 2. It took a month, in an individual whose tail had been amputated, for a tip to grow about four millimeters long, but, as the conditions in this case were artificial, it would not be safe to draw conclusions therefrom as to the rate of regeneration in nature.

We may now return to the question of the physiological significance of the glands. From a comparison of the structure and action of the glands of Plethodon with those of other Batrachia in which the nature of the secretion is known, one is led to suspect that the secretion here is poisonous and protective. Numerous writers have described the product of the various forms of epidermal glands among the Batrachia as milky, acrid, and poisonous. Leydig, for example, as one of the older observers in this field, speaks of it as sharp, irritating, benumbing, and capable of producing death. Capparelli has worked out in great detail the poison of *Triton cristatus*.

In order to test the action of the secretion I made a number of feeding experiments with all three species here treated, the results of which follow.

Batrachoseps is eaten greedily, both by the garter snake, *Thamnophis elegans*, and by the ring-necked snake, *Diadophis amabilis*. At least five tests were made with the Batrachoseps in connection with these two snakes. The taste is perhaps not quite to the snake's liking, for in some cases there was a slight gaping after eating, but in no instance was there the least hesitation in attack. Only once did regurgitation occur and this once it may have been due to over-eating, for the snake had devoured three or four Batrachoseps in quick succession.

Diemyctylus, on the contrary, does not seem to be desirable as food. Out of eleven trials, at periods varying from one hour to a day, an individual of *Thamnophis elegans* only once attacked this

salamander, though the snake was hungry, as was proved by its readily eating Batrachoseps and tadpoles, and though the salamander was by no means too large to discourage an attack. Each time the Diemyctylus was introduced into the terrarium the snake became alert, moved toward the Diemyctylus and apparently made an examination, its nose coming close to the newt's body, its tongue darting out and in. After that the snake withdrew and seldom showed any desire to repeat the test. On the one occasion when the snake did make an attack it had fasted for eleven days. As soon as the Diemyctylus was introduced the Thamnophis made only a hurried examination, then seized the newt by the middle, and, working its jaws from side to side moved up nearly to the head. Then, instead of swallowing its captive, the snake slowly relinquished its hold and finally dropped its intended victim. That this foretaste of its anticipated meal was enough to satisfy the Thamnophis seemed clear, for it went about for an hour afterwards, opening its jaws very wide at frequent intervals, as if trying to get rid of a bad taste; and the lesson was learned so thoroughly that in the three remaining trials it took no notice of the newt.

With Plethodon the tests have been most instructive in connection with the ring-necked snake, *Diadophis amabilis*. This is a favorable subject for experiment, for, its haunts being the same as those of the salamander, it is no doubt a natural enemy. I had made numerous trials with the Plethodon, before finding a Diadophis, such as forcing a frog and a garter snake to swallow either the tail or the entire animal. On one occasion a garter snake, left with two small Plethodons, devoured both, but these specimens were both small and without tails, consequently could be eaten with impunity. In every case of forced feeding both frog and snake went through the act of gagging after eating, and one snake, after three days, regurgitated the whole salamander with only a portion of the head digested. The same frog ate a piece of raw meat of equal size and voluntarily took a number of tiny toads without gaping. On the other hand it is not safe to say that the gagging was in every case due to a bad taste or that the regurgitation was the result of disagreeable or poisonous qualities. The violent methods of feeding in these

experiments made the interpretation of the results doubtful, and, besides, did not fully answer the question whether *under natural conditions* the salamander is really protected by its poison.

After having tried the Diadophis, to see if it was hungry, by giving it a Batrachoseps, I waited a day and then introduced a swollen-tailed Plethodon into the terrarium with the snake. The snake was hungry and a series of encounters ensued. Three times the Diadophis had the Plethodon by the neck and would surely have disposed of it had I not beaten off the snake in order to give the Plethodon every chance to save itself. Three times the Diadophis seized the Plethodon round the middle and worked toward the caudal end of the body. Then each time, but not until then, the salamander poured out the milky secretion on its tail and the snake released its hold. Upon the fourth attack of this kind the Plethodon dropped its tail and wriggled away, only to lose the battle, for then the Diadophis devoured it tail and all, not however without some gagging afterwards.

The next morning, the Diadophis being in the same condition of hunger as on the day before, I put with it another Plethodon. As it crawled up upon the snake's coils, the latter became aroused and glided toward the salamander, its tongue darting out and in. The Plethodon, which had been perfectly motionless for some time, suddenly, without moving the rest of the body, raised its tail and with a *sidewise motion* struck the Diadophis squarely in the face. Somewhat daunted by this reception the enemy retreated, but in a moment or two came up again, this time from behind. When the snake's mouth was very near, the salamander, rigid in every other part of its body, suddenly raised its tail, as a cat arches its back at a worrying dog. At the same time the tail became covered with the milky fluid. Diadophis, making a brief survey, retreated again, and the Plethodon, after remaining motionless in this position for several minutes, long enough for me to make a sketch from which fig. 6, Pl. XVI, was drawn, gradually lowered its tail until it rested on the floor. The snake did not approach the salamander again.

It would be rash in most instances to draw conclusions from a single case or a single experiment, but there may be times when that single case or that one experiment is sufficient to determine

the point at issue. From this experiment, only one, it is true, but crucial, I judge that the tail glands in this species offer a partial protection to the animal. They may, perhaps by some offensive odor or by some irritating volatile product, ward off an enemy at times. But this means of protection is only partial, as shown by the experiments, for at times not even the taste of the secretion prevents the animal's destruction.

To summarize the results of the experiments: We have, in these three species, a graduated series so far as the relation of the power of autotomy and the presence of these poison glands are concerned. Batrachoseps yields comparatively little poisonous secretion when stimulated; Plethodon yields it abundantly on the tail and Diemyctylus pours it out very generally over the dorsal surface of the body. Batrachoseps is eaten with avidity by snakes. Plethodon is not rejected, but Diemyctylus seems not to be taken at all as food. In Batrachoseps, where the secretion is slight, autotomy occurs on *little provocation and at almost any point*. In Plethodon, where the secretion is restricted to the tail though abundant there, autotomy occurs only as a last desperate resource and but in one region. In Diemyctylus where the secretion is copious and general over the body autotomy does not take place.

Finally, passing from the region of fact and entering that of hypothesis, it seems fair to conclude that we have in these three species a case of adaptive correlation between autotomy and protective secretion. Batrachoseps appears to have, in its great tail-shedding power, some compensation for its limited defensive glands. Diemyctylus has no need of this, being sufficiently safe, so far as one means of defense is concerned, in its own abundant secretion. And, finally, it seems probable that when its tail secretion fails the Plethodon, this species sheds that organ to supplement the inadequacy of poison.

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PLATE XVI.

Fig. 1.—*Plethodon oregonensis.* From photographs of two alcoholic specimens, showing the extremes of the swollen as compared with the unswollen condition of the tail.

Fig. 2.—From a photograph of a living individual in process of regenerating the tail.

Fig. 3.—From a photograph of a living individual in process of regenerating the tail.

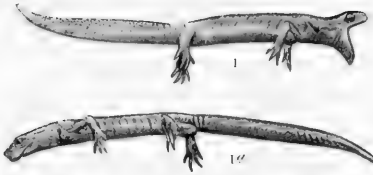
Fig. 4.—Cross section of the swollen tail, drawn with the camera lucida. Enlarged 7½ times.

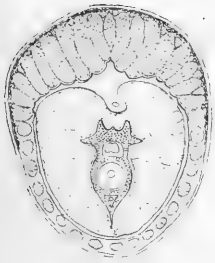
epd.—Epidermis. *l. g.*—Enlarged glands.

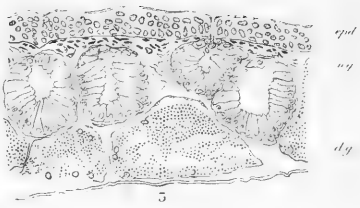
Fig. 5.—Cross section of the skin of the unswollen tail, drawn with the camera lucida under a low magnification.

d. g.—Discharged glands. *n. g.*—Newly-formed glands.

Fig. 6.—Drawing finished from a pencil sketch. This shows the Plethodon in the act of defending itself against *Diadophis amabilis.*







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STUDIES ON THE ECOLOGY, MORPHOLOGY, AND SPECIOLOGY OF THE YOUNG OF SOME ENTEROPNEUSTA OF WESTERN NORTH AMERICA.

BY

WM. E. RITTER and B. M. DAVIS.

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(From the San Diego Marine Biological Laboratory of the University of California.)

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In August, 1893, while the marine biological work of the University of California was being carried on at Santa Catalina Island on the coast of southern California, a few specimens of an undescribed species of tornaria were taken, Ritter, '94. The larva was not obtained again until June and July last. Throughout the period of work at San Diego last summer, the species was one of the most constant organisms of the plankton.

As only a few individuals of the new form were obtained in

* In the original description of this tornaria no name was given it. Spengel,'95, in his notice of the description proposed the name here recognized in accordance with the course pursued by him in naming the older species.

1893, and as through an accident most of these were lost, a brief description of it was all that was published at that time.

The observations made and material collected during the past summer enable us now to materially increase our information about this tornaria, so far as the later larval and earlier metamorphosing stages are concerned. Unfortunately, however, it was impossible, with the aquarium facilities possessed by the laboratory, to carry the metamorphosis through the later stages. We are, conseqently, obliged to leave some of the developmental questions that are in most urgent need of re-examination, practically untouched. Furthermore the earliest larval stages, upon the study of which the answers to several important questions of enteropneust development depend, did not occur in the tow.

What we now present on the structure of this larva is of interest rather from the ecological point of view, to which we have especially directed our attention, than from the morphological and developmental standpoint.

The most notable fact in connection with the distribution of the species during the season was its almost constant absence from the surface waters, and its equally constant occurrence at a depth of from twenty-five to one hundred fathoms. So far as we have definite records in only a single instance were specimens taken during the summer in the surface gatherings, while most of the hauls in depths as indicated above, over the "banks" (to be described later), at least with the large plankton net, secured specimens. It must be borne in mind, however, that closing nets were not used, and consequently that there was always the possibility that specimens came from the surface even when they were present in hauls from the depths. The evidence we have that they were taken below the surface is the fact that surface towings made simultaneously or nearly so in almost all cases secured none. But this evidence is sufficient to justify the conclusion that the larvæ were much more abundant at depths ranging from twenty-five to one hundred fathoms than at the surface. Another noteworthy probability relative to the distribution afforded by the season's collecting is that the parents of the larvæ were not living in the littoral zone, but on the "banks"

about eight miles off Point Loma, the nearest point of main land, in about seventy to one hundred fathoms of water. The observations upon which rest the probabilities here indicated relative to the habitat of the parents, were that the larvæ were always obtained much more abundantly over the banks than elsewhere. While the area covered by our collecting operations was not sufficiently extensive to justify the conclusion that they were entirely limited to this small spot, the constant absence of them from towings made in San Diego Bay and the outside waters between the banks and the main land, makes the point we are now chiefly interested in, highly probable, namely, that the parents did not live in the shallow water along shore, but in a depth sufficient to make it necessary for them to rise through a considerable number of fathoms in order to reach the levels at which they were taken; and, of course, to a still greater height in order to reach the surface. The bearings of this will be seen in connection with our study of the ecology of the larva.

With this as with all other known species of tornaria, we have no information except by inference as to the parent. What relevant facts we have point to *Balanoglossus occidentalis* Ritter (MS.)* as the parent. Of the three species of enteropneusta known to occur on the coast of southern California, we are now sure that *Dolichoglossus pusillus* Ritter (MS.) cannot be the parent (see the section, p. 200, on the embryology of that species). Of the other two species, *Stereobalanus willeyi* Ritter (MS.) seems to be excluded by its possession of two proboscis pores even in the adult, while no trace of a second pore is present even in the larva of the species now under consideration.

As previously stated, our studies on the morphology of the larva have been prosecuted from the standpoint of ecology. In the larval life of the enteropneusta three periods should be recognized; namely, a period of larval *development;* a *climactic* period; and a *metamorphic* period, *i.e.*, a period of development again, but this time development toward the adult animal.

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*For the benefit of those who have not followed the latest gyrations in the synonymy of the enteropneusta it may be stated that the genus *Balanoglossus* as here recognized is a part of the genus *Ptychodera* of Spengel's monograph. *Balanoglossus occidentalis* is a species rather closely related to, though still clearly distinct from, the well-known *B. clavigerus* Delle Chiaje of the European coasts.

Since the specimens collected this summer were none of them early enough to enable us to add anything to what is already known about the first period, namely, that of larval development, what we have to say concerning the structure and form begins with the

SECOND, OR CLIMACTIC PERIOD.

This period is characterized by the *maximum size* and *minimum specific gravity* reached during larval life; and by the height of development of distinctly larval traits, viz., the ciliary bands with their cilia; the several "fields" bounded by these bands; the apical nerve spot and its sense organs; the bulb-like form of the stomach; and the great size of the blastocoel cavity and the mass of secreted material by which this cavity is filled. Negatively the larva is characterized not only by the absence of several structural features which are present in the adult, but what is of more significance, the remaining in developmental abeyance of the whole coelom system, which made its appearance in a comparatively early embryonic time.

In treating of the form and structure of the larva, the full and excellent published accounts of closely related species renders it necessary for us to enter into details here on such points only as a fuller knowledge of the species and the aims of our present study, call for. The larva is somewhat larger than the measurements given by Ritter, '93, indicate. The following figures, in mm., were obtained by measurement of living animals of the largest size, at the climax of larval life, and in full expansion:

No. of Species.	Length.	Thickness at Ciliary Girdle.
1	2.32	.....
2	2.37	2.07
3	2.35	1.08
4	2.35	1.32
5	2.07	1.66

Plate XVII, Figs. 1 and 2, present front and lateral views, respectively, of the same individual. It is seen from these, as from the measurements, that the larva is broad in proportion to its height. Its anterior end is unusually flat, and the anal disc is bulging. The diameter of the body increases rapidly from

the oral field backward to the ciliary girdle, so that the sides form an angle much less than a right angle with the plane of this circle.

The tentacles of the longitudinal bands are short and are capable of very little if any movement. They stand out from the surface of the body, with an inclination, however, toward the circumoral field. As the number of these tentacles on each portion of the band is quite constant, it is worth while to enumerate them. There are about eight on the descending limb of both the ventral lobe and the anterior dorsal lobe, and six on the ascending limb of each of these lobes. There are about three on each side of the narrow lateral isthmus connecting the anterior and posterior transverse portions of the oral field. A single pair of tentacles, somewhat shorter than the longest ones of the series above described, is present at the narrowest part of the lateral lobe.

From our interest in the locomotion of the animal we have been led to study the cilia of the external surface with somewhat more care, it would appear, than has hitherto been bestowed upon them. These cilia are of three quite different sizes. The smallest and most abundant are those of the longitudinal bands. These have an approximate length of .007 mm. They are situated on the anterior longitudinal bands, from which it results that since the tentacles are looped-out portions of the band, each one is not ciliated on its entire surface, but only on opposite sides, Pl. XVIII, Fig. 8, *tent*. The greater height of the ectodermal cells on which the cilia of these bands are borne, and also the distinctness of their nuclei, are shown in this figure. The cilia are entirely confined to these bands. This fact is probably taken for granted by other writers on tornaria, but we have nowhere seen it definitely so stated. It is rather interesting in view of the uniform ciliation of the proboscis of the adult enteropneust, which is derived from the region of these bands of the tornaria.

In the ciliary girdle there are two distinct sizes of cilia. The smaller ones have a length of .08 mm., while the larger ones, the flagelliform cilia, as we may call them, are about .267 mm. long. The flagelliform cilia occupy the middle portion of the band, the

smaller ones being situated on both sides of these. The arrangement is shown in a diagrammatic representation of a cross section of the band in Pl. XIX, Fig. 15, and the size of these as compared with the cilia of the tentacles is shown in Pl. XIX, Fig. 14. In the living, active larva the movement of the large cilia quite obscures that of the small ones.

When the larva is subjected to narcotization with chloretone the movements of the cilia are no longer metachronous, and under these conditions the two sizes may be readily observed. They may also be seen on dying animals, and upon fragments of the band held under compression. The presence of these two sizes of cilia in the girdle seems to have escaped the notice of previous observers, though Morgan, '94, mentions the presence of a line of deeply stained nuclei behind the band that "I should expect to carry cilia during life."

From the physiological point of view the most interesting internal characteristics of the larva are the blastocoel and its contents, and the intestinal tract, the stomach in particular. The great size of the blastocoel cavity, even in comparison with the inflated stomach of all species of tornaria, is a familiar fact to all who have examined either the animals themselves or the figures published by various writers. The following measurements of a typical specimen of *T. ritteri*, together with a reference to Pl. XVII, Fig. 1, will serve to remind the reader of the relations under consideration: Diameter of the animal as a whole, 1.99 mm.; diameter of the stomach, 1.08 mm. From this it is seen that .91 mm., or nearly forty-six per cent. of the entire diameter of the animal is blastocoel space. Or, stated in terms of cubic contents, which of course is the more significant, we find that, in the same specimen, assuming both intestinal tract and the larva as a whole to be cylinders, the first situated within, and concentric with, the second, the blastocoel space is about eighty-four per cent. of the whole. As a matter of fact, however, the proportion would actually be greater, since the intestinal tract departs more from the assumed cylinder than does the body as a whole, both of its ends being much smaller relatively in diameter than is the stomach. A blastocoel space occupying ninety per cent. of the total volume of the animal is

a conservative estimate for a typical full grown larva. When now it is recognized that the blastocoel contains no organs excepting the mesoblastic pouches, and that these occupy but very little space, the two posterior pairs being wholly collapsed and thin walled; and further, that the great part of the bulk comes into existence in the course of the development of the larva, and disappears again in large part as metamorphosis progresses, it becomes quite clear that it must be a positive element in the organization and life career of the larva. Its significance is pretty certainly as a container of the mass of secreted material by which the diminished specific gravity of the larva is brought about. What is the source of this mass?

The sparceness of free cells within the mass is conclusive evidence that it cannot be the product of these cells. In the sections of some specimens scarcely any such cells at all are recognizable while in others they are somewhat more abundant. Nowhere, however, are they numerous. We fail, likewise, to find indications of a secretory activity in any part of the ectoderm that might be the source of the mass, and the mesoblastic pouches show even more clearly than does the ectoderm that they cannot produce it. The walls of these structures remain extremely thin during all the larval period. These three possible sources being excluded there remains only the digestive tract to look to; and here we do not look in vain. The *stomach wall almost certainly produces the mass.* Spengel has called attention to the fact that in some cases the nuclei of the cells of the stomach wall are nearer the inner than the outer ends of the cells, and that in the "basalen Theilen," *i.e.*, the *outer* portion of the cells, "gröbere und feinere Körnchen ansammeln." Plate XVIII, Fig. 10, shows a section of the stomach wall of an individual with the nuclei at the extreme of migration toward the inner ends of the cells. It will be observed that here they are situated in the inner third or even fourth of the cells. The thicker, clearer state of the outer ends is also seen in the same figure, though the full measure of the structural difference between the two ends is appreciated only by an examination of the stained sections themselves; for the inner, smaller ends take the coloring matter with a good deal more avidity than do the

outer ends. It is important to observe that the nuclei never get quite to the extreme inner ends of the cells and that the smaller inner portions of the cells remain distinctly protoplasmic; and further that the nuclei do not become flattened out and crescentic from pressure as so frequently happens in loaded gland cells, but on the contrary that they remain spherical throughout. The significance of this will be seen as we proceed.

The glandular nature of the gastric epithelium does not pertain in equal degree to the entire stomach wall but reaches its most pronounced expression on the two sides of the organ. Dorsally and ventrally the cells though usually having something of the same character, have it in but a relatively slight degree. That these cells are secretory and that the blastocoel mass is the result of their activity scarcely admits of doubt. Naturally, of course, one asks for the direct evidence on the point that would be afforded by observing the discharge of the secretion. While it is true that in a majority of the specimens examined there is an absence of such evidence, in a few instances we have, with little doubt, found it. Such evidence is furnished by the section shown in Pl. XIX, Fig. 13.

Here one finds a thin homogeneous layer on the outer surface of the gastric epithelium, from which there extend off into the adjacent coelomic mass more or less well defined tracts or bands in which the substance shows a fibrillar structure. These fibrils are almost certainly continuous with the homogeneous layer on the one hand, and with the coelomic mass on the other. They are the result of post mortem changes of the secretion in all probability but their relations show, according to our interpretation, the origin and destination of this secretion. In this particular specimen as in one or two others presenting a similar condition, the secretion is considerably more deeply stained than we have ever found it in specimens in which there is an absence of indications that the secretory process is going on.

The gastric cells appear to perform this secretory function up to the time of the initial changes toward metamorphosis; that is, to the first intimation of gill pockets. At least in all the stages studied precedent to the beginning of the pouches, we find the cells in the secretory regions either loaded with the secretion

and their nuclei pushed to the inner ends, as shown in Pl. XVIII, Fig. 10, or the secretion being discharged, as shown in Pl. XIX, Fig. 13. At how early a time, however, in the larval life the secreting begins we do not know, since we have, as already remarked, seen no very young larvae.

With the beginning of metamorphosis a change sets in in the gastric epithelium, and by the time the first two gill pockets are well developed, but before they have broken through the ectoderm, this change has come to be profound. Whereas during larval life proper the epithelium was relatively thin, the cells extending through its entire thickness, and the nuclei being approximately all in the same plane, at the stage of metamorphosis above indicated, the thickness of the wall has very greatly increased, and this increase is accompanied by the irregular scattering of the nuclei through this thickness, Pl. XVIII, Fig. 11. It now appears to cursory observation as though the cells do not all extend through the whole thickness, and perhaps they do not. All have, however, become much more elongated than any of them formerly were, and the distribution of the nuclei is chiefly the result of their having taken their places at different heights in the cells. But the most important change is in the structure of the cells. They are now becoming glandular again, but this time the *inner ends* produce the secretion, the nuclei being pushed towards the outer ends. The final discharge of this secretion into the cavity of the stomach may be readily observed. Pl. XVIII, Fig. 12 shows this state of the epithelium.

The question now arises, What, exactly, has taken place in this change? Have the new gland cells arisen by transformation of the old ones, or have the old ones broken down and been resorbed, the new ones having had their origin in cells that remained in an indifferent state during the larval secreting period? That the first is the method by which the result has been accomplished is capable of easy demonstration. The outer secreting ends of the larval cells break down, the protoplasmic inner ends become longer, and the nuclei, while moving farther away from the inner ends, do not remain at the very outer limit of the protoplasmic part where formerly situated, but come to occupy a position within the protoplasm. Pl. XVIII, Fig. 11

shows a stage in which the larval glandular condition has nearly disappeared, while the cells have become in a corresponding measure protoplasmic. The protoplasmic part stains distinctly though not intensely, while the outer glandular ends, *o. e.*, remain wholly unaffected by the stain, and have the peculiar refractive properties characteristic of lifeless, degenerating cell substance. At a stage a little later than that shown in this figure, the last trace of the larval glandular condition has wholly disappeared, though the cells have not yet become secretory at their inner ends. Then, finally, by the time the first pair of gill pockets has broken through the ectoderm, the cells have become glandular at their inner ends, and have begun to discharge their secretion into the cavity of the stomach. An early stage of this condition is shown by Pl. XVIII, Fig. 12, already referred to.

Whether this interesting two-fold function of the gastric epithelium at different periods in the life of the animal holds good for all species in which the tornaria occurs is not certain, though in all probability it does. Spengel has given us enough on the species studied by him to show that at least the earlier larval condition is there the same as here. His remark, however, which concludes what he has to say on the migration of the nuclei toward the inner ends of the cells, namely, that they "maintain this position in later stages," Spengel, '93, p. 399 seems to indicate that he did not follow the full course of the functional and structural changes of the epithelium. Morgan, '93, describes and figures the gastric epithelium in the species studied by him as composed of tall columnar cells, and in his second paper, Morgan, '94, wherein the metamorphosis is treated in detail, he makes no special point of the change of this epithelium. In this last paper, however, he gives us, under the heading *Growth*, a discussion at some length of a number of interesting developmental questions presented by the career of the tornaria as a whole. He here assumes that the "gelatinous fluid," as he calls it, that occupies the blastocoel increases in quantity during larval life, and through secretion from cells somewhere. "Whether, however," he says, "these cells are ectoderm, mesenchyme, or endoderm, I do not know."

To the interesting question that naturally arises as to whether the stomach carries on digestion at the same time that it is secreting the blastocoel mass we are not able to give a definite answer. It is certain that practically nothing in the way of food is found in the stomachs of any of the many preserved specimens we have examined; but it is likewise true that one may readily observe material in the stomach of the living larvae, though we have never seen it in any considerable quantity. We are of opinion that the animal is but little dependent upon food from outside sources during larval life, and that the gastric cells engaged in secreting the blastocoel mass are not concerned at all with digestion during this period. We have pointed out that not the entire stomach is devoted, in equal measure at least, to the secreting, and it is easy to conceive that those portions not so engaged, and particularly the intestinal wall behind the stomach, may perform the digestive function to the limited extent that is demanded.

Coincidently with the thickening of the stomach wall and its change of function as metamorphosis comes on, there takes place a narrowing of the interval between the ectoderm and the endoderm, and diminution, probably through resorption, of the blastocoel mass.

As we are now sure that the specific gravity of the tornaria is inversely proportioned to the quantity of the blastocoel mass, we can hardly escape the conclusion that the mass is produced *for the purpose of diminishing the specific gravity* of the animal, and so must itself be somewhat lighter than protoplasm. The question, then, of what the physical and chemical properties of the mass are becomes one of considerable interest. We have no information beyond that already possessed on the point. Morgan '94, states that "so far as microscopic examination of dead material goes, it shows that the fluid is much denser in the older stages." Our observations on the present species do not confirm this. But the nature of the mass needs more careful study than it has yet received.

The question of the duration of the climactic period is one of interest. Judging by all the evidence we have, both from the observations of others and of our own, on aquarium kept

larvæ, it is quite short. Full-grown larvæ invariably begin the metamorphosis within a day or two after being taken from the sea.

THE THIRD, OR METAMORPHIC PERIOD.

This, as already indicated, includes the whole series of changes, extending from the climax of larval development to and including the blocking out of all the organs and organ systems of the adult animal. These changes, named approximately in their time sequence, are as follows: (*a*) The bilateral thickening of the wall of the anterior mesoblastic vesicle as the beginning of the proboscis musculature. (*b*) The beginning of resorption of the ectodermal tentacles. (*c*) The reduction in size of the larva. This is initiated *by the narrowing of the anterior end* of the larva, and *is very soon followed* by the first intimation of the *constriction off of the proboscis.* (*d*) The origin of the first pair of gill pockets. (*e*) The transformation of the gastric epithelium (as already shown, for the sake of continuity in description, in the section on the first period); and finally (*g*) the thickening of the somatic layer of the two pairs of mesoblastic vesicles preparatory to the histogenic changes in these.

The purpose of the present study does not require us to follow the details of these changes. We are, to repeat, concerned only with certain points that present themselves with special distinctness from the ecological point of view.

Diminution in size is, as already shown, a general fact of a good deal of interest that characterizes this period. The period is, however, one of true development as well. The development consists of certain retrogressive changes on the one hand, and of progressive changes on the other. The retrogressive changes are, in order of time, first the resorption of the tentacles and flattening out of the ciliary bands and oral field; and second, the loss, at a rather late period, of the cilia of the girdle. It is well known from the published work of other observers that the ectoderm of the oral field is very thin—considerably thinner than that of the other regions of the larval body—and that this is due to the pronounced flattening and concomitant expansion of a

relatively few cells. Plate XVIII, Fig. 5, shows a portion of the ectoderm of both the oral and the extra-oral regions at the climax of larval life. The extra-oral, it will be observed, contains a large number of nuclei closely crowded and occupying the entire thickness of the layer. In the flattening out and thickening up of the ectoderm that takes place in metamorphosis, what happens? Does the thin oral portion as well as the extra-oral contribute to the ectoderm of the proboscis of the adult? If so the oral must, obviously, undergo much greater histological transformation than does the extra-oral.

Spengel believed that the extra-oral, or tentacular field, gives origin to the whole of the proboscis ectoderm, and that the oral field ectoderm undergoes degeneration and resorption. We have examined this point both on living animals and on sections, and are convinced that in this species, at least, the ectoderm of the oral field does not degenerate, but on the contrary thickens and becomes ciliated to form its share of the ectoderm of the adult proboscis. The series of figures, Pl. XVIII, Fig. 8, and Pl. XVII, Figs. 6 and 7, illustrate this. Figure 8 is from a larva at the climax of development and shows at *ec. or.* the thin ectoderm of the oral field with its flattened nuclei far apart; at *ec. ex.-o* some of the thicker extra-oral ectoderm with nuclei much more numerous; at *c. r.* a ciliated ridge with its closely packed, deeply stained nuclei; and at *tent.* a tentacle with the ciliary bands on its opposite sides. Plate XVII, Fig. 6 is from another larva at the very beginning of metamorphosis. Here it will be observed that the ectoderm of the oral field, *ec. or.*, is somewhat thicker, and that the nuclei are nearer together. This structure is now characteristic of most of the ectoderm of this field. Plate XVII, Fig. 7 is from a larva well on the way to metamorphosis. The tentacles are entirely gone, the musculature of the proboscis has reached an advanced stage of differentiation, and the whole ectoderm is much thickened. At *ec. or.* is a section of the oral ectoderm with remnants of the thicker ciliary ridges, *c. r.*, on the two sides. Not only, will it be observed, are the nuclei round and numerous here, but this ectoderm as well as the adjacent extra-oral ectoderm, has taken on the uniform ciliation which characterizes the whole ectoderm of the proboscis of the adult.

The interest in the question of the changes that take place in the ectoderm during larval life lies in the relation of this question to the large problem of growth and development of the larva. It appears that the difference in size and form assumed by the larva at different times in its career is more a question of the *distribution* of a nearly *constant quantity of body substance* than of the *addition* and *distribution* of *new substance*. Morgan, '94, was the first to call attention to this matter. He did not, however, any more than we have, bestow upon it the searching study it certainly deserves. We have not sufficient data, particularly as to the morphology of the first stages of development, and as to the food taken during larval life, to make a discussion of the fundamental problems involved profitable at this writing. We consequently are obliged to leave the subject for the present and rest content with having pointed out that the redistribution of substance in the ectoderm that takes place during metamorphosis is not a process, primarily at least, of the degeneration and resorption of the thinnest parts of the ectoderm, but rather of growth in the thin parts even more active than in the thicker parts. Morgan, '94, p. 61 has recognized stages, or periods, in the life of the tonaria, though he does not mark them off into the three here indicated, and in one respect our observations are at variance with his conclusions in a rather important point of fact. During the second phase of larval growth, he says, a continuous decrease in size takes place, "but," he continues, "*it is interesting to note that no new organs are formed while the larva is decreasing in size*." This last statement does not hold for the present species, for, as we have pointed out, at least one important set of new organs, namely, those of respiration, are initiated during this period. The first pair of gill pockets appear almost simultaneously with, or at least but slightly after, the beginning of diminution in size of the larva; or, in other words, almost coincidently with the beginning of resorption of the tentacles. We must recognize, too, the differentiation of the proboscis as being begun in this period. The very initial change toward the formation of this region of the body is seen in the beginning of the longitudinal musculature of the proboscis. It has been abundantly shown by other writers that

this is developed from the walls of the proboscis coelom, and, as we have pointed out above, the bilateral thickening which initiates the differentiation of these muscles is probably the very earliest step toward metamorphosis.

Although we were unable, with the aquarium facilities at command, to carry the development of the young enteropneust through the stages of most importance to the standing problems of chordate phylogeny involved, and consequently are compelled to leave this whole matter aside for the present, we deem it best to touch two points from this standpoint. We would first direct attention to the tardiness with which the axial skeleton of the adult state comes into existence in this species. (By the axial skeleton we mean the notochord plus the nuchal rod and its two limbs, associated with the notochord.) Although in the most advanced stages obtained, the animal had become distinctly an enteropneust, the three regions of the body being set off, the first pair of external respiratory stigmata and the neural canal both being present, there was still no positive intimation of any of the skeletal parts. With this tardiness in the development of the axial skeleton, there is a corresponding tardiness in the development of the musculature of the collar.

It is instructive to observe the movements of the young animal at this stage. While the proboscis is highly active, the radial muscle plates of this part being already well developed, practically no motion takes place in the collar or the abdomen. This we regard as of importance in connection with the effort of one of us, Ritter, '02, to correlate locomotion and the locomotor musculature in the adult with the axial skeleton.

The other point which we touch we are led to by the remarks in the preliminary communication of Ritter, '94, relative to the possible existence of an endostyle in this species. After describing a thickened ciliated band of epithelium along the floor of the esophagus, and a somewhat similar band joining this on the floor of the stomach, it was remarked that it is "highly probable that the esophageal band is, functionally at least, an endostyle"; and further, that "whether it be homologous with that organ in the chordata, is quite another matter." We regret that in spite of careful attention to the point, we are not yet in

possession of sufficient facts to justify a positive opinion as to the value of the suggestions made at that time. We prefer, consequently, to do no more now than make the following remarks: First, the esophageal band is not, as might be inferred, structurally wholly unique to this tornaria. Morgan, '94, has since figured, Pl. III, Fig. 5 of this paper, what is unquestionably the same thing in the esophagus of the Bahama tornaria, and in all likelihood the ventral wall of the esophagus is somewhat thicker than the lateral walls at least, in all species; and it is further probable that the esophageal cilia will be found to be confined to the ventral and dorsal sides with a preponderant development on the ventral side in most if not all species. Second, the doubt expressed in the preliminary paper as to whether the ventral esophageal band is a direct continuation of the ventral gastral band may now be removed. The two can be looked upon only as parts of one and the same band, though with different degrees of development in the two parts, the stomach part bearing stronger cilia, and being more strongly differentiated from the enteric wall in general, than the esophageal part. Third, the statement that the esophageal band probably has the same function of the endostyle in the Tunicates should be modified so as to include the esophageal and gastric portions together instead of being restricted to the esophageal part alone. Thus modified we would reassert this view, and point out in addition that the particularly large cilia of the gastric band and the posterior end of the esophageal band suggest the well known remarkably long cilia of the floor of the tunicate endostyle; and furthermore that in the gastric portion of the band, at least, there are almost certainly *some secretory cells.*

Fourth, and finally, while our renewed study of this point, so far as we have been able to carry it, has strengthened the suggestion of a general functional similarity between this band and the prochordate endostyle, it leaves the question of true homology as doubtful as ever.

(c) ECOLOGY.

We may now turn to the habits and activities of the tornaria. During at least the first and second larval periods the life

activities are about at the lowest level to which it is possible for them to be reduced and life still be maintained.

The whole round of metabolic processes, including food-taking, digestion, and assimilation, is in its simplest terms, if, indeed, food-taking is not wholly wanting for a considerable part of the time. The respiratory and excretory functions are on the simple protoplasmic level, there being not only no organ for either function, but there is nothing to lead one to suppose that any one portion of either the ectoderm or the endoderm is better fitted than any other for performing them. If there is anything that can be counted as corresponding to the circulatory function, this certainly consists in nothing more than a stirring up to a slight extent of the coeloblastic fluid, or semi-fluid, by the slow rythmical contractions of a simple vesicle contained within the fluid.

The power of response to stimuli is at so low a level as to be detected with difficulty by experiment.

One function, namely, that of body movement, universally recognized as one of the most characteristic marks of animal life, is performed, but only on almost its lowest plane. It is not by muscular, but by ciliary activity.

Really, then, the problems of the life activities of this animal are reduced almost exclusively to those of its body movements. These may be gotten at with a considerable measure of fullness, and in what follows, while we are keenly aware that the subject is not exhausted, we still feel that ground has been pretty well broken.

As has been pointed out in earlier pages, the eggs of this species are pretty surely deposited on the sea bottom in considerable depths of water. The larvae, on the contrary, are pelagic. Two questions grow directly out of these facts: By what means does the larva rise? What are the influences that cause it to rise?

Taking up these questions in order, we may give in a single sentence our conclusions with reference to the first. *The larva rises partly through a reduction of its specific gravity, and partly through swimming by means of its cilia.*

The facts relative to the specific gravity of the larva have been ascertained by experiment.

Specific gravity determinations were made on fifteen individuals. Gum arabic and white of egg were used to increase the specific gravity of sea water to correspond to that of the organism, according to the method employed by Miss Platt. '97 p. 121 footnote, and '99 pp. 31–28. Gum arabic was found to be somewhat more satisfactory than white of egg owing to its greater specific gravity, although for animals having small specific gravity the results were identical for both media.

For convenience of comparison the results may be divided into three groups. Group I will contain young tornaria of the latter part of the first period; group II, those having reached maximum larval development, from 2.00–2.60 mm. in length, corresponding to the second period; and group III, those somewhat advanced into the third or metamorphosing period. The averages are tabulated as follows:

	Group I (5 individuals)	Group II (7 individuals)	Group III (3 individuals)
Specific gravity	1.038	1.033	1.069

The "*overweight*," Ostwald, '02, representing the force by which a plankton organism is drawn downward and which must be overcome if the organism is to rise and maintain itself in the water, is expressed by the difference between the specific gravity of the organism and that of the medium in which it floats. The differences in overweight are relatively somewhat greater than indicated by the above specific gravities, owing to a slight variation of the specific gravity of the water in which the individuals of the three groups are living. The overweights are as follows: Group I, .0147; Group II, .0097; Group III, .0457.

Late metamorphosing stages sank rapidly to the bottom of the aquarium. The specific gravity of these was too great to be determined by the method used for the other stages. The relation of specific gravity to age of tornaria is approximately represented in text figure 1, on the next page.

That active movements are mainly concerned in overcoming the tendency to sink due to overweight is shown by the following comparison of sinking rates of active and narcotized specimens of same specific gravity under similar conditions:

Trials.	Kind.	Distance.	Min. rate per sec.	Max. rate per sec.	Av. rate per sec.
3	narcotized	300mm.	8.8 mm.	7.14mm.	8.33mm.
3	active	300mm.	5.88mm.	3.89mm.	4.83mm.

Swimming takes place chiefly, if not wholly, in one direction only, viz., from below upwards. It is accomplished mainly by the flagellate cilia, for when the action of these cilia is inhibited by chloretone the swimming is correspondingly affected. The motion of these cilia is comparatively slow, the girdle as a whole presenting to the eye a series of saw-toothed waves, Pl. XIX, Fig. 16[a], similar to those for the rows of cilia on the ciliary plates of Ctenophora figured by Verworn, p. 571. These waves travel contra-clockwise. Examination of narcotized animals, where the action of the cilia has become slow enough to permit of being observed, shows that their motion with reference to the entire animal is parallel with the body axis. This conclusion is confirmed by the fact that the direction of the water currents set up by the cilia is parallel to the longer axis of the body and toward the posterior.

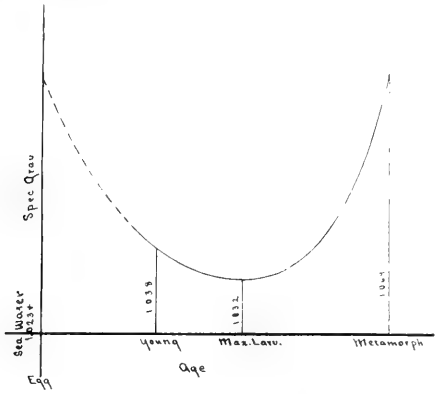

Fig. 1.

The egg probably has nearly the same specific gravity as the late metamorphosing, or adult stage. With this assumption the life history curve with reference to specific gravity is complete, the dotted portion representing the hypothetical decrease from egg to stage actually determined.

Tornaria rarely swims vertically upward but almost invariably takes a spiral course. The importance of this for economy of energy in overcoming the force of overweight of a plankton

organism may be illustrated by comparison with the upward flight of birds. The problem for swimming and flying is essentially the same so far as this element is concerned.

Concerning hovering in bird flight, LeConte, '94, p. 746, says: "In maintaining the body in the same position, as in hovering, the air gives way under each stroke of the wing, creating a downward current, thus diminishing the effectiveness of the down stroke and increasing the loss in recovery or the up stroke. In progressive flight, on the contrary, and more and more as progress is more rapid, every phase of the down stroke is on new air. . . . But if it is difficult, on this principle, to maintain one position as in hovering, it is evidently still more difficult on this principle to raise the body directly upward." Substituting water for air and cilia for wings, this principle applies to swimming and shows the advantage of a spiral course over one directly upward. New areas of water are constantly being put into motion by the cilia in the spiral progression of the animal without the retarding influence of downward currents.

The spiral course may be accounted for as follows: As the animal moves forward in the direction of its axis each cilium pushes sidewise against the water, throwing the body in the opposite direction. This action passes around the animal in successive sidewise pushes corresponding to the crests of the ciliary waves, Pl. XIX, Fig. 16[a]. If these crests are in pairs directly opposite each other, the sidewise push on one side will be neutralized by a counter sidewise push on the opposite side and the animal will thus maintain its axial direction. On the other hand, if the crests are not in pairs directly opposite each other, a spiral instead of an axial course will result. The latter explanation applies to the spiral course of tornaria, Fig. 16.

Besides the body movements just described, the animal slowly rotates around its longer axis. The origin of this action is not clear. Two possibilities suggest themselves which may account for it: The cilia may not strike exactly parallel with the body axis; or the depressions between successive waves may run obliquely across the ciliary girdle so as to form a turbine-like groove. It was impossible to determine by observation which of these, if either, is used. The fact that the rotary motion is slow

makes the former seem more probable, for rotation should, on the assumption of the latter, correspond in rate to that of the ciliary wave, which, however, is more rapid than the rotation.

As has already been indicated, vertically upward swimming is rare. Of the large number of individuals examined such movements occurred in a few instances, but only for very short distances. Usually a spiral course was taken; and likewise when sinking in perfectly quiet water the animal moved slowly in a spiral path until it reached the bottom of the aquarium. A detailed study of the rate and manner of sinking was made to supplement the observations on rising. Sinking rates were determined in two ways. In one, the animals were put in a long test-tube filled with water and corked tightly. Two marks 200 mm. apart were scratched on the tube some distance from the ends so as to give the animal space for orientation, and also to prevent counter influences of small air bubbles which were necessarily, to some extent, present. Trials were made by carefully reversing the tube from one vertical position to another, and the time of falling through the distance of 200 mm. noted by means of a stop watch. In the second method a large battery jar was at first used, but later, in order to get a longer column of water, a tall specimen jar was substituted. A fine line some distance below the surface of the water was marked on the side of the jar for the starting point. Animals were carefully placed below the surface film by means of a large pipette or floated from a watch-glass, care being taken to prevent water currents. By the time the starting line was reached the animals had oriented themselves and were moving normally. The tube method was abandoned because it was thought that the occasional friction against the sides of the tube might be a source of error. The results, however, were practically the same for both methods. Trials were made with individuals of different sizes, with all other factors constant except specific gravity, to determine variation in sinking rate due to difference in size, and to correlate this with variations in specific gravity. It was found that the smallest individuals fell through the distance of 300 mm. 20–30 seconds more quickly than the largest ones. Other trials were made in which specimens of different sizes were started from the same point at the

same time. With but one exception, small individvals reached the bottom first.

Further details may be seen by consulting the tabulation on page 193.

As has been shown, the size of tornaria varies with age. The larva increases in size to a maximum larval stage and then decreases with progressing metamorphosis until by the time metamorphosis is well advanced the young enteropneust is much smaller than the larva at its climactic period. Applying the above observations to age of animals, it will be seen that the rate of sinking is least for individuals of maximum larval development. Individuals of the metamorphosing stages sank more quickly than the larval stages, the older ones falling rapidly to the bottom of the aquarium. These observations are confirmatory of the conclusions drawn from specific gravity determinations.

We are led to recognize, then, that a primary purpose of the swimming operations of tornaria is to enable the creature to rise in the water, and to maintain itself in suspension after having risen. Is this the sole value of these operations, or do they in themselves accomplish something toward the horizontal distribution of the species? The maximum swimming rate of this tornaria, as determined by many observations, is about 6 mm. per second, or about seventy-one feet per hour. Over three days would be required for it to swim one mile. As the animal takes a spiral course and at a lower average rate, the actual horizontal progress is much less than these figures would indicate. The swimming mechanism would seem of importance chiefly in overcoming the pull of gravity, thus enabling the animal to rise and keep itself in suspension within certain levels. Instead of making progress in horizontal directions against waves and currents, it is dependent upon them for transportation.

W. Ostwald, '02, in his "Theory of the Plankton," in which he gives a careful analysis of the subject of flotation concludes that viscosity of the water in which an organism lives is the most important external variable factor concerned in the process. He says where other factors, such as form resistance, specific gravity, etc., are equal, the rate of sinking is inversely

proportional to the viscosity of the liquid in which the organism moves. Viscosity increases at the rate of about two per cent. for each degree of rise in temperature and also with the density of the medium through dissolved salts. In some cases where temperature and rate of sinking were noted we found this theoretical conclusion as to the influence of viscosity in a measure confirmed, *e.g.*, at 16° C the rate of sinking was 3.65 mm. per second; at 20° C 4.77 mm. per second; at 22° C 5.05 mm. per second. These averages are confirmatory to the extent that they show an increase in rate with increase in temperature, but the increase is above the theoretical amount of even three per cent. for each degree of temperature. The following tabulation of some of our typical results shows a still greater discrepancy between the actual and theoretical relation of temperature and viscosity:

No. of trials.	Sp. grav. of water.	Temp. of water.	Distance.	Max. rate per sec.	Min. rate per sec.	Av. rate per sec.
9	1.0242	16 C	200 mm.	5.00 mm.	2.63 mm.	3.53 mm.
10	1.0243	20 C	200 mm.	5.88 mm.	3.63 mm.	4.77 mm.
4	1.0243	22 C	200 mm.	5.55 mm.	3.63 mm.	4.54 mm.

Although these trials were made for another purpose, the conditions as to specific gravity and form resistance were constant enough to give the theory a rough test. A much larger number of observations with special care in controlling other variables will be needed to reach any definite conclusion as to the reaction of viscosity on rate of sinking.

What now, we may inquire, is the stimulus or other immediate influence that leads to the upward migration of the larva? Several possibilities suggest themselves. Pressure of the water, greater at the bottom where the eggs are hatched, and diminishing gradually to the surface, might be a factor in the case; or the presumably increasing oxygen content of the water from the depth upward may be the determining element. Again, the higher temperatures of the upper strata of water, acting directly on the organism or through the thereby diminished viscosity, the matter to which Ostwald has drawn attention, might be the sole or most potent factor.

We have no experimental evidence of our own, nor do we know of any produced by other investigators, upon which to base

definite views relative to these possibilities. As to the first two, however, a number of general considerations lead us to doubt their being real factors in the problem. Concerning pressure there would appear to be no good ground for supposing that this species of enteropneust is not, egg, young, and all, like other bottom dwellers, fully adapted to the pressure conditions under which it lives, and consequently would not be influenced by pressure to swim upward.

As to the possibility of oxygen as a determining factor, the problem presents itself in about the following way: In the first place, the obviously low grade of vital activities of the organism as a whole should be satisfied with a comparatively small supply of oxygen, which should be present at any of the depths here concerned. In the second place, the best information we have concerning atmospheric oxygen in sea water is to the effect that its dissemination is very little if at all dependent upon depth in itself, but rather upon secondary, local conditions, such as, for example, the abundance and kind of organisms. This being so, it is hardly to be supposed that there is a sufficiently constant increase of oxygen from the bottom upward, especially in a locality like that with which we have to do, wherein vegetable life and currents are extremely variable, to bring about so constant a reaction phenomenon as that of the upward migration of this organism.

As to the direct effect of temperature on movements, all our laboratory experience points to the conclusion that increase in temperature above that of the water in which the larvæ are taken, even by the smallest amounts, tends to retard rather than to accelerate the rate of swimming. On the interesting question of the effect on the movements of plankton organisms wrought by change in viscosity of the water due to change in temperature, we have already presented the little evidence we have, and need consequently only refer the reader to what is there said.

It seemed so likely that positive phototaxis might play at least a part in inducing the upward movement that we devoted considerable time to experimental studies on the point. As our results were almost without exception negative, it will not be

worth while to give them in detail. It will suffice to speak, so far as concerns the experiments that resulted negatively, of the methods employed. The one set of experiments that seemed to yield positive results will be given more in detail. To be wholly satisfactory, the following conditions of the experiments would have to be present: (*a*) In some experiments at least, the water would have to be exactly like that in which the larvae live in nature; (*b*) the stages in the larval life would have to be noted, and those of stages one and two would have to receive particular attention; (*c*) the larvae would have to be actively swimming; and, finally (*d*), the results most to be depended upon would be those obtained by light admitted from above in order that the swimming reaction, if induced, would cause the animal to move upward. Condition *a* was secured, so far as could be ascertained, with reasonable exactness. There was no difficulty in securing condition *b* excepting as to the very early larval stages, but this condition may be of considerable importance. The most serious difficulty was with condition *c*, and as a result of this difficulty condition *d* was only imperfectly secured. Our best efforts failed to a considerable extent in keeping larvae swimming with full activity far above the bottom for a sufficient length of time to carry out the experiment as thoroughly as was desired. The cilia were at work constantly, and seemingly with full vigor, but for some unrecognizable reason there was almost always an impairment of progression. Sooner or later the larvae would gravitate toward the bottom. In view of the fact that it was practically impossible to keep the animals constantly suspended, the effect of light on them in their slow downward course was repeatedly and carefully tried. A cylindrical glass jar 20 cm. in depth was arranged with one vertical half darkened, and the other subjected to light of various kinds and degrees of intensity. The larvae were then started on the dividing line at the top, with due care, of course, as to method of starting, and their tendency to either the dark or light sides, in their slow course downward, noted. The result of many trials of this sort showed at least as much tendency to the dark side as to the light. Another series of experiments was made by admitting light into the upper portion of the aquarium

while the lower portion, where the larvae were, was in darkness. The aim here was, of course, to see if the animals could be attracted upward. Although in some of these experiments the lighted zone was brought down to within a few centimeters of the larvae, the results were all negative. As the light rays in some of these experiments were directed horizontally and not vertically, the natural conditions were not exactly reproduced in these particular instances. Still another method of experimentation consisted in placing a glass aquarium containing many specimens indeterminately distributed in their swimming near the bottom, in direct sunlight, to see if they would manifest a tendency to assemble on either the light or the dark sides. Many trials of this kind were made, always, with two exceptions, negative in results. These exceptions were as follows: At the beginning of an experiment on July 8, of a total of thirty-seven specimens under observation sixteen were on the sunny side of the dividing line, and twenty-one on the dark side. At the end of one hour twenty-six were on the sunny side and ten on the dark. The aquarium was now turned 180°, and at the end of another fifty-five minutes twenty-four were on the sunny side and eleven on the dark side. The conditions of experimentation enumerated above as being essential to reliable results were certainly not more favorable in these particular two that produced evidence of positive phototaxis than in numerous others that produced no such evidence. Whatever vitiating effect the departure from ideal conditions of experimentation indicated in *d* and *e* might have, this, it would seem, should apply as well in those cases in which positive results were indicated as to those in which negative results were obtained.

We conclude, therefore, that while our results are not entirely beyond question, they strongly indicate that this tornaria reacts very slightly if at all, either positively or negatively, to light of the intensity to which it is subject in nature.

We come then to our conclusion as to the immediate influence that induces the upward swimming of this tornaria; that causes it to remain in suspension during its larval life proper; and that then determines the manner, *though does not cause*, its return journey to the bottom from which it started.

The cilia, by which alone the *swimming movement* is produced, work in a perfectly invariable way so far as concerns direction of stroke. The *direction* of *the movement* is determined by the orientation of the body, and the orientation is determined chiefly at least, probably wholly, by the *difference* in *specific gravity* of the two ends of the larva. This difference in specific gravity of the two ends is due chiefly to the *distribution* of the *coelomic mass* by which, as has been shown, the reduction of the specific gravity as a whole is accomplished. The anterior end of the larva is, during all the first and second part of the third stage, directed upward, quite vertically at times, but more frequently at a small angle with the vertical. The stroke of the cilia being, then, backward, the body is of necessity driven in general upward.

Concerning the specific gravity of the two ends, it will be seen from our account of the structure of the larva, and by reference to Pl. XVII, Figs. 1 and 2, that while the posterior end is somewhat broader than the anterior, and hence might from this fact by itself contain the larger portion of the coelomic mass, a distinctly greater proportion of the anterior end is occupied by the mass because of the absence from this end of any portion of the digestive tract. This tract contributes to the special reduction of the specific gravity of the anterior half in two ways: first by making room there through its absence for the larger portion of the coelomic mass, and second by its making in the posterior half the larger portion of the protoplasm of the larva. Not only, it will be observed, is nearly all of the voluminous digestive tract in the posterior half, but both pairs of mesoblastic vesicles are not only here, but are situated far back. Pl. XVII, Fig. 3, shows the position of these mesoblasts in *Tornaria hubbardi*, but the same fact would have appeared in quite as pronounced a way in *T. ritteri*, had the mesoblasts been shown in Figs. 1 and 2. Attention should be called also to the extremely small size of the single interior mesoblastic vesicle during the first and second larval periods.

When stating the changes occuring in metamorphosis in their true sequence, we have emphasized the fact that the reduction in size occurs first at the anterior end, and that

the histological changes in the anterior mesoblastic vesicle leading to the proboscis musculature begins very early. The result of these and other changes which affect the anterior end first and most pronouncedly is that this end probably comes to have a greater instead of a less specific gravity before the swimming life is abandoned, and as a consequence the orientation is changed, the anterior end becoming directed downward, so that the downward journey is made anterior end foremost, as was the upward journey.

2. *Tornaria hubbardi** n. sp.

An occasional specimen of a tornaria different from any hitherto described was taken along with *T. ritteri* at various times during the summer. This new species is particularly distinct from all others known in the large number of gill pockets present before any other indication of metamorphosis appears. At least five pairs of these could be seen on the living animal in the youngest larva taken; and at an early stage of metamorphosis seven pairs were present.

Another striking characteristic of the species is found in the ciliary girdle. When in a normal, fully expanded state, this is borne at the edge of a widely flaring portion of the posterior end of the larva, Pl. XVII, Fig. 3. At intervals along this expanded part occur scalloped thickenings, the convex edges of which are directed inward and anteriorward. About ten of these were present on the specimen from which Fig. 3 was drawn. When the animal is in a considerably contracted state, as, for example, was the case with this particular specimen when first seen, the intervals between these scallops stand out in prominent lobes, or flaps, Pl. XVII, Fig. 4.

The course of the anterior, ciliated bands is unusual. Instead of following the simple, typical meander found in such species as *T. mülleri* and *T. agassizi*, or of being produced into distinct tentacles as in *T. grenacheri* and its relatives, they have more

* Spengel's plan of giving tornariae the names of the authors who first describe them cannot be followed in this instance. We, however, come as near conformity as possible and gladly name this one after Miss Marian Hubbard, who rendered valuable assistance in the laboratory work connected with the preparation of this paper.

the character of those of *T. krohni;* that is, they are produced into a small number of broad, low, secondary lobes. These lobes are, however, less prominent in our species than are those of *T. krohni*. Still another distinctive point in the course of the post oral ciliated band is found in the posterior lateral lobe. Pl. XVII, Figs. 3 and 4. This, instead of projecting backward as it does in several species, for example, in *T. grenacheri*, and *T. ritteri*, projects forward as it does in the Bahama species of Morgan. The lobe is, however, much more prominent in the present species than in any other hitherto described. It is long-elliptical, the attachment being at one end of the ellipse. Although in general it is directed forward, it is at the same time inclined distinctly toward the dorsal side of the animal.

As is the case with several other species, the anus in this tornaria is situated excentrically, and is considerably nearer the dorsal circumference of the anal field.

The notochord, like the gill pouches, arises at an unusually early time in the larval life of this species. It could be clearly made out in the living animal, as a forwardly directed outpocketing at the anterior end of the esophagus, Pl. XVII, Fig 5, *n. c.* The nature of the broad shallow pocket shown in the figure between the notochord and the anterior pair of gill pockets, we were not able with the limited number of specimens available, to determine.

None of the other organs present anything noteworthy so far as our observations have gone. One of the specimens obtained was kept alive in the laboratory two days, during which time metamorphosis distinctly set in. At the time of its death seven pairs of gill pouches were present, but none of them had yet broken through the ectoderm, nor had the tongue bars developed on any of them. The proboscis had become clearly marked off and its musculature had begun to develop. No intimation of the collar region was yet visible, however, and the ciliated girdle was still present. The mesoblastic pouches, situated as in most species, far back in the earlier larval stages, already occupied positions relatively considerably farther forward, though the anterior pair had not yet reached the anterior end of the series of gill pouches.

The specimens of this larva did not seem to endure confinement as well as did those of *T. ritteri*.

No specimens were taken in the surface towings. All obtained were in nets that had been down to a depth of forty to seventy-five fathoms.

3. *Absence of the tornaria stage in the development of Dolichoglossus pusillus* Ritter (MS.).

The adult of this species is very abundant at several places on the southern coast of California, particularly at San Diego and in the inner harbor at San Pedro.

It is described by Ritter in MS. soon to be published, and a brief account of some of its habits has been given by him, Ritter, '02.

The following notes were taken from time to time during a period extending over six years. Observations were made at San Pedro where the animals have been very abundant, until recently, near the entrance to the harbor. The area of greatest numbers has gradually shifted toward the mouth of the harbor. None were found in 1902 in places where they were abundant in 1897. In 1900 there were two areas of distribution, one at low tide mark, where large individuals predominated; the other considerably above low tide mark, where small ones predominated.

The sexes differ slightly in color, the male being pale orange and the female somewhat brighter. At the time of the last observations, November, 1902, the males greatly exceeded the females in number. Sperm is discharged in a delicate milky stream through the pores of the ripe genital lobes. This observation was confirmed by detaching some of the lobes and watching the discharge under the microscope. The spermatozoan is small and has a spherical head.

Ova are discharged through the genital pores as observed by Morgan and others, and not through rupture of the body wall as stated by Bateson, '84, for *B. kowalevskii*. The eggs are almost perfect spheres. Their color and that of the young embryos is a light tint of yellow ochre.

Specimens containing ripe sexual elements were collected early in August and as late as December. The breeding season,

therefore, extends over a period of at least four months. Attempts were made at various times to artificially fertilize the eggs but with no success. In spite of careful search for fertilized eggs and developing embryos during each breeding season for several years, none were found until November 15, 1902. At that time, on examining a burrow containing a mature female, about twenty young embryos, some unhatched and some free, were found. Doubtless the failure of previous years was due to attempting to find the eggs in the sand instead of carefully looking for them in the burrows of females. Sickness prevented further search at this time. A little later the entire mud flat over which the animals were distributed was covered by the dredging operations prosecuted in connection with the harbor improvements at San Pedro. This destruction of collecting grounds has made it impossible, so far, to complete the series of stages necessary for a detailed study. Keenly appreciating the importance of such a study we hope to obtain sufficient material at San Diego to carry it out at some future time.

Among the specimens secured were a few stages of development from the late gastrula where the ciliary band was present to beyond the formation of the collar. The observations we were able to make, limited chiefly to the external features, confirm the only recorded description of direct development of Enteropneusta, Bateson, '84, in all important particulars except one: The neural fold makes its appearance later than in *B. kowalevskii*. A few points of minor importance may be added. The first groove, the anterior, of the collar of the embryo becomes distinct in three hours after the first trace of its appearance. The second groove, completing the collar, appears about fifteen hours later. The width of the collar when first formed is .016 mm., the length of the embryo at this time being .127 mm. The tuft of large bristle-like cilia at the end of the proboscis makes its appearance about the time the second groove is fully formed and before the embryo escapes from the egg. Animals do not swim freely but glide about with proboscis pointed forward over the supporting surface. These movements are made mainly by means of the large cilia composing the posterior ciliary band although their action ceases occasionally for short periods. At

such times the animal continues to move by means of the minute cilia with which the body is covered but the motion is very slow. The wave of motion of the large cilia is contra-clockwise when viewed with the animal moving toward the observer. These cilia are about .008 mm. in length.

No specific gravity determinations were made but the animals sank rather rapidly when placed in a vial of sea-water.

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ABBREVIATIONS USED IN THE FIGURES.

c. m.—coelomic mass.
c. r.—ciliary band of ectoderm.
ec.—ectoderm.
ec. or.—ectoderm of oral field.
ec. ex-o—ectoderm of extra oral field.
es.—esophagus.
g. e.—gastric epithelium.
i. s.—inner surface of gastric epithelium.
l. l.—lateral lobe of ciliary band.
m.—mouth.
mes. p.—mesoblastic pouch.
mes'y. c.—mesenchyme cells.
n.c.—notochord.
o. e.—remnant of outer secreting ends of gastric epithelial cells.
o. s.—outer surface of gastric epithelium.
st.—stomach.
tent.—tentacle of ectoderm.

PLATE XVII.

Fig. 1 and 2 are front and lateral views, respectively, of two specimens of *Tornaria ritteri*. These are not drawn to exact measurements, so the difference in size does not necessarily mean that the specimens were thus different. Both were practically at the climax of larval life.

Figs. 3 and 4 are both from the same individual of *T. hubbardi*. 4 shows the larva as it appeared when first brought to the laboratory, while 3 represents the condition it was in after a day's sojourn in the aquarium.

Fig. 5.—Represents, in optical section, the esophagus, *es.*, and a small portion of the stomach, *st.*, of the fully developed larval stage of *T. hubbardi*. Only six gill pockets are shown in this case, but at a slightly later time another, making seven, was present. The notochord is seen at *n.c.* *All remaining figures are from T. ritteri.*

Fig. 6.—Is from a section of the ectoderm partly, *ec. or.*, oral, and partly (the remainder) extra oral, immediately after the beginning of metamorphosis. It should be compared with Figs. 7 and 8.

Fig. 7.—From a section, similar in position to that shown in 6, of the ectoderm of a larva well advanced in metamorphosis.

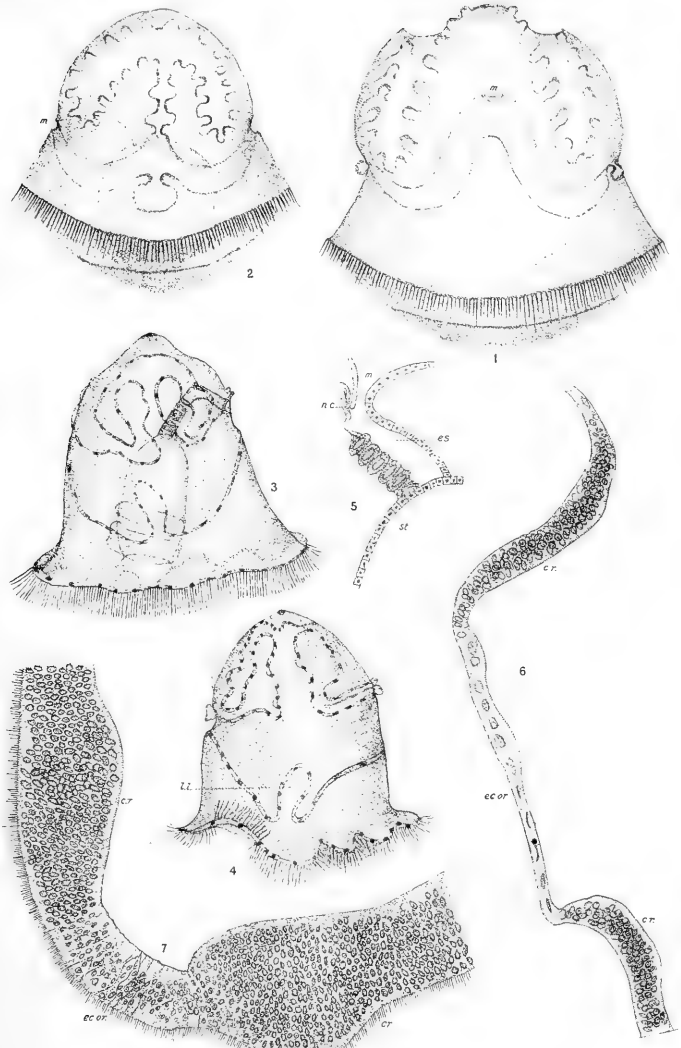

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PLATE XVIII.

Fig. 8.—Section from an individual at the climax of larval life, showing the ectoderm in a region similar to that shown in Pl. XVII, Figs. 6 and 7. The order with reference to stages represented of 6, 7, and 8, should be 8, 6, and 7, with a considerably greater interval between 6 and 7 than between 7 and 8.

Fig. 9.—Section of a larva in the early portion of the third period (metamorphosis but slightly advanced) to show particularly the coelomic mass, *c. m.*, with its few mesenchyme cells, *mes'y. c.*, and the character of the cells of the ectoderm, of the mesoblastic pouches, *mes. p.*, and of the digestive tract.

Figs. 10, 11, and 12 are from sections of the stomach wall at three distinct larval stages. 10 is of a stage rather late in the first period of larval life, and shows the gastric cells filled with secretion *at their outer ends*. 11 is from a stomach shortly after metamorphosis has begun. Here the external secreting ends of the cells have almost though not quite disappeared. 12 is from a larva well advanced in metamorphosis. Here the *inner ends* of the cells are distinctly secretory, and the nuclei are situated at the outer ends.

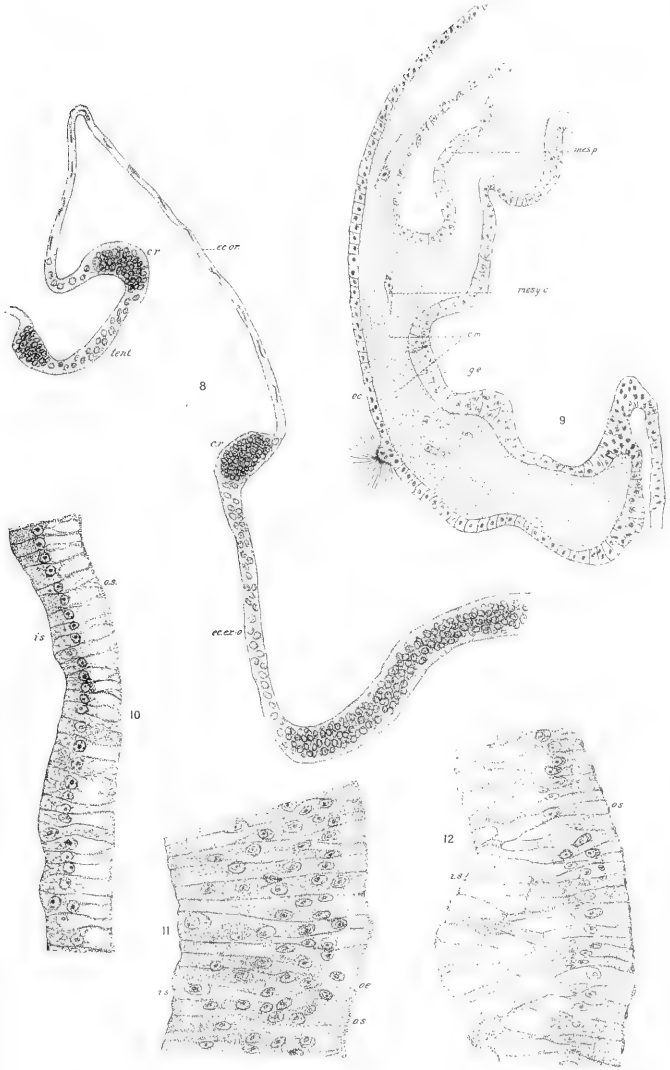

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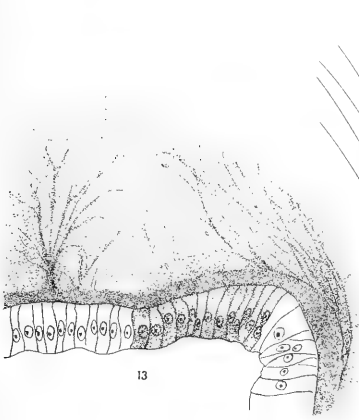
PLATE XIX.

Fig. 13.—Shows the secretion of the gastric epithelium being discharged into the coelomic cavity.

Figs. 14 and 15 are from sections of the ectoderm of a larva in the climactic period. They are drawn to the same scale and are for the purpose of contrasting the cilia of the ciliary girdle, Fig. 15, with those of the anterior portions of the body, Fig. 14.

Fig. 16—Is a diagramatic illustration of the swimming movements of the tornaria. The small circle 16^a represents the larva itself, the radiating lines around the circumference indicating the cilia of the ciliary girdle, and the groupings of different lengths indicate the waves. The arrows in this circle show the direction of travel of the waves. The large circle represents a projection of the spiral described by the larva in its forward progression.



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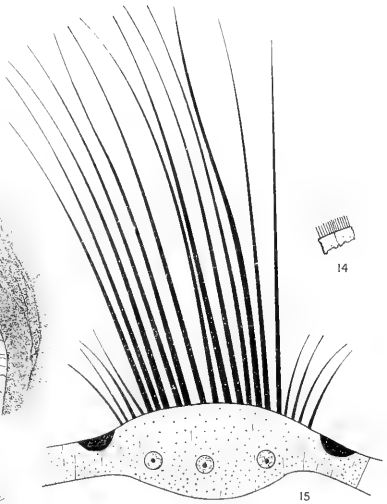

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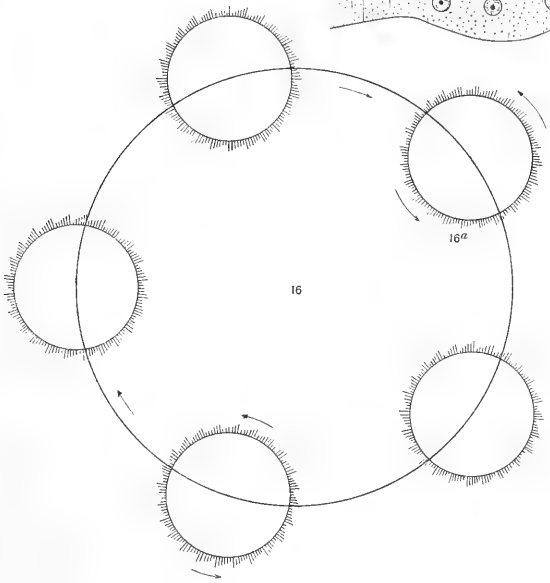

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REGENERATION AND NON-SEXUAL REPRODUCTION IN SAGARTIA DAVISI

BY

HARRY BEAL TORREY AND JANET RUTH MERY

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This paper embodies a preliminary account of investigations, as yet unfinished, the present results of which it has seemed desirable to publish without waiting for the completion of our work.

I. NON-SEXUAL REPRODUCTION IN SAGARTIA DAVISI.

S. davisi reproduces non-sexually by longitudinal fission only, though in some cases the fission resembles rather closely in some respects the process of basal fragmentation so common in *Metridium* and, according to G. C. Davenport ('03), probably occurring in *S. luciae*, the eastern representative of *S. davisi*. Three types of fission are distinguishable in *S. davisi:*

1. Aboral-oral fission by constriction, accompanied by rupture.

2. Aboral-oral fission by constriction alone.

3. Fission proceeding from side to side, by rupture.

McCrady ('58) observed aboral-oral fission in a South Carolina cribrinid which he called *Actinia cavernosa*, but he did not see the completion of the process. G. C. Davenport has recently (:00, :03) observed similar phenomena in *S. luciae*, following the process to completion. In the descriptions of both authors few details are mentioned, and no distinction is made between fission by constriction and fission by rupture. Carlgren ('93) has recorded a case of aboral-oral fission in *Protanthea simplex;* but, as Torrey ('98) indicated in commenting on a

similar case in *Metridium*, such exceptions may be due to accidental rupture of the foot disk rather than to a normal fission process.

The third type of fission enumerated was observed by Mrs. Thynne ('59), in what she asserted to be a species of caryophyllian coral, though it is questionable whether the corals were not really anemones. According to her account, the eggs of *Cyathina smithi*, laid in her aquarium, produced polyps which grew to adult size without forming skeletons. It was among such individuals that she obtained the following facts regarding their non-sexual reproduction. The mouth expands, and the polyp assumes a rectangular shape; the body wall, oesophagus, mouth and foot disk between any two adjacent corners break down; the same thing then occurs between the other two corners, dividing the mother into two portion. Each of the latter ordinarily divides again, so that ultimately four pieces, corresponding to the four corners of the rectangle are isolated and become perfect by regeneration. Occasionally but two or three polyps arise from one in this way. *S. davisi* reproduces similarly; *S. luciae* will probably be found to be in the same category.

In every process of reproduction by fission, a period of destruction (fission) can be more or less clearly distinguished from a period of construction (regeneration). In describing the methods of non-sexual reproduction which are associated with the three varieties of longitudinal fission in *S. davisi*, it will be convenient to make use of this distinction.

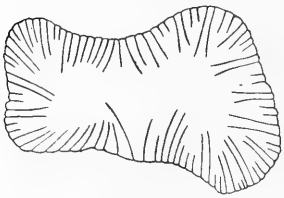


Fig. 1. The elongated foot disk in an early stage of division, the mesenteries arranged in two systems. From below.

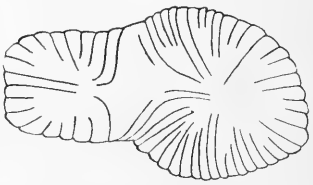


Fig. 2. Foot disk of dividing polyp from below. Tension indicated by course of mesenteries.

1. The first method to be considered may be characterized as aboral-oral fission by constriction and rupture, with subsequent repair.

(*a*) Fission. The first signs of division appear in the rearrangement of the mesenteries on the semi-transparent foot disk, and the elongation of the latter along a line parallel with the major axis of the mouth by the active locomotion of two opposite regions away from each other. The typical arrangement of the mesenteries is strictly radial, around a single center. When division begins, the original center gives way to two (Fig. 1), which move farther and farther apart as division progresses.

A glance at Figs. 2 and 3 may make clear what is very apparent in the foot disks from which they were drawn, that the divergence of the centers is accompanied by a tension, which particularly affects the region between them, and is indicated by the course of the mesenteries. The boundary between foot and column, never sharply marked, becomes less and less distinct, especially in the narrowed intermediate region between the incipient foot disks of the future daughter polyps (Fig. 3).

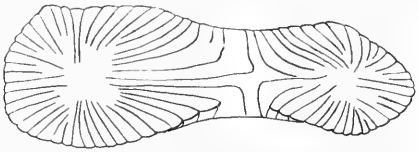


Fig. 3. Foot disk of dividing polyp; a later stage than that shown in Fig. 2. From below.

Fig. 4. Foot disk of a dividing polyp, showing rupture. From below.

As a result of the tension, the attenuated tissue on the foot disk between the centers is ruptured before long, and a gaping, diamond shaped wound is formed (Fig. 4). From this point, the division runs rapidly to completion. The diamond increases

in length, at the same time encroaching in its lesser diameter more and more upon the column, until, with a tear across the mouth disk, the independence of the two moieties is established.

Such, in general, is the process of fission; but there are several facts connected with it which should not be overlooked. The division, which is usually approximately equal, may be very unequal; in rare instances, a polyp is divided into three parts, two large and approximately equal, the third very small. In every case, however, the fission plane passes through the mouth disk, and almost invariably through the mouth also. When the mouth is involved, the fission plane always passes approximately perpendicular to its major axis. If the dividing polyp be diglyphic, the division (into two) gives one siphonoglyph to each portion.* It has been frequently observed that polyps resulting from fission themselves divide, and in every case the second fission plane parallels the first, that is, it also passes perpendicular to the major axis of the mouth. The second division may succeed the first before the regeneration of a second siphonoglyph, as sections show, so that not only may division occur in monoglyphic polyps, but in such cases, may give rise to polyps which have no siphonoglyphs at first. Rearrangements of mesenteries foreshadowing both first and second divisions may occur together in the undivided polyp, in rare cases.

With respect to the relation of the fission plane to the mesenteries, it can be said that among 51 polyps resulting from fission, sections taken before new mesenteries had had time to regenerate and complicate the investigation, showed that ten had resulted from division through exocoels, thirty-two from division through endocoels (in a large but unrecorded majority of cases, between mesenteries which reached the oesophagus), and nine from division through an exocoel on one side and an endocoel on the other.

The rate of fission varies within rather wide limits. The process may begin and end within twenty-four hours, as in *S. luciae* also (Davenport, '03), or it may require weeks for completion. Experiments indicate that the food supply may be

* Cf. M. dianthus (Torrey, '98), in which species the fission plane is parallel to the greater axis of the mouth, and divides the one siphonoglyph in monoglyphic, one or both in diglyphic polyps.

a factor in the result. Davenport has reported that "by feeding to repletion, division already begun could be delayed, even apparently prevented," in *S. luciae*. Our own experiments pointed in a similar direction, but were not conclusive. There is no question that when food in the shape of a small amphipod or morsel of flesh is seized by a dividing polyp, the process of division ceases for a time; the tension in the elongated foot decreases, the centers of the mesenterial systems draw together while remaining quite distinct, and do not move apart until the food is digested and disposed of. But similar delay may be caused by strong mechanical stimulation at short intervals. And it is questionable whether it is the mechanical or chemical stimulation of the tissues of the body by the food, or their abundant nourishment by absorption of the products of digestion, that is at the root of the matter. The fact that aquaria polyps which show the effects of starvation for long periods by actually decreasing in size, do not appear to divide, gives some countenance to the former view.

(*b*) The regenerative processes succeeding fission of this type are not sufficiently distinct from those succeeding those of the second type to warrant a separate description. For this reason they will be described after fission of the second type has been considered.

2. The second method of non-sexual reproduction in *S. davisi* to be considered resembles the process described by Mrs. Thynne.

(*a*) Fission is not preceded by a rearrangement of mesenteries about two centers, and is usually completed within twenty-four, often within fifteen hours (i.e., over night). It may result in the formation of two, three, four or five independent pieces which may be equal in size but are usually unequal, especially when there are more than two. The tear begins on one side, involving all tissues from column wall to oesophagus inclusive. Meanwhile, the moieties separate as in fission of the first type, and the tissues on the other side of the body between the two are put upon the stretch. The prompt completion of the division leads ordinarily to but two individuals, the tear proceeding in general perpendicularly to the major mouth axis. It occasion-

ally happens, however, that before the division is completed, an area of the foot disk near one of the free edges produced by the tear, becomes secondarily attached and ceases to follow the migrations of the moiety with which it is connected. A new strain in the intermediate tissue results, ending in complete rupture and the establishment, by regeneration, of a third polyp, usually much smaller than the other two, but possessing from the first a portion of the oesophagus, mouth disk and a few tentacles. A fourth and rarely a fifth fragment may be formed similarly before the division may be said to have given way to a period of repair. In the last case, the fission plane passes quite irregularly with respect to the original major mouth axis. The process as a whole is strikingly irregular, and appears to differ from the basal fragmentation of *Metridium* only in so far as each fragment retains a bit of the oesophagus and a few tentacles.

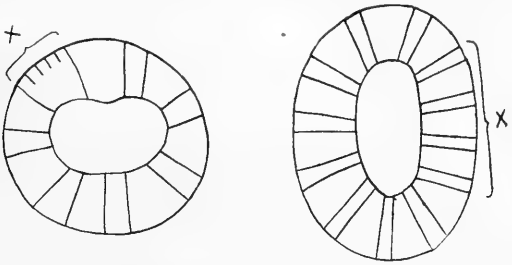
(*b*) Regeneration succeeding fission of both foregoing types. As soon as fission has been accomplished, the torn edges of the body wall roll in and the wound closes, with the tentacles retracted. In fission of the second type, the edges begin to roll in on one side as soon as formed, without waiting for the completion of the division on the other side. In a day or two, each new polyp now expand, and the edges of the wound may be seen to have fused. Along the line of fusion a strip of new tissue begins to appear, easily recognizable by its color, which is many shades lighter than the rest of the body wall. This is the zone of regeneration, in which new tentacles and mesenteries soon make their appearance.

The mesenteries are the first to develop, but there is no constant relation between the appearance of mesenteries and tentacles, the latter appearing now earlier, now later, and in no absolutely fixed order. The first pair of mesenteries arises in the middle of the zone, and is soon followed by two other mesenteries, one on each side of the original pair. This stage with four mesenteries of approximately equal size is so frequently met with that it was some time before it was discovered that they do not appear simultaneously. Next, stages with six mesenteries are obtained, due probably to the addition of a mesentery on each side of the first four. But beyond this point we can say

nothing definite as to the order of their appearance. The first pair, second pair, or all of these first six mesenteries, and indeed of the first eight or ten mesenteries, may reach the oesophagus. There is no fixed order of increase in size.

The first tentacle appears between the first two mesenteries. Two tentacles follow simultaneously, one on each side of the group of the first four. Then four tentacles appear, not always simultaneously, however, one on each side of each of the last two. Beyond this point the regeneration of tentacles was not followed.

We have been unable as yet to ascertain definitely whether the process of regeneration results in bringing the polyp back to its original condition as regards number and arrangement of mesenteries and tentacles; or, to state the question in a different form, whether the number and arrangement of new tentacles and mesenteries are in any way conditioned by the number of old tentacles and mesenteries at the beginning of the regeneration. These problems will admit of ready solution as soon as a further supply of material is obtained. It may be definitely said, however, that regeneration does not tend to restore a particular structural type. The sexual type, at present unknown, is probably itself variable. A small percentage of regular hexamerous diglyphic polyps is found. If this be assumed as the sexual type, which will then be the fundamental type of the species, in all probability, it is clear that such regeneration as shown in Figs. 5 and 6 does not tend to establish it. Many polyps are



Figs. 5 and 6. Semi-diagrammatic cross sections of polyps in process of regeneration, showing perfect mesenteries and zone of regeneration (X).

met with also which show no signs of a zone of regeneration, but possess only two pairs of perfect mesenteries. If they are products of fission, as is probable, then in them regeneration seems to be at a standstill. Such cases suggest the influence of external factors; lack of food, for instance, might alone prevent the return to the parent condition which might otherwise have occurred.

3. The third method of non-sexual reproduction in *S. davisi* may be described as aboral-oral division by constriction. This is the least conspicuous method of the three, occurring so rarely that we have never seen the completion of the process in a *normal* individual. In consequence, we cannot demonstrate its normal occurrence, but are strongly inclined, from indirect evidence, to believe that it does actually play some part, though a very small one, in the propagation of the species.

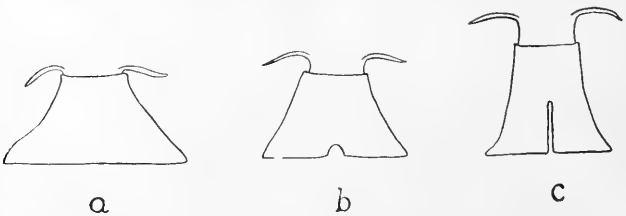


Fig. 7, a, b, c. A series of polyps which may represent different stages of aboral-oral fission by constriction.

In the first place, cases that appear to represent stages in the process have been found which can be arranged in a progressive series (Fig. 7 *a*, *b*, *c*). Case *c* might have risen as the result of an accidental tear through the foot disk, a condition we have mentioned as sometimes occurring in *Metridium*, where it has no connection with normal methods of non-sexual reproduction. Against this view, results of experiments to be described below may be brought, indicating that a tear of such proportions would probably initiate a fission that would reach a speedy completion. We have no facts to indicate that *c* represents a double monster sprung from an abnormal embryo, and do not favor such a view.

On the other hand, the condition represented in *a* has been met with many times as a *resting* condition, though identical

with that early stage of fission of the first type which immediately preceded a tear (Figs. 2, 3). The condition represented in *b* may be readily derived from *a*, and there is evidence that it is so derived. For the condition represented by *b* has been seen to merge into the condition represented by *a* as a result of a separation of the two foot disks and a consequent stretching of the intermediate tissue. We think it highly probable that during a period of comparative inactivity in such a case as *a*, two foot disks have been differentiated from the tissue of the isthmus connecting them, this isthmus being formed largely if not exclusively by tissue of the body wall (cf. Fig. 3.)

The best evidence, however, is to be obtained from the actual division of one polyp, abnormal, it is true, but doubly interesting on that account. This polyp was abnormal in that it possessed a second mouth and set of tentacles on the side of the column. It was unique in this respect among the many hundreds of polyps we have examined; and since budding is unknown in the species, we are disposed to believe that the supernumerary structures were produced as the result of a wound on the column; that they can be so produced experimentally will be shown later.

When the abnormal polyp was first observed, no signs of division were noticed in the foot disk. A few days later the mesenteries on the foot disk were seen to be arranged around two centers. The foot disk had lengthened along the line passing through both centers. Two foot disks were soon distinguishable, separated by a constriction which proceeded slowly upward. Without sign of rupture, a complete division was finally effected. Instead of passing as usual across the mouth disk, however, the fission plane passed *between the two mouth disks*, a peculiarity for which the presence of the supernumerary mouth and tentacles must be in some way accountable. The direction of the fission plane with respect to the major axis of either mouth was not observed, so that it still remained to be determined whether or not the doubling of the mouth disks, besides modifying to some extent the direction taken by the fission plane, might not also have precipitated the division. By way of solution, wounds were made in the columns of a number of polyps in whose foot disks there were no signs of division.

Simple cuts and punctures healed readily without the production of new structures. When pieces were cut out of the body wall, and the fusion of the edges of the wound was thus hindered, better results were obtained—six double-headed polyps in all. None of these showed any tendency to divide in any way, though they were watched for three weeks. This result looks like a demonstration of the view that division is not initiated by a doubling of mouth and mouth disk, and is consequently little less than a demonstration of the normal occurrence of fission by constriction in *S. davisi*. We shall repeat the experiments on a larger scale.

II. CAUSES OF FISSION.

Fission of the first two types in *S. davisi* depends to such a degree upon active movements of different areas of the foot disk in opposite directions that the idea readily suggests itself that the establishment of some sort of physiological discontinuity between these areas may be the key to the causal problem. A solution was attempted by experimentation.

Two sets of experiments produced slightly varying results. In the first set, twelve polyps were cut from foot half way to mouth, the cut being perpendicular to the major mouth axis (*i.e.*, parallel with the course of a normal fission plane); one had divided in six days, two more in twelve days. Eight polyps were cut from mouth half way to foot, also perpendicular to major mouth axis; two had divided in three days. In the second set, eight polyps were cut from mouth half way to foot, parallel with major mouth axis. In one of these, the wound was repeatedly reopened, but healed again in every case, and no division resulted. Three polyps were cut half way to foot disk, across the major mouth axis; no division resulted.

Six polyps were cut from foot half way to mouth, across major mouth axis; in twenty-four hours three had divided. It was found also that if a polyp which is beginning to divide be cut parallel with major mouth axis half way to the foot, the division is inhibited until the wound is healed, and if the latter is reopened, as was done repeatedly in one case, the division takes place only after the wound has finally closed.

The difference between the two sets of experiments lies in the facts that according to the first set, 25 per cent of the polyps cut from the mouth toward the foot disk, across the mouth, divided as against 25 per cent of those cut from the foot toward the mouth, perpendicular to the major mouth axis, and they divided more rapidly; while according to the second set, *none* of the polyps cut across the mouth toward the foot disk divided, although *50 per cent* of those cut from foot toward mouth, perpendicular to the major mouth axis, did divide. This discrepancy may disappear with farther experimentation on larger numbers of polyps and with especial care to keep the wounds open.

It appears to be clear, however, from these experiments, that an interruption of the physical continuity of two portions of a polyp by means of a cut parallel with the course which would be taken by a normal fission plane, tends to interfere with the physiological interaction of the separated regions and initiate the process of fission. This is especially true when the cut follows the aboral-oral course of the normal fission plane (second set of experiments.)

Double structures have been produced in various animals by similar experiments: in Hydra notably by Trembley, in planarians by Duges, Morgan, Van Duyne and others, in lizards by Tornier. The partial separation of the first two cells of the sea urchin (Driesch) and Amphioxus (Wilson) leads to even more marked results.* In all of these cases, normal physiological connections have been broken; Morgan is disposed to believe that these physiological connections are in the shape of some sort of tension. The doubling of parts, however, never involves the entire body; there is no evidence of a stimulus to division. Perhaps this is because division of the types made possible by the experiments does not occur normally in any of the species concerned. Yet in *Corymorpha palma*, separation of the two individuals developed heteromorphically on the opposite ends of a fragment of stem has been observed; the discontinuity between the two ends shown by the development of two hydranths was further emphasized by the subsequent division, which never occurs under normal conditions.

*See Morgan, ('01) for an account of these cases and the literature of the subject.

But while discontinuity of some sort is probably at the basis of the phenomenon of fission in *S. davisi*, it is apparent that the experiments go no farther than to point out this fact. Why the mesenteries in an unharmed polyp begin to group themselves about two centers, and why opposite areas in the foot disk move away from each other constantly only in polyps which are to divide, are problems which still await solution. A possible explanation of the *direction* of the fission plane may be suggested, however. This plane passes perpendicular to the line of greatest strain. This line of strain is parallel with the major mouth axis, and at the ends of the mouth lie the directive mesenteries. There can be little question that the arrangement of the muscle bands on the outer sides of the directives and near the oesophagus leads to mechanical results which are different from those achieved by all the other muscle bands, which lie on the inner sides of the non-directive mesenteries and farther from the oesophagus. This mechanical difference is always correlated with the shape of the mouth and may be sufficient to determine the direction of the line of greatest strain and consequently the direction of the fission plane in a dividing polyp. The uniform failure to divide of polyps which were cut perpendicular to the direction of the normal fission plane lends support to this view.

III. HETEROMORPHOSIS.

Until the last few years heteromorphosis has been quite unknown among the *Anthozoa*. A typical example was recently obtained by Wilson (:03) in Renilla, a new hydranth regenerating on the aboral end of an extirpated axial polyp of a young colony. Hazen (:02), in discussing the factors which determine the orientation of regenerating pieces of *S. luciae*, says that a pedal disk is produced at the point of contact with the substratum, no matter how the piece falls, provided it is not subsequently disturbed. There is no specific statement that a pedal disk was ever regenerated at the oral end of a piece, and the brevity of the account leaves this in doubt. There appear to be no published observations on the appearance of a hydranth on the aboral end of a regenerating anemone, though attempts have been made on several species, notably by Loeb, to bring about

this result. *S. davisi* offers no difficulties in this direction; more than 50 per cent of the anemones operated upon gave positive results. The facts obtained up to this time are given below.

Twenty polyps were divided by transverse cuts into oral portions which included mouth and tentacles, and aboral portions which included the foot disk. Nine were cut through the capitulum, so that the oral portions were very short. Eleven were cut so that the oral portions were each half the length of the original column.

Of the nine shorter pieces, four rested with mouth disk upward, five with aboral end upward; two of the former, but none of the latter, had developed hyranths in five weeks.

Of the eleven longer pieces, four rested with mouth disk upward, seven with aboral end upward; in less than four weeks all of the former had developed aboral hydranths, while of the latter five had developed aboral hydranths, one had produced both foot and hydranth aborally and one was a normal polyp.

With respect to the factors involved in these results, Hazen has suggested that the position of the axis in regenerating pieces of *S. luciae* might be determined by a geotropic influence or by a combination of geotropism and stereotropism; the foot disk being formed at the point of contract (itself determined by gravity), the hydranth at the opposite (upper) end. This suggestion hardly fits the facts of heteromorphosis which have been enumerated. Gravity cannot determine the presence or absence of an aboral hydranth when the latter develops regardless of the orientation of the piece. We cannot speak so surely about the factor of contact. It is possible that the aboral cut surfaces of the pieces in our experiments which are resting mouth up, did not touch the substratum for a sufficient length of time to determine the development of a foot disk; they certainly did not adhere. On the other hand, it is odd that the only foot disks developing on the aboral ends of pieces, appeared on two longer pieces, both of which rested on their mouth disks, not on the aboral cut surfaces. Internal factors seem to have been more potent than external in this case. It is probable, however, that future experiments will show a certain influence of contact upon the development of the foot disk in regenerating pieces to

S. davisi, as Hazen has already shown it for *S. luciae*. We have obtained, so far, one case which supports this view. The aboral portions of the polyps used in the previous experiments were inverted, so that their oral cut surfaces came in contact with the substratum. In every case but one the pieces righted themselves and regeneration of hydranths ensued. The single exception remained as it was placed and developed over the cut end a smooth surface which resembled a foot in appearance, though it did not adhere. The piece finally died.

Two other factors should be noticed: size of piece and region of cut. The longer pieces developed heteromorphically much much more readily than the shorter ones. We have not been able as yet, owing to difficulties of manipulation, to compare pieces of similar length from different regions of the column to determine directly the relative value of the two factors. It is highly probable, however, that size is the more important of the two, since the shorter pieces produced neither foot disks nor hydranths in 75 per cent of the cases, indicating a regenerative capacity in general inferior to that of the longer pieces.

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THE STRUCTURE AND REGENERATION OF THE POISON GLANDS OF PLETHODON.

BY

C. O. ESTERLY.

It has long since been held that the skin glands of both the Urodela and the Anura are of two kinds. This distinction was first made by Ascherson '40 in an investigation of the glands in the web of live frogs, and was based upon the size, shape, and location of the glands without regard to function or microscopic structure. That the skin of Amphibians secretes a substance other than the well-known mucus, and clearly poisonous, has been shown by many physiological and toxicological experiments and investigations (Albini '56; Boulenger '92; Calmels '83; Capparrelli '83; Dutarte '89; Gratiolet and Cloez '51–'52; Hubbard '03; Phisalix-Picot '00), and the facts gained from experiment are upheld as far as possible by histological evidence. Microscopic examination shows that there is more than one kind of gland. (Ancel '02; Coghill '99; Eberth '69; Eckhard '49; Engelmann '72; Hensche '56; Leydig '76 *a*; Paulicki '85; Phisalix-Picot '00; Schultz 89; Seeck '91; Stieda '65; Szezesny '67; Wiedersheim '86). These have generally been distinguished as granular (Körnerdrüsen) and clear, according to the appearance of the secretion contained in them, the former having been almost unanimously looked upon as making the poison series, the latter the mucous series. The suggestion has been made, however, that the various glands are only the young and old stages of one sort of gland (Junius '98), and this question will receive further consideration in the present paper.

The poison glands are in most cases much larger than those of the mucous variety, and their enormous cells (Riesenzellen of Leydig) completely fill the interior of the gland so that there is no lumen. This character distinguishes these glands from the others, which are provided with a low, cubical epithelium surrounding a capacious lumen. (Pl. XX, Fig. 2.) The mucous secretion filling the lumen is very distinct from the heavily granular contents of the cells of the poison glands. (Pl. XXIII, Fig. 31.) The two sorts of glands are further distinguished by other features, chief of which is the staining reaction of the mucous secretion (Nicoglu '93; Hoyer '90). These observers used thionin as a specific stain for mucus and found that the small glands stain rose-red while the others are uncolored.

The foregoing general facts have been determined chiefly upon the Anura and the various European Salamanders, especially Triton and Salamandra. But *Plethodon oregonensis*, a salamander found about Berkeley, forms a particularly interesting object for the study of the poison glands because of their unusual development on the tail of this animal. This seems to be a protective character associated to some extent with the ability of the animal to throw off its tail under stress of circumstances. It has been shown by experiment that the secretion of the glands of the tail is poisonous or obnoxious to certain animals, a character which probably belongs to the dorsal glands (Hubbard, '03), which are very large and much more developed than elsewhere on the body. In this respect Plethodon appears to resemble *Triton cristatus*. (Capparelli '83.) However, the poison glands of Plethodon are not confined to the dorsum of the tail; much smaller ones are found on its ventral surface and also on the trunk and head of the animal, intermingled with mucous glands, which occur in all situations where the poison glands are found.

The principal question considered in the present paper concerns the changes occurring in the formation of the secretion and its expulsion from the glands. In Plethodon this involves the death of the glands, as Seeck ('92), Nicoglu ('93), Vollmer ('93) and others have shown for other Amphibia. The exhausted glands are here renewed or replaced in the manner described by

Heidenhain ('93 *a*), Vollmer ('93) and Nicoglu ('93). This process consists in the growth into the old glands of a new and smaller gland, which, however, is mucus in character, contrary to the statements of Nicoglu ('93), so that the poison glands develop from the mucous to the poison variety. This has been suggested but not definitely shown by Hoyer ('90) and Junius ('98), and distinctly denied by all other investigators of the regeneration of these glands. Under the histological structure of the glands will be considered some new points in the musculature, especially as to the presence in the epidermis of an apparatus for closing and opening the duct. The innervation of the muscles and epithelium of the glands will also receive attention.

This work was done under the direction of Professor C. A. Kofoid, and my heartiest thanks are due him for very kind assistance in every way and for criticism of results.

MATERIAL AND METHODS.

In order to obtain the best insight into the structure of the glands of the tail, sections in three planes have been made of that entire organ. The tissue was in all cases perfectly fresh and was fixed in Zenker's fluid, which has been satisfactory in all respects. Washing in 70% iodine-alcohol followed the use of the fixative.

That bony tissue might not hinder the passage of sections in any plane through the whole tail, the tissue was subsequently decalcified in a 5% aqueous solution of nitric acid for from twelve to twenty-four hours, followed by immersion in a 5% aqueous solution of sodium sulphate for the same length of time, and thorough washing in running water for from twenty-four to forty-eight hours.

Paraffine sections have alone been used, varying in thickness from $3\frac{1}{8}$ to 10 microns. The sections were fixed to the slide by the water-albumen method, and in all cases where possible staining was done on the slide.

A considerable variety of stains has been employed. The most successful have been Mallory's ('00) connective tissue stain (acid fuchsin, phospho-molybdic acid, anilin blue-orange G),

Van Gieson's haemalum and picro-fuchsin, and the iron-haematoxylins of Benda and Heidenhain. I have found it of considerable advantage to increase the percentage of fuchsin in Mallory's stain to as much as 1.5 or 2%. This stain, as a whole, when successful is very beautiful, but its action varies most unaccountably. The staining and differentiation will be perfect in some sections, while in others on the same slide the differential coloration will fail completely. But the range of application of the stain seems to be almost unlimited except for purely cytological work.

Other stains have been used, such as Mayer's neutral and acid haemalums followed by eosin, orange G, erythrosin and Congo red; safranin alone or in combination with light green; ferric chloride haematoxylin, and such special stains as the phosphotungstic acid haematoxylin of Mallory and Cajal's ('03) silver nitrate-pyrogallic acid method for nerves, Tänzer's orcein for elastic fibres, and Mayer's muci-carmine as a mucus stain.

As has been said, the largest poison glands of Plethodon are situated on the back of the tail, and in cross sections (Pl. XX, Fig. 1, *p.gl.*) it may be seen that they lie in that portion of the skin covering the dorsal half of the tail. Here the greatest development is in the glands at either side of the mid-dorsal line, while farther down on the sides they gradually diminish until they are considerably smaller and not readily distinguished by their size from the larger mucous glands. (Pl. XX, Fig. 1, *m.gl.*) The coloration also of the tail gives a clue to the location of the largest glands. The dorsal half of the tail is black or brown, while the ventral half is orange or yellow, and the glands under consideration are confined almost entirely to the darker portion. The mucus glands are found largely on the ventral side of the tail, but they also occur along the dorsal surface. In this region they lie between the necks of the large glands.

The poison glands form large sacs, extending from the epidermis to the inner layer of the corium. (Pl. XX, Fig. 1.) In shape they are elongated, with oval or even somewhat rectangular outline. The ducts are short, and the transition from the body of the gland to the neck and duct is not sharp as in the mucous glands, which are regularly flask-shaped.

It has been shown (Hubbard '03) that the swollen appearance of the tails of some animals is due to the increased development of the poison glands posterior to the well-marked constriction found just behind the cloaca in such cases. That this is really true appears in the study of a series of sections of a swollen tail passing from the tip up to and including part of the cloacal aperture. In the constriction the dorsal glands are very small comparatively, and are here no larger on the back of the tail than on the ventral side. But behind the constriction their development is much greater, and one may trace the regular increase in size as the series passes from the constriction back to the enlarged portion of the tail. Everywhere in the tail, except in the constriction at its base, the difference in size between the glands on the dorsal and ventral surfaces is maintained.

As is well known, the bodies of all the glands lie in a spongy connective tissue, the middle layer of the corium, which in the region of greatest development of the poison glands is increased enormously in thickness (Pl. XX, Fig. 1, *m.c.l.*), being alone from one-sixth to one-fourth or more of the dorsal-ventral dimension of the tail. (Hubbard '03.) The bottoms of the large glands rest upon or come very close to the inner layer of the corium. (Pl. XX, Fig. 1, *i.c.l.*)

The ducts of both mucous and poison glands pass through the outer corium layer and the epidermis, the long axis of the gland which passes through the duct and its mouth being perpendicular to the surface at the point where the duct opens to the exterior.

The histological structures found immediately surrounding the ducts of the poison glands are in no essential points different in Plethodon from those in other salamanders. The funnel cells and their processes (Pl. XX, Figs. 1 and 2, *fl.c.*) are present as in Triton (Nicoglu '93) and in Salamandra (Ancel '02). The membrane-like structure lining the duct belongs to a specialized cell of the epidermis, corresponding to the "stoma cell" of Eberth. As Nicoglu has shown, the mouths of the glands lie within these cells, processes of which extend down in the ducts about as far as the lower limit of the epidermis or a little farther. (Pl. XXIII, Fig. 27, *p.fl.c.*) The prolongations stain black in iron haematoxylin, reddish in Mallory's and yellow in Van Gieson's stain.

In addition to the funnel cells proper, Nicoglu has described the arrangement of the cells in the epidermis which are to replace the funnel cells as they are thrown off at the time of moulting. The same condition is found in Plethodon and does not differ at all from that in Triton (Nicoglu '03) or in Salamandra (Ancel '02). (Pl. XX, Fig. 4; Pl. XXIII, Figs. 27, 28, 29, 30. *rep. c.*)

As further evidence that the cells described as replacement cells really have that function, Plethodon shows that the lower ends of the replacement cells, especially those nearest the duct, extend inward as do the prolongations of the funnel cells. (Pl. XXIII, Fig. 27, *rep. c.*) The arrangement of the former very strongly suggests that they are of the same nature and function as the funnel cells. And in cross sections of the ducts the replacement cells are shown rolled one within the other as in Pl. XX, Fig. 4; Pl. XXI, Fig. 16, *rep. c.* The cell first to replace the one thrown off at moulting immediately surrounds the duct; the cell next to replace this one lies concentrically outside it, and so on. In Mallory's stain the cell boundaries are very distinct, and there can be no doubt of the structure as described either in cross or in longitudinal section of the ducts.

The walls of the gland sacs proper are composed, in many Amphibia, of a number of elements which have been described and all of which need not be discussed at length here. In the most peripheral layer are connective tissue and elastic fibrils, as is shown by the use of Mallory's connective tissse stain for the former and orcein for the latter. Nerves, lying in this layer, also extend over the gland. Inside the connective tissue sheath, as it is generally called, lie the muscle fibres, and next to them the epithelium of the gland.

(See in this connection Drasch '92, '94; Eberth '69; Eckhard '49; Englemann '72; Heusche '56; Leydig '76, *a*, *b*; Paulicki '85; Phisalix-Picot '00; Schuberg '03; Schultz '89; Seeck '91; Stieda '65; Tonkoff '00; Wiedersheim '86.)

Because of the intimate relation between the connective tissues of the gland wall and those of the corium, it is necessary to consider in more detail the structures of the inner, middle and outer layers of the corium. Schuberg ('03) has studied the corium of Axolotl most minutely. I have confirmed his results

in general in Plethodon, and particularly as to the relation of the connective tissue bundles of the inner layer of the corium to those of the middle layer. He found (p. 222) that columns of connective tissue pass perpendicularly from the inner into the middle layer, and seem to serve as mechanical supports for the glands, since under each one such a column of tissue is found. The same arrangement occurs in Plethodon except that the perpendicular bundles do not stand beneath the glands, but around them, as can be seen in longitudinal sections of the glands. (Pl. XX, Fig. 5, *c.t.b.*) In spaces between the large glands or on the ventral side of the tail, the bundles from the inner layer of the corium can be seen especially well. The connective tissue fibres from the wall of the gland unite with the outer layer of the corium which then, lying next the muscle layer of the gland, passes toward the surface of the epidermis and ends on the side of the neck of the gland about a third of the distance between the inner and outer boundaries of the epidermis. (Pl. XX, Fig. 8; Pl. XXIII, Figs. 27, 31.) This appears in both longitudinal and cross sections of the ducts. In the latter can be seen a crescent of connective tissue on each side of the duct between the muscle fibres and one of the replacement cells. (Pl. XXIII, Figs. 28, 29; Pl. XXI, Fig. 16, *c.t.*) Ancel ('02, Pl. IX, Fig. 22) seems to have shown the same in longitudinal section.

The elastic fibres pass through the inner layer of the corium into the middle layer in company with the connective tissue bundles as Schuberg ('03, p. 231) has described. The elastic fibres can be followed around the glands, and over them in tangential sections. The fibres are of nearly the same calibre throughout and all of them take the same general direction, from the inner corium layer perpendicularly or sharply turned toward the outer layer. As in the case with the connective tissue bundles the elastic fibres pass at once around or over the large glands, and are not found arranged perpendicularly beneath them as in Axolotl. (Schuberg '03, p. 232, Fig. 14.) On the surface of the gland they are branched in a few cases; usually, however, only single fibres of wavy, curving and regular outline are visible, ending before the outer corium is reached (Schuberg '03, Pl. XXI, Fig. 9, *el.f.*).

Between the connective tissue layer and the gland epithelium lies the layer of contractile or smooth muscle fibres. These were first shown histologically by Heusche ('56), though before him Ascherson ('40) had observed movements of the living glands. Since this time there has been no doubt of the existence of muscles in the walls of the poison glands (Coghill '99; Drasch '89, '92, '94; Eberth '69; Eckhard '49; Englemann '72; Heidenhain '93 *a*, *b*; Leydig '76, *a*, *b*; Massie '94; Nicoglu '93; Paulicki '85; Phisalix-Picot '00; Schultz '89; Seeck '91; Stieda '65; Szczesny '67; Vollmer '93). As regards the smaller series of glands the question seems to be open. The absence of contractile fibres on them has been used as a character to separate them from the large glands. The muscles of the large glands are arranged in a single layer and have a general meridional direction on the gland, converging toward the upper pole. The fibres are usually simple but may be branched (Pl. XX, Fig. 7); this occurs mostly on the lower part of the gland. Neither do the muscles form a continuous sheet about the gland; the individual fibres are separated by spaces of greater or less extent. I have not been able to find with certainty muscles on glands which are mucous in nature.

The nuclei of the contractile cells, contrary to the description of Nicoglu ('93, p. 437,) and such figures as his and those of Vollmer ('93), lie in the upper region of the glands just outside the uppermost gland cells, yet still well beneath the epidermis (Pl. XX, Fig. 6; Pl. XXIII, Fig. 31, *m.n.*). The first observer mentioned has shown (his Pl. XXII, Fig. 12) the nuclei of the muscle cells in *various locations about the periphery of the glands;* but *in Plethodon the nuclei have a constant position as described and are found only there*. In the region of the nuclei the muscle fibres are considerably larger than elsewhere on the gland, as is shown in Pl. XX, Fig. 8, *m.f.*, or Pl. XXIII, Fig. 31, *m.f.*, so that the muscle, especially in longitudinal sections of the glands, seems to bear a flask-shaped expansion. From this point it is possible to trace a single fibre very nearly to the base of the gland, and also outward around the neck of the gland into the epidermis. (Pl. XX, Fig. 6.) The connection of the muscles with the epidermis has been reported by Nicoglu ('93) and Heidenhain

('93 *b*), and the arrangement in Plethodon is a similar one except as regards the presence of the "Schaltstück" cells described by them. In Plethodon the "Schaltstück" is not demonstrably present except in one or two questionable cases in all my preparations, and Vollmer ('93) found that it is very often absent even in Triton. There can be no doubt, however, that the muscles send processes into the epidermis. This is especially well shown in longitudinal and cross sections of the ducts.

The statement that the muscle nuclei of the poison glands in Plethodon lie only in the necks of the glands, instead of generally distributed about the periphery as held for other animals, may be supported by several facts. In the first place, longitudinal sections of the glands through the duct and mouth show two nuclei, one at each side of the gland where the sac begins to pass over into the duct. In sections of the same plane which pass a little to one side of the duct (Pl. XXI, Fig. 10, *mf.*, *mn.*) may be seen in some cases the obliquely cut ends of as many as seven muscle cells each with its nucleus in situ, and occupying exactly the position relatively of the two lateral nuclei which are shown in the median section. There can be no doubt of their structure.

Cross sections of glands and ducts are also very instructive on this point. In such, especially if stained in Van Gieson (Pl. XX, Fig. 12), there are shown in many cases the light yellow muscle fibers between the gland cells and the connective tissue, when the plane of the section passes more deeply through the gland than the position of the nuclei of the muscles. But when the gland is cut across at the level of the nuclei, the evidence gained from longitudinal sections is even more strikingly upheld. In such cross sections can be seen as many as twelve or fourteen muscle fibres stained light yellow (in Van Gieson), and in very sharp contrast to them the brown or black nuclei. And in this region the section of the muscle is larger than it is deeper in the gland; this corresponds to the flask-shaped enlargement seen in median longitudinal section (Pl. XX, Fig. 8, *mf.*). If a series of frontal or cross sections of the tail is studied, it will be found that while the muscles themselves can be traced until the bottom of the gland is reached, nuclei never appear again which are unmistakably those of the muscle fibres. The only place in

which one can be sure that he is dealing with nuclei of the contractile fibres is in the location above described. Hundreds of sections have been carefully examined and there has never been a case of a fully formed gland in which the muscle nuclei are situated in any position except that described. Not only is this true in stains such as Mallory's and Van Gieson's but also in clear nuclear stains like iron haematoxylin.

That those observers who describe muscle nuclei on the periphery of the gland sacs have mistaken connective tissue nuclei for them, seems to me very probable. Nicoglu ('93, p. 438) says that the nuclei often occupy an eccentric position, so that even with oil immersions one cannot see that there is any protoplasm of the muscle cell about them. His description ('93, p. 436) of the flattened narrow nuclei of the muscle cells applies more to connective tissue nuclei. That these occur in the walls of the glands has been observed by Paulicki ('85, p. 158), who says: "An die Drüsen treten gewöhnlich . . . sich nach oben erstreckend bindegewebige Stränge mit Kernen." And the figures of Schuberg ('03), especially Fig. 28, show that this is true for the glands of Axolotl. From these facts and from my observations on Plethodon it is clear that connective tissue nuclei closely invest the glands, and evidence is added to that already brought forward to show the location of the nuclei of the muscle cells.

The processes of the muscles passing into the epidermis serve to connect the fibres with the outermost layer of the skin. This has been shown, as said before, by Heidenhain ('93) and Nicoglu ('93), as well as by Ancel ('02), and there is nothing to be added to the description given by the former except, as before stated to mention the frequent non-occurrence of the Schaltstück as such. This is a structure described as containing about four cells which are arranged in a ring about the neck of the gland at the lower boundary of the epidermis. The cells form seemingly the principal points of insertion of the muscle fibres, but this cannot be so in Plethodon where the Schaltstück is virtually absent. Otherwise it may simply be said that the upper or outer ends of the muscle fibres pass into the epidermis and end between the replacement cells of the funnel. This can be seen fairly

well in cross sections of the gland ducts in the epidermis where the cut ends of the muscles are seen close beside the funnel cell (Pl. XXIII, Figs. 28, 29, *prol. m.f.*). In good longitudinal sections of the ducts the muscles (Pl. XXIII, Fig. 27, *prol. m.f.*) are seen to end between the older replacement cells which are already elongating into their typical form (same, *rep. c.*). Nicoglu ('93) represents the endings as between the cells, but Ancel ('02) seems to consider them as special parts of cells. At any rate he has shown (Fig. 22) the fibrils as within cells in the epidermis. I have not been able to find such structures as he shows; there can be hardly any doubt that the prolongations of the gland muscles into the epidermis end between the replacement cells. Nicoglu and Heidenhain ('93) and Ancel ('02) have remarked upon the existence of intercellular bridges between the muscle cell on the one hand and ectodermal epithelial cells on the other, as Nicoglu says (p. 440), "von ganz ähnlicher Art wie zwischen den Oberhautzellen selbst."

I have not found the intercellular bridges in Plethodon between epithelial and muscle cells, but all the facts concerning the connection of muscle and epidermal cells have been taken as evidence of the ectodermal origin of the muscles of skin glands. This has been so often commented upon that it is useless to more than call attention to it here. The evidence gained from a study of the development of the glands shows that the muscle fibres come from the Malpighian layer of the epidermis (Ancel '02; Vollmer '93; Junius '98). This, added to the facts already cited, and coupled with the observations of many investigators (Engelmann '72; Seeck '91; Heidenhain '93; Nicoglu '93) seems fairly conclusive that the muscles of the dermal glands are of ectodermal origin: (Compare also in case of sweat glands, v. Kolliker '89; Handbuch des Gewebelehre des Menschen, pp. 138 and 258).

The existence of a sphincter or constrictor muscle for the glands has been claimed by Schultz ('89), who described a band of muscle fibres running around the neck of the gland beneath the meridional layer. This observation has been disproved by Drasch ('94) and Nicoglu ('93), and I have been unable to find such a structure in Plethodon. And there is no evidence of the

epithelial plug of Drasch ('94) for restraining the contents of the gland under pressure. Phisalix-Picot ('00) mentions (pp. 44–45) an orbicular muscle, but gives no description or drawing of it, so that her meaning is obscure. Dilator muscles for the ducts or mouths of the glands have never been described.

However, both dilator and constrictor muscles occur about the mouths of the poison glands of Plethodon. These are best shown in sections of the epidermis parallel to the surface, stained in Mallory's connective tissue stain, which are, of course, also cross sections of the ducts. All three sets of gland muscles may very often be seen in one such section (Pl. XXIII, Fig. 30, *con. m.*, *dil. m.*, *m.f.*; Figs. 28, 29 also). In these cases it will be seen that the duct (*l.d.*) in the epidermis is oval in cross section, and that at each end of the oval is a triangular mass of fibres, staining red in Mallory, as do the muscles on the body of the gland. The fibres converge toward the duct and insert upon the replacement cells nearest the funnel in such a way that by contracting they will bring the lips of the duct together and so close or greatly diminish its lumen (Pl. XXI, Fig. 16). The constrictor fibres are differentiations of the cell whose large nucleus (Pl. XXI, Figs. 14, 16; Pl. XXII, Fig. 28, *nuc. ep. m.c.*), stands at the ends of the elliptical opening of the duct. The fibres lie within this cell as can be especially well seen in longitudinal sections of the glands which do not pass through the duct. Here it appears that the cell of which the constrictor fibres are a part, together with its nucleus, lies in the deepest layer of the epidermis immediately upon the outer layer of the corium. This cell seen in surface view is equal in extent to several of the neighboring epidermal cells, but in cross section it is very much flattened (Pl. XXI, Fig. 13). Ancel ('02) has figured such a cell, but gives no clue as to its function.

The dilator fibres belong to the same cell of which the constrictors form a part, and are at a slightly lower level seemingly than the latter. The action of the dilator is two fold. Some fibres pass around the ends of the oval opening of the duct (Pl. XXIII, Fig. 28, *dil. m.*; Pl. XXI, Fig. 14) and when they shorten they tend to separate the lips of the lumen more widely, by pressing at the ends of the ellipse. This is evident when it

is seen that the mass of dilators is often concave in outline toward the center of the duct (Pl. XXIII, Fig. 28; Pl. XXI, Fig. 15, *dil. m.*), so that in contraction the fibres first mentioned pull in the general direction of the major axis and toward the center of the ellipse. Other dilator fibres attach at the edges of the duct near the end (Pl. XXI, Fig. 14), and in shortening pull in the direction of the minor axis of the ellipse, thus widening the lumen by spreading its walls at the tips of the oval. (Pl. XXI, Fig. 14.) The entire effect of the dilator fibres is to make the aperture of the duct nearly circular, thus offering freer exit to the secretion. Their action would be to open the duct from the form shown in Pl. XXI, Fig. 16, to that, for example, in Pl. XXIII, Fig. 30.

The fact that the constrictor and dilator fibres lie entirely within the epidermis need not militate against their having the function of muscles, for in the case of the intrinsic gland musculature it has been well established that it has an ectodermal origin. It is certain that the arrangement and appearance of the fibres described as constrictor and dilator muscles are such as to suggest very strongly both that nature and function. The coloration in Mallory is exactly that of the smooth muscles of the glands; and the convergence of the constrictor fibres to their insertion in a position where contraction would close the duct; the endings of the dilators in places to be of greatest advantage in widening it when the muscles contract—all these facts lead one to conclude that he has to deal with an apparatus for closing and opening the ducts of the glands.

The muscles of the poison glands, as has been said, immediately envelop the secretory cells. The entire gland is filled with enormous cells, the generally recognized "Giftzellen" of many authors or the "giant cells" of Leydig. In such glands a lumen does not exist; this is especially well shown in sections of the tail of a tadpole 38 mm. in length, in which the cell boundaries are distinct, the secretion not yet being present in sufficient quantities to obliterate them. There it will be seen that the ends of the cells are in contact with the middle of the gland, thus doing away with any trace of a lumen (Nicoglu '93; Seeck '91; Calmels '83). A glance at the figures will serve to distinguish

in this respect the poison and mucous glands; the latter have capacious lumens (Pl. XX, Fig. 2), often filled with a clear secretion. The large gland cells each have a number of nuclei (Nicoglu '93; Drasch '92), not over four in Plethodon. They are round or oval, of regular outline, and lie normally upon or very near the wall of the gland, and so at the base of the cells. The internal structure of the nuclei is simple. There is a scanty network and few chromatin granules; usually also one or two nucleoli.

The cells and nuclei of the small or mucous glands are distinct in every way from those of the poison glands. The cells are low and cubical and show a filar structure (pseudo-filar, Nicoglu '93). This is seen in sections stained either with Van Gieson, Mallory or iron haematoxylin. The nuclei are smaller than those of the poison glands, and angular instead of regular in outline. They invariably stain intensely black in iron haematoxylin, remaining so when the nuclei of the giant cells have decolorized to a very faint gray (Pl. XX, Figs. 2, 3; Pl. XXII, Figs. 18, 19, 20).

A general comparison of the two sorts of glands might be instituted in some such terms as these. The poison glands are very much larger than the mucous glands, and have contractile walls; the mucous glands lack this character. The extreme dimensions of the former on the tail are approximately from 1400 microns in length and 380 microns in breadth to 680 microns in length by 200 microns in breadth, and half the latter figures on the body. The mucus glands vary from 93 by 90 microns on the tail to 60 by 40 microns on the body. This alone, without closer inspection, would serve to generally distinguish the two varieties of glands; but in addition the poison glands have no lumina, the cells and nuclei are much larger than in the other glands (mucous average about 11 microns in greatest diameter, poison about 20 microns) and stain differently; and above all the character of the secretion is vastly different.

As might be gathered from the name often applied to them, the secretion in the poison glands is composed of granules. These are of varying size, and the cells are entirely filled with them. The mass stains from red (Pl. XXIII, Fig. 31, *sec.*) or reddish yellow to a dark purple in Mallory; in Van Gieson the

color is as a whole yellow with a tinge of red. In iron haematoxylin some granules stain (Pl. XXII, Fig. 18) black; but at times one can detect in some granules a clear outer portion which takes the counter stain (erythrosin, etc.), while the central part stains dark black, and others which take only the counter stain.

The mucous secretion, on the other hand, reacts very differently, as does the cytoplasm of the mucous cells, which can be easily distinguished from their secretion. Here the reactions are typically those of mucus. Mallory's stain, which colors mucus in the sublingual of a cat a clear blue in two minutes, stains in the same way both the cells and the secretion of the small glands. This same stain beautifully differentiates the mucus in the goblet cells of the oesophagus and intestine of Plethodon. I have not been able to obtain the reaction in these gland cells with thionin, in which Nicoglu places so much confidence as a mucous stain. Hubbard ('03) has had the same difficulty. However, mucicarmine, a specific mucous stain, gives the mucous reaction after twelve or twenty-four hours in both the glands of Plethodon and the sublingual of the cat. The use of Van Gieson's stain clearly differentiates the small gland from the large ones. In the former the cells and the secretion are stained a clear red or pink, without a trace of yellow as in the poison glands. Orcein also, which has been described as a mucous stain, colors the cytoplasm of the mucous gland cells a deep brown, and has absolutely no effect on the granular secretion of the poison glands. The iron haematoxylin is of little use in revealing the mucous nature of the small glands, since they take only the counter stain except for the nuclei. These become a deep black as already said. But this method at least serves to distinguish the two sorts of glands aside from the nuclear staining, in that the secretion of the small glands never takes the haematoxylin, as do the granules of the large glands.

From these distinctions as to the primary character of the two classes of glands, we are led to consider the histogenesis of the secretion. It has been generally held that this process is not the same in the mucous and poison glands. Seeck ('91), p. 55, holds that the secretory cells are of two sorts, "solche die als

Zellen erhalten bleiben und Drüsensecret secerniren (Schleimdrüsen), und andere, deren Protoplasma sich in feinkörniges Drüsensecret metamorphosirt wobei die Zellen vollkommen aufgebracht werden, zu Grunde gehen, so dasz man ihre in Zerfall begriffenen Kernen in Drüsensecret finden kann (Körner-oder Giftdrüsen)." Nicoglu ('93), p. 447, finds that the cells of the poison glands "wenn ihre Stunde gekommen ist, wandeln sie sich in toto in Secretmasse um." But up to this time they act as other gland cells in elaborating and retaining a secretion in their interior, as the pancreas cells do zymogen granules. Schultz ('89) does not think that all the cells of a gland are destroyed at the same time, but such as do form a part of the secretion mass must be regenerated; indicating that they are destroyed in the process of secretion. Drasch ('94) merely states that the poison glands of the salamander, if completely emptied, pass entirely away, and are replaced by new glands. Observations of the glands at various times after emptying show regressive changes in all the layers. Vollmer ('93) also has described the process of solution of the Leydig cells after strong electrical stimulation of the glands, and has made careful statements regarding the appearance of the emptied glands. The conditions in Plethodon almost duplicate those he has described.

It seems pretty well founded, then, that the poison gland cells pass bodily into the secretion mass. But a distinction should be made here, as Nicoglu has done, between the secretion mass as that thrown out, and the secretion material, which is the formed substance in the cells. There is no evidence of the disintegration and solution of cells in the full but not discharged gland. It is only when for some reason the glands are emptied that the degenerative processes are discerned. Otherwise the formed secretion is retained within the cells, which remain in a normal condition at such times.

This review of the literature describes very well the processes which go on in Plethodon; Pl. XXI, Fig. 17, will show the appearance of a gland on the day it was emptied. It has shrunken greatly in size; as compared with others of the same animal which, for some reason were not emptied, from three hundred microns in diameter, say to one hundred microns. The

nuclei which in full glands lie at the bases of the cells, are in this case in the inner parts of the cells, and are larger and clearer and in a state of disintegration. In some places only outlines or shadows of nuclei can be seen. Often they became shrunken and irregular in outline when the gland is emptied. The entire appearance of emptied glands would lead to the conclusion that their time of functional activity is at an end.

The mucous glands, on the other hand, never reveal such changes. It seems correct to say that the processes there are like those in milk glands, where parts of the cell bodies are thrown off as secretion, while the remaining portions in time repeat the same processes of secretion. Nussbaum ('82, p. 302) speaks of the heads or inner portions of the mucous gland cells of Salamander as discharged on stimulation.

If it is true then, as it seems to be, that the poison glands are changed bodily into the mass of secretion, we must look to some source for their replacement, if the animal is to have their continued protection. Nussbaum's conclusions should be cited here ('82, p. 336) as bearing on the general topic of death of gland cells through secretory activity, and their renewal. He says secretion consists in the formation and elaboration of the mother-substance of the secretion material, the changing of this in the cells and in emptying the secretion when ready, out of the cells. "Wie alles Lebende aus uns unbekannten Ursachen abstirbt und neuen Generationen Platz macht, so gehen auch nach einer gewissen Zeit Drüsenzellen zu Grunde und werden von lebenskräftigen Nachbarzellen ersetzt. Sterben aller Zellen gleichzeitig ab, so ist die Drüse vernichtet wie eine Protozoen Colonie. . . . . Die Secretion mag wohl die Zelle abnützen; die Zelle wird altern. Der Ort der Secretion ist aber nicht gleich bedeutend mit Zellentod; er ist eine energische Lebensthätigang."

In this particular case of the skin glands of Amphibia, a definite process of replacement goes on, occurring in Plethodon in the way described for other salamanders by Nicoglu ('93), Heidenhain ('93) and Vollmer ('93), and not as Junius ('98) claims, by entirely new origin. The former observers find that inside the old poison glands there lies a second smaller gland, possessing a lumen. This small sac is to replace the older gland

and lies always between the musculature and epithelium of the latter. Nicoglu ('93) finds that the new glands possess "all the epithelial parts of the old gland with the exception of the "Schaltstück." Whether this statement is to include also the muscle fibres, he does not say; his figures show muscle cells lying upon the ingrowing gland, but there is no reference to prove that they belong to it rather than to the old gland. However, Vollmer ('93) says that the new gland contains both gland cells and smooth muscle fibres, which arise as does the gland bud, from the Malpighian layer of the epidermis.

The place of origin of the replacement glands is found by Nicoglu ('93) and Heidenhain ('93*a*) in the very small, flattened cells immediately adjoining the Schaltstück and lying inside the gland. Vollmer ('93) on the other hand concludes that the place of origin of the new gland "ist das Keimlager des Rete Malpighi. Auch die von Heidenhain erwähnten unscheinbarer Zellenelemente, denen er die Bildung der Drüsenknospe zuschreibt stammen vom Rete Malpighi." There is no reason, he says, why the new glands inside the old ones should not differentiate as do the first glands in the course of their development.

In Plethodon the method of renewal of the worn-out glands is as these authors have described, but there is no evidence showing the source of the replacement glands, and the subject must be dismissed with the above references to the literature.

But whatever the source of the new glands, there can be no doubt that in every old gland without exception there is a small sac or replacement gland. This is always found in those glands which have not been discharged (Pl. XXIII, Fig. 31), as well as in those which have been and show the most extensive degenerative phenomena. In this respect Plethodon seems to differ from Triton (Vollmer '93). This author states that the growth of the new gland is initiated when the old glands are emptied. Nicoglu ('93) mentions the fact that the old poison glands contain the smaller sacs, but does not say definitely whether or not the destructive processes must have set in before the the new gland makes its appearance. But in Plethedon the *presence* of the replacement gland is not dependent on the secretory processes in the large glands. The former are present in the glands of an

animal thirty-eight mm. long which are not filled with secretion.

We have to deal then, in these cases, with the regeneration of a gland by a gland. Individual cells are not broken down, and then renewed by the growth of new cells as Schultz ('89) maintains, and as seems to be implied by Calmels ('83), who finds that the young gland cells are indifferent elements which may develop into either poison or mucous cells, so that a gland may be poisonous only in part.

The question, however, as to whether a poison gland is replaced only by a poison gland is still to be considered. May not these be renewed by glands which to begin with are mucous in character? That is, may not a specific poison secreting epithelium be replaced through mucous cells, and gland by gland instead of cell by cell? These inquiries have been raised by Nicoglu, and he says ('93, p. 425) that a mucous cell never goes over into a poison cell, or vice versa, and Schultz ('89) also says that mucous glands are always only mucous glands, and poison glands only poison glands (p. 33), and therefrom we are to suppose that the same is true of the individual cells, as he finds that cells replace cells.

Still the evidence gained by a study of the poison glands of Plethodon indicates rather strongly that we have to deal with *a production of poison glands from mucous glands entirely*. Nicoglu has already shown that in Triton a mucous gland may sometimes replace a poison gland entirely, but he very strongly opposes the idea that the function of such a gland ever changes. He holds (p. 435) that the condition of mucus within poison gland is a functional adaptation, because the animal needs more mucous glands than are on hand. Everything goes to show that in Plethodon, on the other hand, the occasional method of regeneration described by Nicoglu is the only one. The replacement glands already described stain blue without exception in Mallory, which has been shown to be a mucous stain. The contrast between the blue of the mucus and the red of the granular secretion is very sharp (Pl. XXIII, Fig. 31). The mucous reactions described for Van Gieson, orcein and mucicarmine, are shown invariably in the replacement glands as in the mucous glands outside, and the correspondence of the replacement

glands stained in iron haematoxylin with the other mucous glands is just as complete (compare Pl. XX, Figs. 2 and 3).

There can be nothing clearer than the reaction of the new glands to Mallory's stain. The blue color is present in every case as shown by a study of hundreds of glands. In the very large glands on the back of the tail the ingrowing glands never reach beyond a certain size, such as is shown in Pl. XXIII, Fig. 31. This may possibly be due to some effect of the poison which would hinder the growth of the small gland, or, as seems more likely, the new gland does not develop because it is hemmed in and hindered in its growth by the pressure of the large amount of secretion in the old gland. Drasch ('94) has made this suggestion previously, but does not say where the replacement glands are located. But in all the small poison glands which lie along the sides of the tail and also on the dorsal and ventral surfaces, particularly in the constriction, can be seen all stages of development of the mucous glands within them, from the small buds to new glands which have almost entirely replaced the old ones. The small poison glands differ from the largest ones in no other respect than in size, and for that reason it seems fair to conclude that the processes of regeneration going on in them are characteristic, and typical of those believed to occur under certain circumstances in the large glands of Plethodon, and as observed in other salamanders. There are many cases to be seen in Plethodon in which some glands are so far replaced by a new mucous gland that only a faint crescent of granular secretion can be seen, the rest of the contents being mucus. In other cases the amount of granular material is a little greater, and in still others we may see the gland half granular and half mucus (Pl. XX, Fig. 3; Pl. XXII, Figs. 18, 19, 20). In all these the granular portions stain as do the same parts of the large glands, while the remainder reacts to Mallory and the other stains as do the small sacs in the large glands and the mucous glands outside of these.

To sum up the foregoing we may say that the small glands within the large ones react like known mucous glands to Mallory's stain and mucicarmine, and in the same way so far as the nuclei of the replacement and mucous glands of the tail are concerned,

to iron haematoxylin. That is, both the mucous cells and those of the replacement glands stain blue in Mallory, red or pink in Van Gieson, and both have a fibrillar structure. The mucous reaction is also given with mucicarmine. And finally, the nuclei of the ingrowing gland fundaments always stain intensely black in iron haematoxylin, as do the nuclei of the mucous glands.

The facts just related have been gained entirely from a study of preparations made from material taken from unstimulated animals, that is those not irritated prior to immersion in killing fluids. The evidence along this line is stronger and more convincing in the case of an animal which, without stimulation of any kind other than such as might have occurred in nature, got rid of a great deal of the secretion in the glands of the tail and then cast that organ off, as if it could be of no further use. The animal in question, when first observed, was seen to be entangled head down between some pieces of bark in the terrarium in which it was confined. This seemed to irritate the salamander very much, for when it freed itself it began moving quickly about, swinging its tail from side to side like an angry cat. The tail, during this time, became covered with a very abundant white secretion, After about five minutes of such behavior on the part of the animal, when I merely touched the tail it was suddenly thrown off, the break being in the constriction back of the cloaca.

The tail was put into Zenker's fluid after about fifteen minutes, and sections made later. Here the likeness between the fundaments in the empty poison glands and the mucous glands could not be more complete. In all the stains used the appearances are exactly the same. The cells of the mucous glands are much higher than in other animals seen, stain a lighter blue in Mallory, and have a vesicular structure approaching granular, rather than the filar structure usually seen. Even so, the replacements glands cells are their exact counterparts, and show the same reactions to Van Gieson, mucicarmine, and iron haematoxylin, as well as Mallory's stain.

It seems hardly possible that the cells of the mucous glands could have so changed their structure and appearance in fifteen or twenty minutes, though the increase in height and consequent

diminution in size of the lumen of the gland, together with the vesicular structure of the cells, would lead one to think that they are in the way of becoming granule or poison cells. But whatever the interpretation put upon this appearance, and to whatever source it is due, it must be admitted that the fundaments in the old poison glands have undergone the same processes and their histological characters are now exactly similar to those of the mucous glands.

Further evidence that the glands are originally all of the same character may be gained from the literature. Ancel ('02), who has followed very closely the development of the skin glands in salamander, considers that the large glands represent organs more completely differentiated than the small glands toward a special functional adaptation, though both in early development are absolutely alike (pp. 269, 283.) Junius ('98) believes that there is but one kind of gland in the skin of the frog and probably of all Amphibia, and that the various glands of the authors are young and old forms or developing stages of them. He says further that in the frog he has not seen the regeneration described by Vollmer and Nicoglu, and declares that atrophied glands are replaced by wholly new ones developed by downgrowths of epiderm cells into the cutis. According to him, small glands represent young stages of large ones, and the former are equivalent to the non-contractile or mucous glands, while the latter are the dark, contractile, granule or poison glands.

Again, Hoyer ('90, p. 354) finds that in some poison glands of the salamander single cells or groups of cells lying between the non-staining large granular cells take on a red-violet color in thionin (which he employs as a specific mucous stain). He makes the suggestion merely: "Möglicher Weise deutet dieses eigenthümliche Verhalten auf eine genetische Beziehung der in den Drüsenzellen enthaltenen mucinähnlichen Substanz zu dem giftige Secrete." And finally, the observation of Phisalix-Picot ('00) that the secretion of the mucous glands of the Salamander is poison, seems to me to bear along this line of a correlation between the so-called mucous glands and the poison glands.

Evidence in this direction also, further than that already advanced seems to be indicated in the poison glands of Plethodon.

Here there is very frequently a distinct blue tinge to the *granular* secretion. This may possibly be because the metamorphosis from "a mucus-like substance to the poison secretion" is not entirely completed. At any rate one is impressed with the likelihood that there is mucous material in the poison glands outside of that contained in the replacement glands.

In the discussion of the replacement of the poison glands by those of the mucus variety, it has been shown that every large gland has within it the fundament of a new gland which to all stains for mucus except thionin gives the mucous reaction, and which is also the exact counterpart of the small glands having the mucous secretion. The fact that only in poison glands of smaller size are found evidences that they are entirely replaced by mucous glands, may be explained on the ground that there the amount of granular secretion is not sufficient to mechanically hinder the growth of the new replacement gland. The actual transition stages from mucous to granular secretion have not been observed in my material.

If we make the assumption in view of these facts that the glands of mucous character in the poison glands develop only into mucous glands on the death of the latter, we are forced to one of two conclusions: either that the small glands *outside* the large ones, especially in Plethodon on the dorsal surface of the tail, become the poison glands, or, on the other hand, that when the latter are once destroyed there is no return to such structure except by developing anew according to the embryonic type.

The latter process is going on continually in large as well as in small animals, as can be readily seen by inspection of sections. But it seems that the fundaments are all alike to begin with (Ancel '02); as this author says, the solid gland buds in which a cavity is formed do not undergo further important morphological transformations, and constitute the mucous glands. Those which remain solid, however, continue their development in other ways and form the poison glands (p. 269). It seems to me that this is equivalent to saying that in embryological development the poison glands pass through a mucous stage to reach their final form and character. It certainly lends evidence to the view

expressed, that the glands which are to replace the worn-out poison glands are originally mucus in character.

There is no reason to believe, however, that the replacement glands are functionless during the life of the poison glands in which they lie. Even the smallest replacement glands have distinct ducts and epithelium, and in some cases it is absolutely certain that they have elaborated a secretion similar in every respect to that of the mucous glands.

It is very probable that under all ordinary conditions the small glands in the large ones secrete mucus, and in this sense are adaptations; not because the animal through some unusual external conditions has come to need more mucous glands as Nicoglu ('93) says, but rather because under normal environment there is always need of more mucus than can be secreted by the glands outside the poison glands, especially when the latter are so closely crowded together as on the back of the tail in Plethodon. And much evidence goes to show that under stress of necessity such mucus secreting glands become by replacement the more highly specialized poison glands and take on a particular function, that of forming a substance protecting the animal from its enemies (Hubbard '03.)

The nerve supply of the skin of Amphibia has been a favorite subject of study for many years. Most investigators have limited themselves to the terminations in the sense organs of the skin and in or on the ordinary epidermal cells (Pfitzner '82; Canini '83; Frenkel '86; Massie '94; Herrick and Coghill '98; Coghill '99). The innervation of the glands has received less attention.

Eckhard ('49) first showed that the glands could be emptied by stimulating the anterior roots of the cerebro-spinal nerves, but did not consider the structure of the nerve endings. Eberth ('69) found that there is a network of very fine fibres close upon the glands; Englemann ('72) came to the same conclusion and showed farther that from the nerves about the gland fine twigs are given off to the contractile cells. Openschowski ('82) describes a network of nerves surrounding the glands, as well as an intracellular net; but from his figures it is hard to believe that the structures he shows are nerves. Drasch ('89) also experimentally proved the efficacy of nerve stimulation in obtaining

secretion from the glands, as does Phisalix-Picot ('00). Eberth and Bunge ('92) have described free nerve fibres which seem to end with knobs outside the epithelium of the ball of the thumb of the male frog. Loeb ('96) has also shown how closely the glands of Amblystoma are connected with the central nervous system. In 1898 Herrick and Coghill were able to show the existence an intimate connection of nerve fibres with the walls of the glands, but were unable to discover the exact relation of the fibres to the gland cells. They also described the plexus of nerves beneath the corium as being composed of two sorts of fibres; larger ones connected with the nerve bundles of the central system, and smaller ones which in part, at least, originate in ganglion cells in the corium. Schuberg ('03) has criticised the results of these authors, contending that many or all of the nerve bundles described are really connective tissue bundles, and that the ganglion cells are the "Mastzellen" he himself figures.

Massie ('99) continuing the work of Herrick and Coghill, considers the same arrangement of fibres beneath the corium, and also shows that nerves end on the muscles of the "ental" glands. He finds that nerve fibres passing from the nerve bundle plexus under the corium are intimately connected with the ental glands, and seem distinct from the nerves supplying the muscles. "It seems, therefore, that there are two groups of nerves passing to the glands of the ental series; the one attaching by the typical endings to the enveloping muscle cells, the other ramifying promiscuously over the surface of the gland." (p. 59.)

In the study of the nerves of the poison glands of Plethodon, three methods have been relied upon; namely, the silver nitrate-pyrogallic acid method of Cajal, and Mallory's phosphotungstic acid haematoxylin and fuchsin-orange G-anilin blue methods. The last named gave most excellent results, while of the other two Cajal's was only indifferently successful.

The haematoxylin of Mallory stains only the sheaths of the nerves and so it is of no value in tracing the axis cylinders, since, as is well known, the nerves lose the medullary sheaths on passing into the corium. Beneath the corium, however, the nerves can readily be followed by this method. In some instances fibres

are shown running for long distances beneath the corium, and branches can even be seen to turn toward the epidermis, but all traces of them are lost as soon as they enter the corium.

The other method of Mallory gives like results as far as the distribution of the nerves beneath the corium is concerned. In cross sections of the tail it is often possible to trace a fibre from the roots leaving the cord out to the corium. Sometimes this may be seen in one section; in many cases two or three neighboring serial sections will show the same. The plexus beneath the corium is shown best, as a whole, in frontal sections of the tail. Here it will be seen that the nerves are *very numerous*, and with the method in hand can be traced to their connections with the cord. There can be no question as to the presence of the nerve-bundle layer of the plexus that Herrick and his pupils have shown; but as regards the stratum of glanglion cells, it seems to me that Schuberg's criticism holds good. At any rate neither of Mallory's methods reveals such a structure, and this would at least seem strange in view of the beautiful staining of other nervous elements. In cross sections of the tail, Mallory's fuchsin method shows nerves running in or immediately beneath the inner corium layer. At times several fibres are in view at once, being, however, of different sizes.

Within the corium the distribution of the nerves to the glands is not apparent in sections which pass through the gland, owing to the exceedingly small size of the fibres. But when the periphery of the gland is just denuded, the nervous elements are shown very clearly. In such cases it will be seen that there is a feltwork of many *very fine fibres* closely investing the gland, *ending upon the muscle fibres* and *around the nuclei of the gland cells.*

The endings upon the muscles are shown both by Cajal's method and Mallory's fuchsin stain, and in some cases are typical (Pl. XXII, Figs. 25 and 26) as described by Huber and Dewitt ('97) and Coghill ('99). That is, they are equipped with terminal expansions or bulbs which lie on the muscles. In many cases fine branching fibres can be clearly seen lying upon the muscle layer. These pass over ultimately into the finest of slender twigs which without terminal expansions always lie on a muscle fibre and end there (Pl. XXII, Fig. 26.)

The fibres in the perinuclear endings are of much the same character as those of the muscles. There are many instances which are very clear of basket structure about the nuclei of the large glands (Pl. XXII, Figs. 21, 22. Pl. XXIII, Fig. 30). I have not been able to discover connections between the fibres and the nuclei, though in at least one case (Pl. XXII, Figs. 23, 24) the fibres end in knobs which lie directly on the nucleus. The latter seems usually to be surrounded only by a basket of fine fibres. Bethe ('94) has described three sorts of endings on cells. Of these he finds that in the unicellular glands of the frog's palate one frequently finds under the nucleus a small blue knob which is connected with a fibre. The latter cannot, however, be followed farther.

In the case of the gland cells under consideration, there can be no doubt that the nuclear basket is connected with nerve fibres. That there should be a nerve supply to the gland cells, seems evident from the experiments of Drasch ('89), Eberth ('49) and Loeb ('96) on Amphibian glands, and we have in Plethodon histological evidence of such supply. The well-known influence of the nervous system on the secretion of sweat, for example, may be also mentioned in this connection. Herrick and Coghill ('98, p. 51) have suggested the possibility of a connection between the nerves enveloping the glands, and the gland cells, but were not able to demonstrate it.

The objection may be raised that we are dealing here with elastic instead of nerve fibres. This does not seem possible for several reasons. The elastic fibres, as has been said, show very little variation in size, and never, as shown by staining in orcein, reach the excessive fineness of the nerve fibres. The branching of the elastic fibres is much less frequent than that of the nerves, and, in clearest distinction the former, as seen upon the glands, take an almost uniform direction even in branching, straight toward the epidermis, while the nerve fibres cross and recross and branch in all directions, and the finest twigs show varicosities which are never seen on the elastic fibres. The general effect of the brown fibres in an orcein stain is entirely different from that of the red ones in Mallory's stain, and leaves no doubt of the distinction here set forth between the elastic and nervous fibres.

SUMMARY.

1. The skin glands of *Plethodon oregonensis*, as of most Amphibia, are of two kinds: granular and mucous. The two are distinguished by the character and staining reaction of their secretions, and by other histological features, as well as by the sizes of the glands.

2. The bodies of the large glands possess an investing musculature, and in addition the ducts have both dilator and constrictor muscles lying in the epidermis.

3. The granule glands are poison in character.

4. In the elaboration and ejaculation of the secretion the poison glands are destroyed.

5. Renewal takes place by the growth into all the old glands of a new and smaller gland, which is mucous in character. The presence of this smaller sac is not dependent upon the removal of the secretion of the large glands, for whether this occurs or not, the fundament giving the mucous reaction is found in all glands; in those which show no degeneration as well as in those where it is wide-spread.

6. The growth of the new gland is dependent upon the removal of the secretion about it. There is evidence that even in case the glands are hindered in their development, they still secrete mucus. But when not hemmed in by the heavy granular contents of the large glands they grow and take the place and very probably assume the function of the old glands which they replace.

7. Both musculature and epithelium of the granule glands have a direct nerve supply. The gland cells are surrounded by a basket work of fibres, which in some cases have terminal expansions lying on the nuclei. The muscles are supplied by nerves with typical endings of expansions or bulbs, as well as by fine twigs without terminal expansions.

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LIST OF ABBREVIATIONS USED IN THE PLATES.

con.m.—constrictor muscle fibres.
c.t.b.—connective tissue bundles.
c.t.l.—connective tissue layer of gland walls.
c.t.—connective tissue in epidermis.
c.w.—cell walls.
d.—duct of gland.
dil.m.—dilator muscle fibres.
el.f.—elastic fibres.
ep.—epidermis.
ep.m.c.—cell containing musculature of duct.
fl.c.—funnel cell.
i.c.l.—inner layer of corium.
l.d.—lumen of duct.
l.gl.—lumen of gland.
m.b.—muscle bundles.
m.c.l.—middle layer of the corium.
m.f.—muscle fibres.
m.gl.—mucous gland.
m.n.—muscle nucleus.
n.c.—nerve cord.
n.e.—nerve endings.
n.fl.c.—nucleus of funnel cell.
n.f.—nerve fibre.
nuc.m.c.—nucleus of mucous cell.
nuc.p.c.—nucleus of poison cell.
nuc.ep.m.c.—nucleus of muscle cell in epidermis.
o.c.l.—outer layer of corium.
p.fl.c.—processes of funnel cells.
p.gl.—poison glands.
pig.—pigment.
prol.m.f.—prolongations of muscles into epidermis.
rep.c.—replacement cell (and nucleus).
rep.gl.—replacement glands.
sec.—secretion.

All the figures were drawn with the Abbé camera lucida.

ERRATA

P. 251, l. 31: *For* fuchsin-orange G-anilin blue,
read fuchsin-orangeG- anilin blue.

P. 259, under Zalesky 1866: *For* Bd. J 1, *read* Bd. 1; *for* Saeyler, *read* Seyler.

P. 264, under description of Fig. 16: *For* × 1650, *read* × 825.

P. 266, under description of Figs. 21, etc.: *For* × 1850, *read* × 925.

PLATE XX.

Fig. 1.—Cross section of entire tail, showing position on dorsum of large poison glands (*p.gl.*) and the mucous glands (*m.gl.*) chiefly on the ventral side. Diagrammatic except in outlines and proportions of parts. Van Gieson. × 22

Fig. 2.—Mucus gland from ventral side of tail, showing large lumen (*l.gl.*), and dark staining, angular nuclei (*nuc.m.c.*). Lower part of funnel cell (*fl.c.*) shown in epidermis (*ep*) which is not reproduced entire. Benda's iron haematoxylin. × 342

Fig. 3.—Poison gland (*p.gl.*) of small size partly replaced by ingrowing mucous gland (*m.gl.*). Funnel cell (*fl.c.*) shown in epidermis (*ep.*); nuclei (*nuc.m.c.*) of mucous gland darkly stained as in Fig. 2. Benda's iron haematoxylin. × 342

Fig. 4.—Outline drawing of cross section of duct of poison gland showing replacement cells of the funnel (*rep.c.*) rolled one within the other, the funnel cell (*fl.c.*) and the lumen of the duct (*l.d.*) Mallory's conn. tissue stain. × 875

Fig. 5.—Portion of lower part of poison gland showing bundles of connective tissue (*c.t.b.*) passing from the inner layer of the corium (*i.c.l.*) to the connective tissue layer of the wall of the gland (*c.t.l.*) Nuclei (*nuc.p.c.*) and walls (*c.w.*) of gland cells. Secretion not shown in detail. Mallory's conn. tissue stain. × 342

Fig. 6.—One side of median longitudinal section of duct of poison gland showing muscle fibre (*m.f.*) and its nucleus (*m.n.*) and the prolongation of the fibre (*prol.m.f.*) into the epidermis (*ep.*). Compare with Pl. IV, Fig. 27. Mallory's conn. tissue stain. × 280

Fig. 7.—Branching muscle fibres (*m.f.*) from lower part of gland. Mallory's conn. tiss. stain. × 342

Fig. 8.—Longitudinal section of poison gland through the mouth showing two expansions of muscles (*m.f.*) in which the nuclei lie, and portions of muscle fibres. Nucleus of funnel cell (*n.fl.c.*) at duct (*d.*). Secretion of gland not shown. Ferric-chloride haematoxylin. × 342

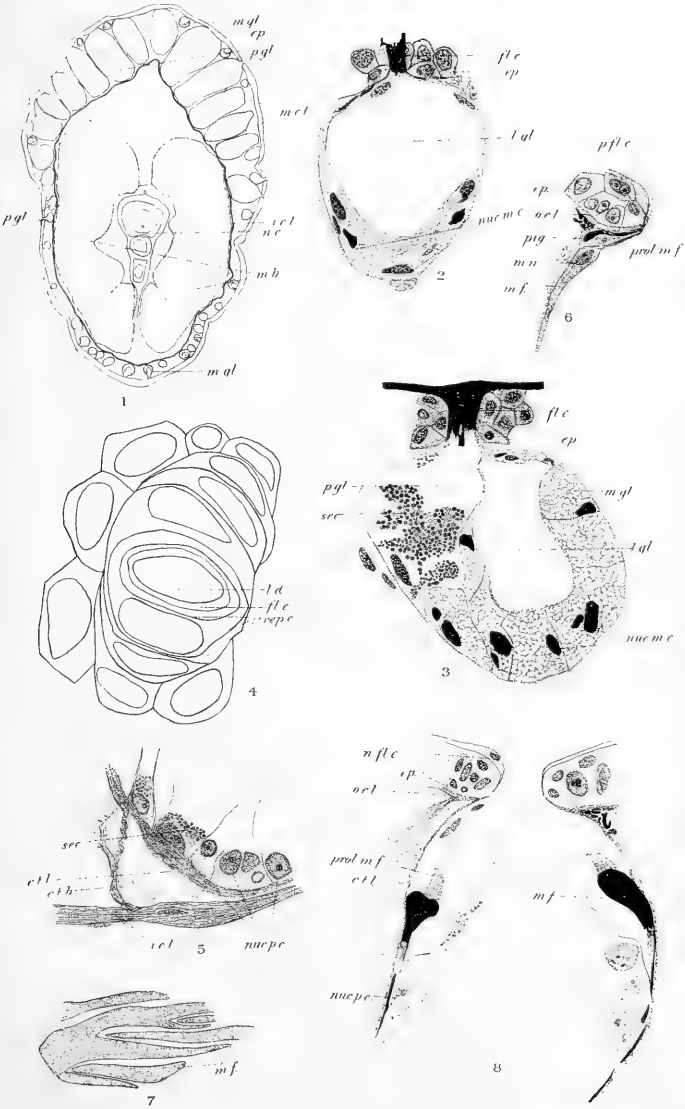

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PLATE XXI.

Fig. 9.—Elastic fibres (*el.f.*) on surface of gland. Gland wall (*e.t.l.*) in section indicated; also nuclei of gland cells. The elastic fibres pass through the inner layer of the corium (*i.c.l.*). Tänzer's orcein. × 342

Fig. 10.—Section through upper pole of gland at one side of the duct, showing cut ends of muscle fibres (*m.f.*) and their nuclei (*m.n.*). From cross section of tail. The nuclei in this figure correspond in position to that shown in Pl. XX, Fig. 6, and to the enlargement of the fibres shown in Fig. 8. Mallory's conn. tissue stain. × 342

Fig. 11.—Tangential section through wall of gland and the mouth, from frontal section of tail. Muscle fibres (*m.f.*) and nuclei (*m.n.*) shown. Funnel cell (*fl.c.*) lining duct and some secretion (*sec.*) in lumen of duct (*l.d.*). Mallory's conn. tissue stain. × 342.

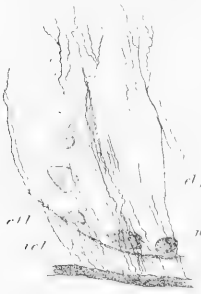
Fig. 12.—Cross section of gland from frontal section of tail, at level of muscle nuclei (*m.n.*). Compare with Figs. 10 and 11. Van Gieron's stain. × 400

Fig. 13.—Cross section of epidermis at upper pole of poison gland, showing deep lying epidermal cell (*ep.m.c.*) which contains the constrictor and dilator muscles of the duct. Mallory's conn. tissue × 342

Figs. 14 and 15.—Cross sections of ducts at level of cell described in Fig. 13, showing constrictor (*con.m.*) and dilator muscles (*dil.m.*). In Fig. 14, only the outer ends of the constrictor fibre appear. In both figures are shown the ends of the muscle fibres (*m.f.*) of the glands, in the epidermis, and the connective tissue (*c.t.*) outside the muscles. The nucleus of the epidermal muscle cell is shown in Fig. 14. Mallory's conn. tissue stain. × 875

Fig. 16.—Description as for Figs. 14 and 15. But one set of constrictor fibres shown; lumen of duct (*l.d.*) nearly closed. Mallory's conn. tissue stain. × 1650

Fig. 17.—Longitudinal section of nearly empty poison gland. Secretion (*sec.*) very small in amount, cell walls (*c.w.*) distinct, nuclei clear and of irregular shapes. Semi-diagrammatic in unimportant details. Benda's iron haematoxylin. × 342



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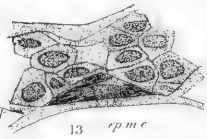

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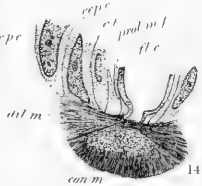

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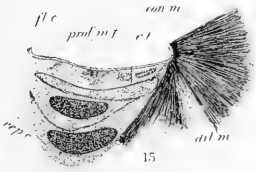

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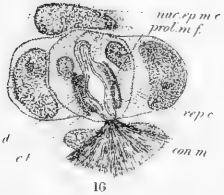

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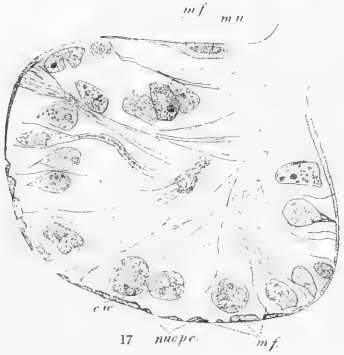

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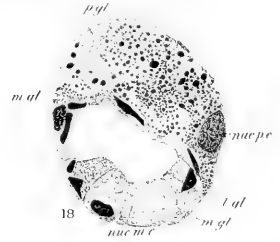
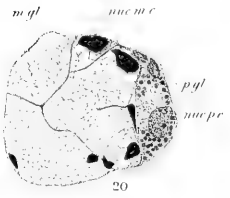
PLATE XXII.

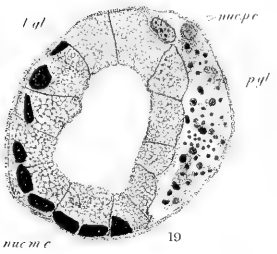
Figs. 18, 19, 20.—Stages in replacement of small poison gland (*p.gl.*) by mucous glands (*m.gl.*) from sides of tail. Mucous nuclei dark. Secretion (*sec.*) shown in poison part only. Benda's iron-haematoxylin. × 342

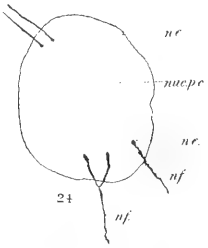
Figs. 21, 22, 23, 24.—Tangential sections of poison glands, showing nerve endings (*n.e.*) on nuclei of poison cells (*nuc.p.c.*). Mallory's conn. tissue stain. Figs. 21, 22, 24. × 1850. Fig. 23. × 875

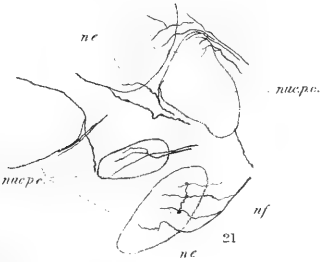
Figs. 25 and 26.—Tangential section of wall of poison glands, showing nerve endings (*n.e.*) on muscles (*m.f.*). Fig. 25, Mallory's conn. tissue stain. Fig. 26, Cajal's silver nitrate-pyrogallic acid. × 875

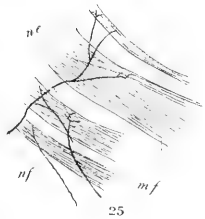












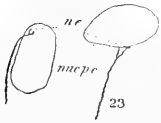


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PLATE XXIII.

Fig. 27.—Median longitudinal section of duct of poison gland, showing prolongation of funnel cell (*p.fl.c.*), prolongation of muscles (*prol.m.f.*) into the epidermis, and the connective tissue (*c.t.*) outside them. Replacement cells (*rep.c.*) shown with processes extending down as far as funnel cell. Mallory's conn. tissue stain. × 1650

Figs. 28, 29, 30.—Cross sections of ducts, showing funnel cells (*fl.c.*), gland muscles (*prol.m.f.*), connective tissue (*c.t.*) at sides of duct (*d.*), and constrictor and dilator muscles (*con.m*, *dil.m.*). Mallory's conn. tissue stain. × 1650

Fig. 31.—Longitudinal section of poison gland, showing small mucus gland (*m.gl.*) inside it. Large gland 440 microns by 180 microns; small gland 90 microns by 43 microns. Mallory's conn. tissue stain. × 1650

Fig. 32.—Nerve-endings (*n.e.*) about nucleus of poison cell (*nuc.p.c.*). Mallory's conn. tissue stain. × 1650

Fig. 28

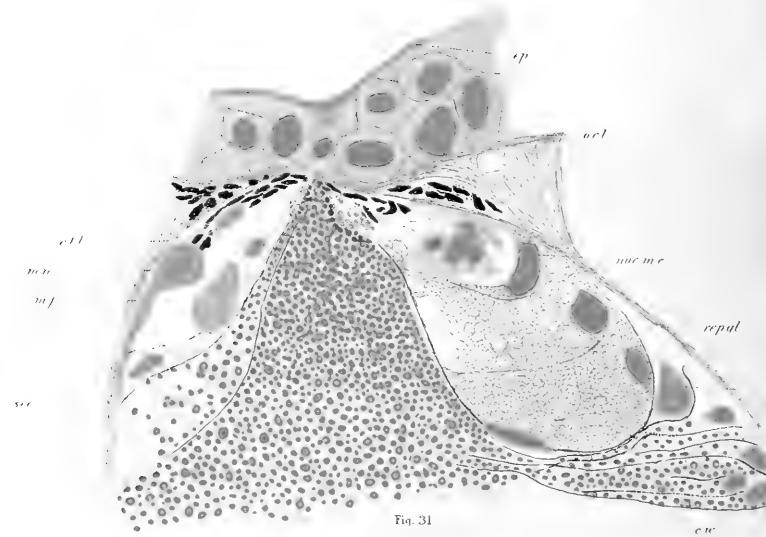

Fig. 31

Fig. 29

Fig. 32

Fig. 30

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Fig. 28

Fig. 27

Fig. 29

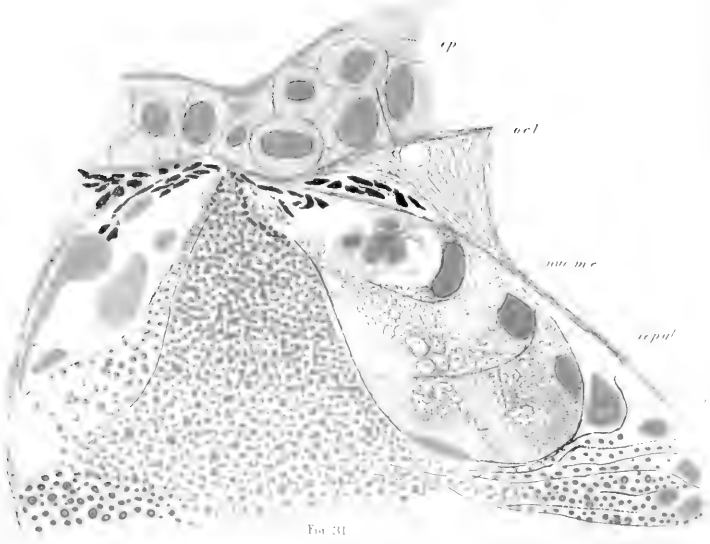

Fig. 31

Fig. 32

Fig. 30

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ZOOLOGY

Vol. 1, No. 8, pp. 269-286, Pls. 24-25 December 17, 1904

THE DISTRIBUTION OF THE SENSE ORGANS IN MICROSCOLEX ELEGANS

BY

JOHN F. BOVARD

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THE DISTRIBUTION OF THE SENSE ORGANS IN MICROSCOLEX ELEGANS

BY

JOHN F. BOVARD

(Zoological Laboratory, University of Oregon)

The sense organs of the earthworm were discovered by Leydig ('65), who described them as spots, each made up of a group of cells, five or six times larger than the surrounding cells and often times limited by pigment. Mojsisovics ('77) was the first to accurately describe these cells. His figures do not show them to be any different from ordinary epithelial cells except for the possession of sense hairs which pass through the cuticle. Schultze, a contemporary of Mojsisovics, has the credit of discovering the canals through which the sense hairs protrude. For nearly twenty years the question was debated whether or not these were really sense organs. Cerfontaine ('90) settled this by giving accurate and detailed descriptions and illustrations. He likened the arrangement of cells to the manner in which onion leaves overlap each other. This character may be seen but it is not to be observed regularly throughout the whole worm. Although the connection of these organs to the nervous system was conjectured, the proof was not brought forward until 1895, when Miss Langdon published her paper on the sense organs of *Lumbricus* in the *Journal of Morphology* for May of that year. She demonstrated conclusively the direct connections of the cells of the sense organs with the nervous system and described the distribution of these organs over the body.

It is the purpose of the present paper to describe the distribution of the sense organs over the body of *Microscolex elegans*, a California earthworm, and to make some comparisons with *Lumbricus agricola* as described by Miss Langdon. These two worms are quite different as regards structure and habits. No effort was made to work out the connection of the sense organs to the nervous system of *Microscolex*.

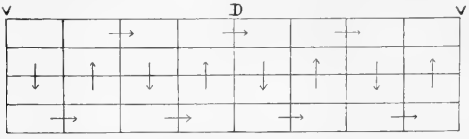
MATERIAL AND METHODS.

Microscolex is a small worm with apparently a limited distribution. It has been found in Berkeley, but is far more abundant in Golden Gate Park, San Francisco. Dr. Eisen ('94) has reported it also from Mount Diablo and Sonoma County regions. The worm is usually found in manure piles or amongst decaying leaves. In Berkeley a pile of leaves was found which contained no other forms than *Microscolex elegans*, while in the park in San Francisco it was associated with *Allolobophora foetida*. It was noted that *Allobophora caliginosa*, a worm very common throughout the State, was seldom found in the immediate vicinity with these worms.

Fresh material was used wherever possible, but after the dry weather came preserved material had to be resorted to. The worms were allowed to swim about a while in water to free them from grit and dirt, and were then killed by allowing alcohol to drip into the dish at the rate of 60 drops to the minute. In this way the worms were stupefied in from two to three hours. From the drip they were transferred to 80 per cent. alcohol and held between glass rods to keep them straight while hardening. When hardened they were preserved in 95 per cent. alcohol. Material to be used in sectioning was taken directly from the drip and killed in Flemming's solution or corrosive sublimate and acetic acid. Sections 2 to 5 microns in thickness were stained with Mayer's haemalum or Delafield's haematoxylin. On the whole, material stained in toto with Delafield's hematoxylin gave the most satisfactory results.

The cuticle was prepared in the following manner. Freshly killed worms were split open along the mid-ventral line from the mouth to the anus. They were then put into 30 per cent. alcohol or water to macerate, when after two or three hours the

cuticle could be removed. They are very delicate and easily torn, so as to insure removal without tearing the worm was cut transversely into two parts and the cuticles handled with camel's hair brushes. This is practically the same method used by Miss Langdon ('95). They were then carefully spread out on slides and allowed to dry. When thoroughly dry the cuticle sticks to the slide and is ready to be examined. The spots which indicate the areas of the sense organs are thinner than the rest of the cuticle, and perforated with minute holes where the sense hairs project. At best these areas are not clearly defined. Staining the cuticle was tried with very good results, this bringing into stronger contrast the sense areas and the remainder of the cuticle. The staining was done before the cuticle was spread on the slide. The cuticle was dipped into a strong stain two or three times, rinsed with pure water and then mounted. A few cuticles were stained after mounting, but on account of their hardness when dry, they did not take stains well. Nigrosin, iron haematoxylin, Ehrlich's haematoxylin and methylin blue were used. Nigrosin was the most satisfactory. The staining of the cuticle is an important aid to accurate study of the distribution of the sense organs.



Text Fig. 1. The small rectangles indicate the areas as seen with the small diaphragm in the eyepiece of the microscope. The arrows indicate the order in which the areas were examined.

The plan was to count all the sense organs found in the entire cuticle and to plot these so that their distribution in any part might be seen at a glance. It was also desired that the count of the sense organs should be as accurate as possible. In order to see the sense areas well a high magnification was necessary. Under these conditions a whole metamere could not be in the field at once, so a method was devised whereby a small area

could be counted at a time. A rectangular diaphram of such dimensions that its width was one-fourth the width of the metamere and its length one-eighth the length of the metamere, was put in the eyepiece. By means of a mechanical stage, the whole area of each metamere was gone over, and plots were made of all sense organs in each of these small divisions. The entire surface of one worm was gone over in this way, and parts of four others were enumerated for comparison.

The work, for the most part, was carried on in the zoölogical laboratory of the University of California, but was completed in the laboratory of the University of Oregon. The problem was suggested by, and the work carried on under the guidance of, Professor C. A. Kofoid of the University of California, and I wish here to express my sincerest appreciation for his kind advice and for his help in the final arrangement of the paper.

STRUCTURE OF THE SENSE ORGANS.

The structure of the sense organs of *Lumbricus* and *Microscolex* is practically the same. In *Microscolex* each organ (Plate XXIV, Fig. 4) is made up of a group of sense cells lying loosely in a cavity surrounded by a layer of boundary cells which form a continuous layer usually one cell thick, but it may be thicker. They are the same as the supporting cells of the epidermis, with the exception that they are usually greatly flattened. The boundary cells are somewhat longer than the epidermal cells, because they are bowed outward and stretch from the elevated area just under the cuticle to the thinned part of the basement membrane beneath. The sense organs are ovoid, the greatest transverse diameter being a little closer to the proximal than to the distal end. The smaller distal end forms a raised spot on the cuticle, which is here thinned and has canals for the passage of the sense hairs. The basal end is usually somewhat flattened, and rests on the basement membrane of the epidermis.

The size of the organs is about the same for both worms. They measure from 80 to 100 microns in height, 18 to 20 in diameter at the top and 40 to 60 in the widest part. In *Microscolex* there is a wider range of variation in the diameter of the top as indicated by the dimensions of the sense areas in the

cuticle. These areas above the organs measure from 6 to 35 microns in diameter. Their average size, however, is about 15 microns.

Lying within the membrane formed by the boundary cells, are the sense cells proper. These are greatly elongated and narrower at the ends than in the middle. The widest part is just below the middle, which contains the nucleus. Their distal ends, which are broader than the proximal, carry stiff bristles, which extend through a short canal in the cuticle. The basal end of the cell is very narrow, and runs out into one or two long processes. Among the basal ends of these cells may be found low cuboidal and sharply pointed columnar cells, which rest on the basement membrane and project upward into the cavity of the organ. Several of these have been observed to have long processes running up along the sense cells, thereby suggesting transition stages in their development. It is often difficult to find the cell boundaries near the top of the sense organ, but in the lower end the cells are quite far apart and sharply defined. The internal structure of the sense organ of *Lumbricus* differs from that of *Microscolex* in that in the former species the cells have the same diameter at the distal and the proximal ends, and stand entirely apart, not showing the close approximation at the distal ends. Miss Langdon found no basal cells with processes projecting up into the cavity of the sense organ, while in *Microscolex* these were plainly seen.

The cuticle has three kinds of openings. We note first the largest openings, such as the nephropores (Plate XXV, Fig. 6), the sexual openings, and the chaetae sleeves (Plate XXV, Fig. 5). When the cuticle is stripped off the cuticular sheathes of the chaetea are removed with it, and in the preparations these lie bent over and close to the cuticle, so that the position of each chaeta is definitely marked on the metamere. The second class of openings includes the sense areas (Plate XXV), which mark the positions of the sense organs. These areas are circular, or slightly oval, and thinner than the rest of the cuticle, and each containing near its center openings for the sense hairs, which became more scattered toward the periphery. The third kind of opening is that of the gland cells of the epidermis. These are

the very small and numerous openings found all over the cuticle. They are about the same size as the openings for the sense hairs. The cuticle is made up of two layers, an outer dense and an inner loose, fibrous layer. The thinning of the cuticle for the sense organ is at the expense of the inner layer. The outer layer contains two sets of fiber, which cross each other at an angle of about 60 degrees, each fiber running spirally about the worm. The openings for the gland cells and the sense hairs are made by pushing the fibers to one side, while for the larger openings there is a distinct rupture of the fibers.

DISTRIBUTION OF THE SENSE ORGANS.

The sense organs were found in all parts of the surface of the body of *Microscolex*, while in *Lumbricus* none were found in the clitellum. The organs were not distributed equally, certain regions having more than others. The largest numbers are present in the anterior segments. Passing caudad they gradually decrease till in the middle region of the worm (segments 18 to 90) they reach a degree of constancy for each successive segment approximating 220. Continuing caudad beyond segment 90, the numbers again increase, but do not become so abundant as in the anterior segments. Thus in one worm the second segment had 511 sense organs, the thirty-fifth had 218, while the ninety-third had 310. The ninety-third was next to the last segment in this worm. The lowest number in any segment was 136, in the fiftieth; the highest was 569, in the fifth. In *Lumbricus* the anterior metameres have the largest numbers, but from here on to the caudal end there is a gradual and uninterrupted diminution in numbers. The total sense organs in corresponding metameres are unequal. *Microscolex elegans* contains on an average 103 segments, while *Lumbricus* has over 150. The following table shows some of the figures for corresponding segments:

	Prostomium and 1st Seg.	10th Seg.	56th Seg.
Lumbricus agricola.....	1900	1200	799
Microscolex elegans.....	536	324	218[1]

[1] This is the number of sense organs in the thirty-fifth segment, which corresponds with the fifty-sixth of *Lumbricus*, whose length is twice that of *Microscolex*.

The total number of sense organs in a single *Lumbricus* was approximated by Miss Langdon ('95) at 150,000, while for a *Microscolex* of 103 segments only 14,787 were found. Thus *Microscolex*, with approximately one-fourth the surface of *Lumbricus*, has only one-tenth as many sense organs.

The largest sense organs in *Microscolex* (35 microns in diameter) are on the prostomium, and the smallest (6 microns) on the clitellum. For the rest of the worm, the organs have about the same average size (15 to 19 microns). Those of the posterior end do not increase in size as do the numbers. In *Lumbricus*, on the other hand, the largest are on the prostomium and the first metamere, and caudad they gradually diminish in size, the smallest being on the caudal segments.

Besides these differences in distribution over the general surface of the worm, there are certain zones in each metamere where there is a perceptible grouping of the sense organs. This distribution differs both antero-posteriorly and dorse-ventrally. In the antero-posterior direction three zones are to be seen. The first, the cephalic or anterior zone, extends from the septal furrow in front of the median zone of the metamere. The surface of the anterior zone is an arc, the convexity of whose surface points in the anterior direction. The nephropores occur in this zone close to the septal furrow. The largest numbers of sense organs are in this zone, and passing caudad they decrease in size and numbers in the successive metameres. For the most part the organs of this zone are most numerous near the septal furrow. They do not occur in a distinct line along the anterior margin, as in *Lumbricus*, but are scattered over a small area or belt. The numbers become fewer as we approach the succeeding zone, making a gradual transition from a region of large to one of comparatively small numbers.

The second zone is a narrow one extending through the middle of the metamere, and consisting of a single row of the largest sense organs found in line with the chaetae sleeves. This is true in all the metameres except the first, where the largest organs are in the anterior zone. It is impossible to make out any distinct groupings about the chaetae sleeves, as was shown in the case of *Lumbricus* by Miss Langdon ('95).

The third zone is the caudal, or the posterior. It occupies an area between the median and the septal furrow, and covers an arc the convexity of whose surface points posteriorly. The distribution here is exactly the reverse of that in the anterior zone. Excepting in the prostomium and the first metamere the posterior zone has the fewest and smallest sense organs. In this zone the organs decrease in number caudad till we reach the sixtieth metamere, where they begin to increase in both size and number, though they continue to decrease caudad in the other zones, resulting in the approximation to the constant number previously noted. The anterior and the posterior margins of this zone have the organs scattered, the majority being in the central part.

In all the segments except the first five and the last five the average diameter of the sense organs in the anterior zone is 16 microns, in the median they are 19 to 22 microns, and but 10 in the posterior. Again turning to *Lumbricus,* we find that, beginning in the second, third and the fourth metameres, a median line of sense organs is prominent, and diminishes caudad. No distinct median zone is here recognized, the median line of organs in line with the chaetae are not separated from the posterior zone as they are in the anterior, so that only two zones are distinguishable, a cephalic and a caudal. Around each opening of the dorsal pores, nephropores and sexual ducts of *Lumbricus* groups of organs were found guarding these entrances. No such distribution was found in *Microscolex,* each opening, on the contrary, being surrounded by a small clear area containing no sense organs at all (Plate XXV). In both the worms the surface of the prostomium and the first metamere are covered with sense organs, so that no distinct zones can be made out. In *Microscolex* the posterior margin of the first metamere contains many smaller sense organs, while the rest of the surface of the prostomium is covered by very large organs. The following table shows the distribution in the antero-posterior direction in the metameres of *Microscolex.*

Segment.	Number of Sense Organs in Zones. Anterior.	Median.	Posterior.
6	293	135	101
8	228	83	70
10	180	81	63
12	148	73	52
[1]14	101	69	34
20	102	64	57
30	92	58	65
40	116	57	74
50	53	32	58
60	78	72	100
90	82	76	107
91	67	61	105
[2]93	88	88	134

The dorso-ventral distribution was not mentioned in *Lumbricus,* but is a striking feature of *Misroscolex,* where four regions—a dorsal, two lateral, and a ventral—may be distinguished. The dorsal surface always has fewer organs than the ventral, while the lateral surfaces always have more than either the dorsal or the ventral. For example, metameres 10 to 20 contain on the dorsal surface a total of 483 sense organs, on the ventral 632, and on one of the lateral zones 724. Recording these as they occur in different metameres of a *Microscolex,* we have the following table:

Number of Segment.	Number of Sense Organs on Surface. Dorsal	Lateral.	Ventral.
10	72	76	60
12	47	80	75
13	44	60	58
15	48	63	55
17	19	63	45
20	29	71	60
35	27	67	36
50	18	50	31
80	30	61	55
93	39	89	78

The only exception to this type of dorso-ventral distribution is in the prostomium and the last segments, and here the organs are more evenly scattered over the surface. The ratio of the number of organs in the ventral zone to that of the dorsal varies

[1] Clitellum.

[2] Next to last segment.

from 6 : 5 to 5 : 3. The greatest contrast is in the middle of the worm, where the ventral organs out-number the dorsal 5 to 3.

The distribution of the sense organs in *Microscolex* is significant when viewed in the light of the habits of this worm. *Microscolex* is a small, frail worm, and its movements are quick and rapid. Backward movement is almost as free as movement in the other direction. Many times during experiments on these worms they have covered a distance of more than half a meter in a continuous movement. While the common *Allolobophora caliginosa* has the ability to move backwards, it never shows this in so marked a degree as does *Microscolex elegans.* I have seen these worms moving backwards freely, not only in the burrows, but also on free surfaces, when no experiments were being tried and there was apparently no occasion for such action. Naturally, we should expect the anterior end of the worm to be the most sensitive, and therefore have more sense organs than do the other parts of the worm. There being in *Microscolex* this backward movement, the posterior end should also be particularly sensitive. Actual count of the organs of these regions shows an increase in the number of organs posteriorly and on the posterior arc of the rear segments. The anterior segments have the largest numbers, which decrease till a region of constancy occurs behind the clitellum; then follows an increase in the numbers from the nintieth segment on to the end of the worm.

Another noticeable habit of this worm is its marked squirming movement, especially noticeable on a smooth surface. There are two reasons why the lateral zones should have more sense organs than the dorsal or the ventral zones. First, along the sides of the worm the nephropores occur. If these pores are places of great sensitiveness, then we should expect to find, as in *Lumbricus,* each nephropore provided with a distinct grouping of the sense organs. As Plate XXV, Fig. 6, plainly shows, there is no grouping at all about these openings. On the contrary, the area just about the pore is usually quite free from organs. There are no other openings on the lateral surfaces of the body. The lateral sense organs are scattered in *Microscolex,* and the whole surface must do the duty that a group of the

organs immediately about the opening does in *Lumbricus*. Secondly, in the burrow or on a rough surface, the side to side motion, so characteristic of the worms, would make the sides also a region of first contact with the environment, consequently we might expect the body to be sensitive here and to have more sense organs. The ventral surface is seldom off of the substratum, first, because a better hold is gained here with the chaetae; and second, because gravity tends to keep that side in contact with the earth. For these reasons the ventral surface would have more use for sense organs than the dorsal, whose surface would be stimulated only by occasional rather than by constant contact.

The distribution of the sense organs suggests that the surface of the worm is not equally sensitive in all parts. Experiments to determine the sensitiveness were made, with alcohol and acids as irritants, sugar and quinine as taste stimulants. A fine capillary pipette was used for applying alcoholic solutions of 1 per cent. and less, so that a small quantity could be applied to a small area. The time between the application and some direct manifestation of irritation was recorded by a stop watch. The records show that the anterior end is more sensitive than the posterior, and the posterior more than the middle part. Solutions of quinine of one thousandth of 1 per cent. and even less gave the same results as the alcohol. The fact that the animals reacted to the quinine may indicate that the sense organs have some gustatory function. This might be expected, for the difference in structure between sense organs on the outside of the body and those of the pharynx is very slight. The sense organs of the pharynx are lower and a great deal broader than the others. The results of the last set of experiments are of importance because they show that the degree of sensitiveness inferred from the differences in time reactions of a given region is correlated with the number of sense organs found therein. The ratio of the number of organs in the anterior end to those of the posterior is 3 : 2, while the ratio of time reactions is approximately 4 : 7. Thus the ratio of the numbers of sense organs in two given areas is approximately inversely proportional to that of the time reactions. This relation is shown in

the comparison of the anterior and the middle parts of the worm. The ratio of the sense organs in the two regions is 3 : 1, while the ratio of the time reactions is 4 : 9. In the following table some of the time reactions are given, the time being given in seconds:

Stimulant.	Time Reactions of Different Portions of the Worm.		
	Anterior.	Middle.	Posterior.
Alcohol	2	7.8	5.6
Alcohol	3.8	10.2	7
Alcohol	1.8	10.8	8.6
Alcohol	4.8	8	8.6
Alcohol	5	6	4
Quinine	4.8	5.6	5.6
Quinine	4.6	7.8	6.2
Quinine	7.6	8.6	13.6
Quinine	6	13.6	9

SUMMARY.

1. The anterior metameres contain the greatest numbers of, and the largest sense organs.

2. In the middle of the worm (metameres 18 to 90) a region of constancy is found where each metamere contains about 220 sense organs.

3. Toward the posterior end the number of sense organs per metamere increases to about two-thirds that found in the anterior end.

4. Every metamere shows an antero-posterior and a dorso-ventral distribution of the sense organs.

(*a*) In the antero-posterior direction there are three zones—anterior, median and posterior.

(*b*) In the dorso-ventral direction there are four areas—two laterals, a dorsal and a ventral. The number of sense organs in the ventral area exceeds that in the dorsal, and that in the lateral surpasses the ventral.

5. In the posterior end of the worm the antero-posterior distribution is just reversed, the larger number of organs being in the posterior arc of the metamere. This distribution is correlated with the habits of the worm.

6. The largest sense organs are in the prostomium, and the smallest in the clitellum.

7. In each metamere except those of the posterior end the largest sense organs are found in the median zone, the next in the anterior zone, and the smallest in the posterior zone.

8. The total number of sense organs in *Microscolex elegans* is less than 15,000, to 150,000 in *Lumbricus agricola.*

9. There are no groups of sense organs about the nephropores, sexual ducts, or the chaetae sleeves.

10. The sense organs are the most numerous and the largest on those parts of the worm which most frequently come in contact with surrounding objects.

11. The ratio of the numbers of sense organs in two given areas is approximately inversely proportional to that of the time reactions.

University of Oregon,
Eugene, Oregon, May 14, 1904.

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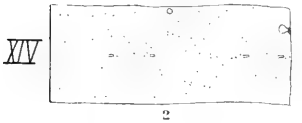
EXPLANATION OF PLATE XXIV.

Fig. 1.—Prostomium and six metameres between the mid-dorsal and mid-ventral lines. The chaetae are represented in the median line in the median zone. The nephropores are seen near the septal furrow. The size of the black dots represents the size of the sense organs only approximately.

Fig. 2.—A metamere from the clitellum. Near the mid-ventral line is the oviducal pore.

Fig. 3.—The next to last and the last metameres of the body, showing the reversed antero-posterior distribution.

Fig. 4.—Sense organ cut in longitudnal section. *cut.*, cuticle; *gl. c.*, gland cell; *b. m.*, basement membrane; *cir. m.*, circular muscle; *b. c.*, basal cell; *s. c.*, sense cell showing one of a group of sense cells and the tapering basal ends; *bd. c.*, supporting cell next to the sense organs; *epi. c.*, epidermal cell; *s. h.*, sense hair protruding through the thinned cuticle.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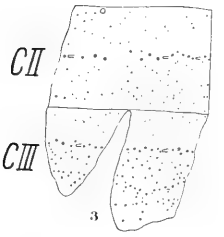
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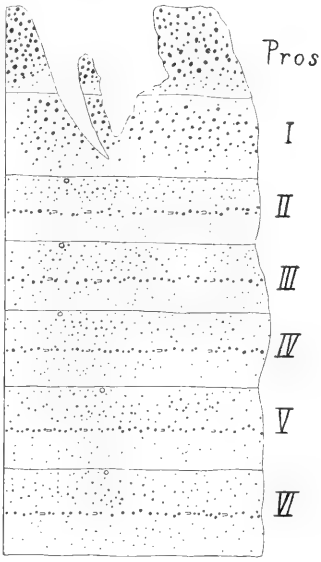
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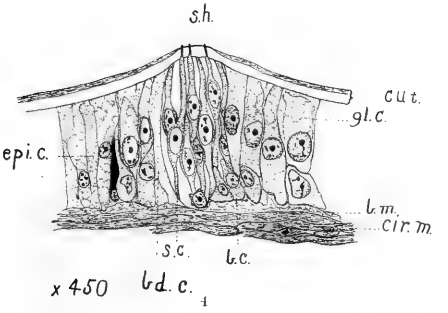
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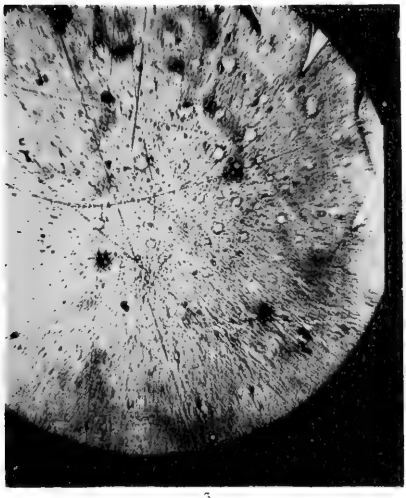
EXPLANATION OF PLATE XXV.

Fig. 5.—Chaetae sleeve, showing the absence of any special distribution about it. The glandular openings appear as black dots in regular rows.

Fig. 6.—Area about the nephropore.

Fig. 7.—The posterior portion of the prostomium, showing the size of the organs in that part.

These micro photographs were taken with a Zeiss microscope, AA objective, and the No. 12 compensating ocular. The magnification in each case is about 88 diameters.



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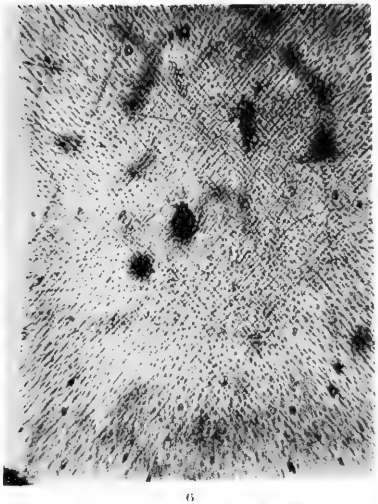

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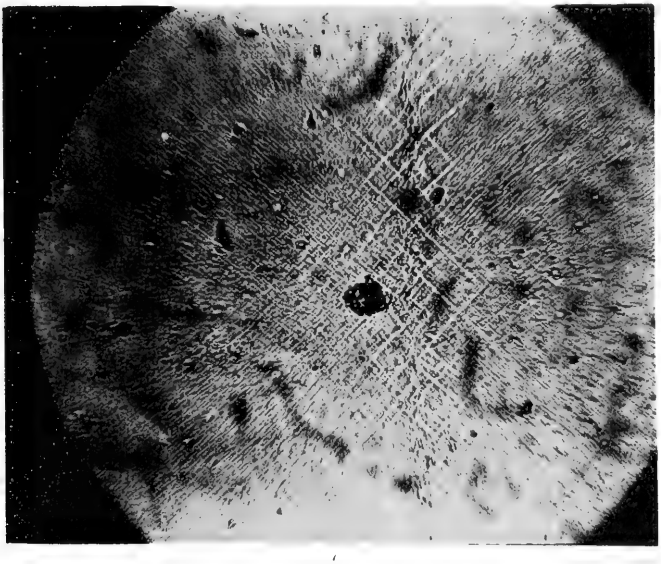

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BY

CHARLES ATWOOD KOFOID

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SOME NEW TINTINNIDAE FROM THE PLANKTON OF THE SAN DIEGO REGION

(From the San Diego Marine Biological Laboratory of the University of California.)

BY

CHARLES ATWOOD KOFOID

The following Ciliates belonging to the family *Tintinnidae* have occurred in the collections made at the San Diego Marine Biological Laboratory in 1903-1905. They appear to be as yet undescribed and are of considerable interest in several instances owing to the highly specialized nature of the external shells or loricae which these simple unicellular animals have formed in adaptation to a pelagic life.

I am indebted to Mr. R. D. Williams and Mr. John F. Bovard, assistants at the San Diego Laboratory, for some of the observations recorded and several of the sketches utilized in this paper.

Tintinnus serratus sp. nov.

Pl. XXVI. Fig. 1.

The lorica of this species is tubular, with slightly flaring ends. Its length is about twelve times its least diameter which is near the aboral end. It gradually enlarges anteriorly, attaining just behind the anterior flare a diameter one and one half times that in front of the posterior flare. Both ends are open, the diameter of the aboral aperture being three-fifths of the oral. Within a short distance of each the wall of the lorica flares

gradually in a regular curve, approximately 30° from the axis, increasing the diameter about 20%. The aboral margin is perfectly smooth but the oral is deeply and regularly incised, forming a serrate margin of twenty erect, acute teeth.

The wall is unusually thin and hyaline even for this thin-walled genus and shows only the faintest traces of structure.

The animal has not been found in the lorica.

The number of adoral ciliary plates in the genus Tintinnus is stated by Daday ('87) to be 18-20. There are 20 circumoral teeth in the lorica of this species, a fact which indicates that there is some correlation between the structure of the adoral apparatus and the formation of the serrate oral margin of the lorica.

This species belongs to the form-cycle of *T. fraknoi* Daday, differing from it in the possession of the serrated circumoral margin of the lorica, and in attaining less than one half its size. As figured by Daday ('87) the ends in *T. fraknoi* flare more gradually and are less differentiated than in *T. serratus.* In the Pacific plankton, however, I find that *T. fraknoi* generally has the flare better developed than it is in Daday's figures of the species from the Mediterranean.

Dimensions:—Length, 150 μ; diameter inside of flare, anteriorly 18 μ, posteriorly 12 μ; of oral opening, 25 μ; of aboral, 15 μ; length of teeth, 4 μ.

Taken in the plankton at the surface inside the kelp belt off San Diego in June. The structure of the lorica indicates a eupelagic distribution.

Tintinnopsis reflexa sp. nov.

Pl. XXVI. Fig. 2.

The lorica of this organism is cylindrical, finger-shaped, its length two and one-half times its diameter, with rounded fundus and reflexed oral rim. The sides are straight and at the mouth the wall is reflexed, forming a broadly rounded oral perimeter, and continues aborally parallel to and outside of the cylinder for one-tenth of its length, terminating in a smooth unmodified edge. The wall is thin, translucent and has the primary reticulations described by Biedermann ('93) and Brandt ('96) but

no secondary fenestration. The outer surface of the wall is sparsely strewn with numerous, small, irregular particles of a more highly refractive character than its own structure.

The animal has the form and structure usual in *Tintinnopsis*. There are two ellipsoidal nuclei centrally located and in the posterior end a single vacuole whose diameter at diastole equals half that of the lorica.

A reflexed oral margin is not found in any other species of *Tintinnidae*. The nearest approach to it appears in the flaring rims of such species as *Amphorella steenstrupi*, *A. acuta*, *Petalotricha ampulla*, *Tintinnopsis mortenseni*, *T. bütschlii*, and *T. campanula*. In none of these forms has this flaring rim much greater relative proportions than has the reflexed rim of *Tintinnopsis reflexa*. An exception to this limitation in extent appears to be presented in the problematical organism described by Cleve ('99) as *Fungella arctica* and referred by him to the *Tintinnidae*. The significance of this limitation in proportions lies, it seems, in the dependence of this projecting portion of the shell upon the *length of the cilia and intercalary cirri of the adoral ciliary plates*. In *T. reflexa* the distal edge of the lorica is located approximately at the line where the ends of the cirri of the adoral plates would fall when reflexed.

The general form of the lorica of this species approaches most nearly to that of *T. nitida*, described by Brandt ('96) from Karajak-Fjord in Greenland waters. It differs, however, from this species in the posterior reflexion of its more extended rim, in the minuteness and sparseness of the attached particles and in its smaller size.

Dimensions:—Length, 50 μ; diameter, 20 μ.

Taken in a vertical haul from 70 fathoms to surface off San Diego in July. The structure of the shell is indicative of a eupelagic distribution.

Tintinnopsis dadayi sp. nov.

Pl. XXVI. Figs. 3-5.

Lorica campanulate with expanded fundus, spreading margin and cylindrical central portion. Its length from apex to primary oral rim is 2 to 2.5 times its central diameter, 1.3 to 1.8

times that of the fundus and 1.1 to 1.35 times that of the oral margin. In some individuals the lorica is continued beyond the primary oral rim by a cylindrical extension whose diameter is the same as that of the body behind the oral rim as seen in Pl. XXVI, Figs. 4 and 5. A secondary oral rim may appear on the cylindrical extension. No trace of annulation was found in the lorica.

The wall of the lorica is formed by a single hyaline lamella to whose outer surface numerous highly refractive angular particles adhere.

This species is most nearly related to *T. bütschlii* Daday but differs from it in its smaller size, in the absence of annulations, in the more sharply differentiated and sometimes repeated oral rim and in the swollen fundus.

Dimensions.—Length, 80-108 μ; diameter of fundus, 55-65 μ, of the cylindrical part, 40-48 μ, of the oral rim 60-80 μ.

This species was taken frequently in the summer months in shoal waters near shore and evidently belongs to the coastal plankton.

Cyttarocylis quadridens sp. nov.

Pl. XXVII, Figs. 8-11. Pl. XXVIII, Fig. 18.

The lorica is elongated, vase-shaped, tapering abruptly one-third of the distance from the aboral end to a slender attenuately pointed pedicel which bears in its aboral half an expansion armed with four more or less salient tooth-like projections. The oral opening is about one-fifth of the total length in diameter, is squarely truncate, with a thick, very slightly flaring rim. From the mouth the body of the lorica tapers slightly to the sloping shoulders which contract to the slender sub-cylindrical pedicel whose greatest diameter is about one-sixth that of the mouth. The pedicel tapers gradually to about one-half its initial diameter and then spreads into a quadrangular skirt-like expansion which bears the four posteriorly spreading spines on its angles. The diagonal width is here about equal to the initial diameter of the pedicel. From the recessed posterior face of this expansion arises an attenuate terminal spine. The cavity of the lorica is constricted abruptly in the expanded

region of the pedicel and is continued as a slender tube nearly to the tip of the terminal spine.

The wall of the lorica is relatively thick, especially toward the oral margin where it measures 5 μ. It grows slightly thinner posteriorly especially in the expanded region of the pedicel and the terminal spine, where it measures only 2-3 μ in thickness.

The wall is composed of minute subregular prisms mainly hexagonal with occasional pentagonal or irregular ones, placed so that their ends form the inner and outer surfaces of the lorica. Their sides form the coarse subregular hexagonal meshwork which Brandt ('96) has designated as the secondary reticulum. The slightly rounded ends of the prisms form the whole, or at least a part, of the inner and outer lamellae of the wall. Under high magnification (Pl. XXVIII. Fig. 18) the outer lamella exhibits a very minute faint reticulation which Brandt has called the primary one. The diameter of the meshes of this primary reticulum is less than 1 μ, and that of the secondary about 5 μ. In the pedicel the secondary reticulum becomes indistinct and on the expansion and terminal spine it disappears altogether, apparently as a result of the greater thickness in the walls of the prisms.

Well preserved specimens of the inhabitant have not been observed within the lorica, though moribund individuals have been found there in a few instances.

This species varies considerably in the prominence and angle of divergence of the four salient spines on the pedicel and in the length of the terminal spine. The four spines are usually symmetrical with respect to each other but instances of asymmetry are occasionally seen (Pl. XXVII. Fig. 9). It belongs unquestionably to the form-cycle of *Cyttarocylis treforti*, described by Daday ('87) from Naples, which, however, has two lateral apophyses in place of a quadrangular expansion of the pedicel. Similar lateral apophyses also occur on the spirally striate form described by Cleve ('99*a*) as *C. hebe* var. *apophysata*. *C. treforti* occurs occasionally in the plankton of the Pacific off San Diego, but it does not appear to intergrade with the form here described as *C. quadridens*.

Observations on the method of formation of the lorica in *Cyttarocylis* are not to be found in literature and I have been unable to keep this species alive for prolonged examination in a microaquarium. It seems probable from the form of the lorica that this is built up from the terminal spine anteriorly, and that the quadrangular expansion on the pedicel with its four spines may in some way result from the presence of the four spiral lines of cilia on the body of the animal which pass from the adoral circlet toward the posterior end. They would form the natural lines of transit of substances gathered by the adoral circlet or extruded from the body and utilized in the formation of the lorica. The posterior ends of these lines of cilia may be regions where the shell-forming substances gather in the form of this quadrangular expansion with its more or less prominent spines. Anterior to this region the spiral course of the cilia and the greater freedom of movement on the part of the body of the animal would tend to facilitate the more regular distribution of the material and to bring about a transition from the quadrangular to the circular cross section of the shell.

Dimensions.—Total length, 430-450 μ; diameter of oral end, 90-100 μ; length of terminal spine, 35-50 μ; diagonal diameter at the expanded region of the pedicel, 12-18 μ.

This species is found generally, though rarely in large numbers, in the summer plankton of the Pacific off San Diego. It has been taken in vertical hauls from 185-35 fathoms to the surface very generally, and less frequently in surface catches. It appears to be a eupelagic species.

Cyttarocylis pulchra sp. nov.

Pl. XXVIII. Figs. 19-23.

This differs from the preceding in its proportions, in the possession of one to three rings about the anterior part of the lorica and in its very stout pedicel with a four-sided posterior portion. The lorica is vase-shaped, being cylindrical in its anterior third with a very slightly flaring mouth whose lip diminishes to a sharp edge. This section of the lorica bears one, or two, but more generally three external annulations which

result from a symmetrical increase of the wall to from 2 to 2.5 times its thickness in adjacent regions. The anterior ring is about one-fourth of the diameter of the mouth behind the rim, the second ring three-fourths, and the third a little less than five-fourths. The second and third are thus slightly nearer together than the first and second. The total length of the lorica is seven times its diameter between the rings and five times that on the rings.

The lorica tapers very gradually near its middle to the stout pedicel which with its terminal spine forms the posterior half of the total length. This pedicel is about one-third of the diameter of the anterior part measured between the rings, and changes in the posterior third of its length from a cylinder to a rectangular prism from whose flaring end arises the stout terminal spine. The four angles of the pedicel are carried out (on the skirt-like expansion) in projecting points like those of *C. quadridens* and in addition one similar point is intercalated on each margin of the overhanging ledge midway between the two corners of each face. The width of the faces is about one-fourth the diameter of the mouth of the lorica.

The cylindrical spine projects from the center of the recessed region at the base of the pedicel and ends in an acute tip. Its length is nearly one-half the diameter of the mouth, and its diameter less than one-fifth of its own length.

The cavity of the lorica conforms to the external contour with the exception that there are only very slight annular expansions beneath the rings, and that in the prismatic portion of the pedicel the lumen contracts suddenly to a slender canal which extends as a straight tube nearly to the end of the terminal spine.

The structure of the lorica is essentially similar to that of *C. quadridens*. It is composed of similar elements having a similar arrangement in all parts but the rings. In *C. quadridens* the wall is everywhere composed of a single layer of prisms but in *C. pulchra* the rings, as shown in Pl. XXVIII, Fig. 20, are formed by 2-3 layers of prismatic elements, which pass over into the single layer on either side. In the quadrangular sec-

tion of the pedicel the prisms which are thin-walled elsewhere become very thick-walled so that their central cavities are almost obliterated, giving a pitted appearance to the wall in this region. This wall is, as before stated, much thickened, but I have found only a single layer of prisms in it. It has a yellowish brown color which is in strong contrast with the hyaline character of the rest of the lorica. The presence of rings on the lorica of this species and the occurrence of loricae having only one or two rings raises an interesting question as to the method and significance of their formation. It seems probable that there occurs during the period of lorica formation a temporary suspension in the factors leading to its elongation without concurrent diminution in the supply of the materials from which the hexagonal prisms are formed, resulting in a local aggregation of the prisms in a ring. This process may, it seems, occur two or three times and at an approximately uniform interval. The structure in these particulars is probably correlated with some phase of activity of profound importance in the animal's economy which is subject to rhythmic repetition. Naturally the suggestion arises that division or possibly conjugation may afford the basis on which these features of shell structure rest. Observations on this point are lacking because of the great difficulty of keeping these most delicate pelagic organisms under laboratory conditions.

The animal has not been seen in a normal condition. Moribund individuals have three or more ellipsoidal nuclei.

Dimensions.—Total length, 405 μ; diameter of oral end, 70 μ; length of terminal spine, 35 μ; width of face of pedicel, 20 μ; diameter of rings 82 μ; thickness of wall, 6-8 μ; diameter of prisms, 2-4 μ.

This species has been found generally in the plankton of the Pacific off San Diego at all seasons of the year but more frequently in the summer. It is never very common and is more frequent in vertical catches than in those taken at the surface. It appears to be a eupelagic species.

Cyttarocylis torta sp. nov.

Pl. XXVII, Figs. 12-15. Pl. XXVIII, Figs. 16, 17.

This species has many points in common with the preceding. In proportions and form of the lorica, the relations of cylindrical portion and pedicel, and in the form of the expansion and terminal spine the two species are counterparts. *C. torta* differs from *C. pulchra*, however, in two prominent details of structure which have been constant in all of the numerous individuals of the species which have come under my observation. In the first place the annulation is not formed by 1-3 distinct rings as in *C. pulchra* but by a very broad thickened band whose anterior and posterior margins are somewhat enlarged, a condition which might arise by the thickening of the region between the first and second rings in *C. pulchra*. The anterior thickening is usually less prominent than the posterior and the intermediate belt is not uniformly or symmetrically thickened on all sides, thus presenting a variety of margins as the lorica is rolled about. A second narrowed ring is found in some individuals behind the broad band, and as in the two ridges in front of it, its anterior face is less abrupt than the posterior one, differing in this particular from the evenly rounded rings on *C. pulchra*.

The second structural feature differentiating this species from *C. pulchra* is the marked torsion of the quadrangular portion of the pedicel, which makes a turn of 90°-180° from right over to left (*cf.* Figs. 14 and 15). The torsion appears in the prominent lines which form the angles of this part of the pedicel and also in the several—usually three—fainter lines distributed on each face between the angles. These lines in common with those upon the angles, terminate in projecting points along the margin of the skirt-like expansion. There is some irregularity among different individuals in the number and distribution of these intermediate lines. The direction of the torsion is uniform in all loricae examined.

The finer structure of the lorica is essentially similar to that of *C. pulchra* as shown in the figures. The quadrangular portion of the pedicel is thick-walled occluding the lumen to a

slender tube which has, however, an ovoidal expansion just before it enters the terminal spine (Pl. XXVII, Fig. 12).

This species belongs to the form-cycle of *C. pulchra* to which species it is evidently closely related. The existence of two constantly present differential characters in the individuals of this species under my observation leads me, however, to regard it as distinct from *C. pulchra*. The nearest approach to intergrades appears in one individual of *C. pulchra* (Fig. 23) in which the second ring is slightly widened.

The formation of the twisted end of the pedicel in this species may be due to the rotation of the animal during the early period of shell formation. If so, the rotation must be in one direction constantly, or at least nearly so, during this period of formation. In locomotion the *Tintinnidae*, in common with other free-swimming ciliates, rotate about the long axis. I have not observed *C. pulchra* in activity, but in other species which I have seen in motion reversals in the direction of this rotation are not infrequent. It is difficult to find an explanation of the difference between the broad anterior band and the smaller posterior ring in *C. torta* on the supposition made in the case of the rings in *C. pulchra,* that they are attendant upon the repetition of some phase such as division or conjugation in the life history of the organism.

The structure of the lorica is similar to that of *C. pulchra* with the exception that there are 2-3, and sometimes as many as 5 layers of prismatic elements in the rings and collar and that the thickened region of the pedicel is relatively longer.

The animal has not been seen in normal condition.

Dimensions.—Total length, 450 μ; diameter of mouth, 65 μ, on rings, 90 μ; of pedicel, 18-25 μ; diagonal of pedicel expansion, 30 μ; thickness of wall, 2 to 4 μ; length of terminal spine, 40 μ.

This species has been taken sparingly in both summer and winter plankton of the Pacific at San Diego, but more abundantly in vertical than surface catches. It is apparently eupelagic in its distribution.

Cyttarocylis fasciata sp. nov.

Pl. XXVI. Figs. 6, 7.

Lorica elongated, subconical, its length five times its oral diameter. The posterior third contracts more rapidly than the anterior to a blunt, somewhat irregular, apex. The terminal third is curved slightly to one side so that the apex is asymmetrical. Near the mouth the lorica widens a little to a partially and irregularly everted lip.

The wall of the lorica is formed by a band of substance laid in a spiral of about 17 turns from right over to left (leiotropic) from the apex toward the mouth. The width of this band is not uniform; it varies from 0.2 to 0.6 of the oral diameter, being widest in the fourth and fifth turns from the apex, the region of most rapid diminution in calibre, and narrowing abruptly in the three apical turns, and more gradually toward the mouth. The band is placed somewhat obliquely to the trend of the side so that the posterior margin of each turn is set on the inner face of the anterior margin of the turn behind it (Pl. XXVI, Fig. 7). In the last turn at the oral end the width of the band diminishes gradually so that the mouth is squarely truncate.

The wall is composed of minute prismatic elements of very irregular form, with a varying number (3-6) of sides of irregular and unequal length. As with other species of *Cyttarocylis* here described, the ends of the prismatic elements form the inner and outer faces of the lorica. The irregularity of the pattern which they form in this species stands in strong contrast with the regular hexagonal type seen in species previously described in this paper.

The inhabitant of the lorica has not been observed.

This form belongs to that group of species of *Cyttarocylis* in which the material of the shell is laid down in bands as a result of intermittent activity of secretion or of spiral rotation or torsion of the body. Intermittent deposition yields the annulated type of lorica. When the process of extrusion of the prismatic elements or other lorica-forming substances is intermittent only during the latter part of shell formation, such loricae are produced as that of *C. annulata* of Ostenfeld and Schmidt ('01)

where the rings are limited to the anterior end. When intermittent deposition continues throughout the whole of shell formation, the entire lorica is composed of superposed rings of equal or unequal width as in *C. annulata* of Daday ('87) and *C. fistularis* [*Tintinnus fistularis* of Moebius('87)]. Jörgensen is probably correct in regarding the latter species as identical with *C. helix* (Clap. et Lach.) Jörg. in which the structure of the lorica is imperfectly known, but appears from the figure of Claparède and Lachmann ('58-'59) and the discussion of Jörgensen ('99) to consist of an apical portion, which is formed by a broad band spirally wound, and a superposed oral portion made up of a number of narrower transverse rings.

When the deposition of shell material is continuous and attended by torsion we may have the spiral type of banded lorica in the anterior end as in *C. claparedi* of Daday ('87) and the nearly related if not identical *C. ehrenbergi* var. *subannulata* of Jörgensen ('99), or throughout the whole lorica as in *C. pseudannulata* of Jörgensen ('00) and in the species here described.

The type of shell structure in *C. fasciata* suggests the slow rotation of the animal in a constant direction during the deposition of the shell-forming substance (from which the prismatic elements are formed) and the localization and limitation of the region of its extrusion to a single place upon the animal. It seems desirable that all annulate forms of the *Tintinnidae* should be reinspected carefully for spiral structure.

It is evident that the spiral structure of the shell is of great importance in assisting in the rotation of this structure during active locomotion of the animal and maintaining it during passive movement through the water, as for example during its sinking, and that with the rotation there comes a corresponding increase in the molecular friction and that the flotation of the organism is thus facilitated.

This species is most nearly related to *C. helix* (Clap. et Lach.) Jörg., from which it differs in its much greater size (length 520μ to 150-200μ in *C. helix*), and in the greater width of the anterior bands which are also plainly spiral, while in *C. helix* they are probably transverse and are very narrow. The proportions of the two species are also different. *C. fasciata* is conical,

while *C. helix* is cylindrical with more or less pronounced curvature of the tapering apex.

Dimensions—length, 520μ; diameter of mouth, 100μ; at apex, 20μ; width of spiral band, 20-60μ.

This species was taken but once, in a vertical haul from 35 fathoms to surface, 8 miles off Pt. Loma in June.

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EXPLANATION OF PLATE XXVI.

Fig. 1.—Lateral view of lorica of *Tintinnus serratus*, ×615.

Fig. 2.—Lateral view of lorica of *Tintinnopsis reflexa*, ×600.

Fig. 3.—Lateral view of lorica of *Tintinnopsis dadayi*, ×375. Individuai with primary oral rim only.

Fig. 4.—The same of a second lorica, showing both primary and secondary oral rims, ×190.

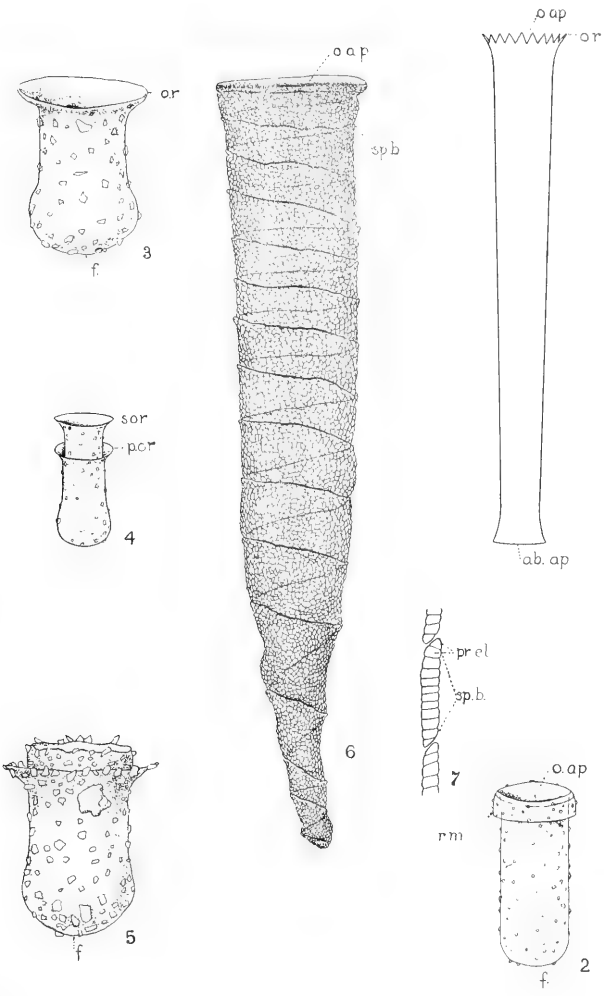
Fig. 5.—The same of a third lorica, in which the secondary oral rim is only partially developed, ×375.

Fig. 6.—Lateral view of lorica of *Cyttarocylis fasciata*, ×490.

Fig. 7.—Longitudinal optical section through wall of lorica of *C. fasciata*, ×1225.

ABBREVIATIONS.

ab. ap.—aboral aperture.
f.—fundus.
o. ap.—oral aperture.
o. r.—oral rim.
p. o. r.—primary oral rim.
pr. el.—prismatic elements.
r. m.—reflexed margin.
s. o. r.—secondary oral rim.
sp. b.—spiral band.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EXPLANATION OF PLATE XXVII.

Fig. 8.—Lateral view of lorica of *Cyttarocylis quadridens*, ×250.

Fig. 9.—Lateral view of posterior ends of lorica of *C. quadridens*, showing asymmetry and degrees in development of the lateral spines, ×250.

Fig. 10.—Lateral view of posterior end of lorica of *C. quadridens*, showing lumen, ×1200.

Fig. 11.—Optical section of wall of lorica of *C. quadridens*, showing prismatic elements, ×1200.

Fig. 12.—Optical section through posterior end of lorica of *Cyttarocylis torta*, showing lumen, ×600.

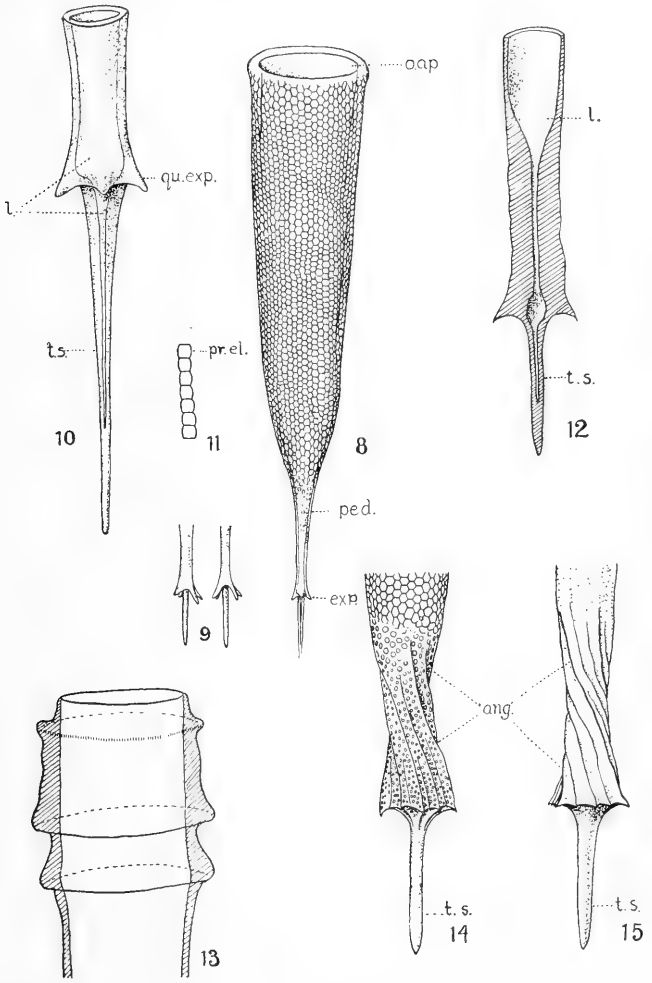
Fig. 13.—Anterior end of lorica of *C. torta*, viewed as a transparency. Lorica with additional posterior ring, ×320.

Fig. 14.—Posterior end of lorica of *C. torta*, showing 90° of torsion, ×600.

Fig. 15.—Another lorica of the same, showing 180°, ×600.

ABBREVIATIONS.

ang.—angles of quadrangular pedicel.
exp.—expansion of pedicel.
l.—lumen of lorica.
o. ap.—oral aperture.
ped.—pedicel.
pr. el.—prismatic elements.
qu. exp.—quadrangular expansion of lorica.
t. s.—terminal spine.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EXPLANATION OF PLATE XXVIII.

Fig. 16.—Lateral view of lorica of *Cyttarocylis torta*, having no additional ring, ×250.

Fig. 17.—Optical section and inner surface of anterior end of lorica of *C. torta*, showing prismatic structure, ×375.

Fig. 18.—Surface of lorica of *C. quadridens*, showing primary and secondary reticulations, ×1100.

Fig. 19.—Lateral view of lorica of *Cyttarocylis pulchra*, having three rings, ×250.

Fig. 20.—Optical section and inner surface of lorica of *C. pulchra*, showing prismatic structure, ×500.

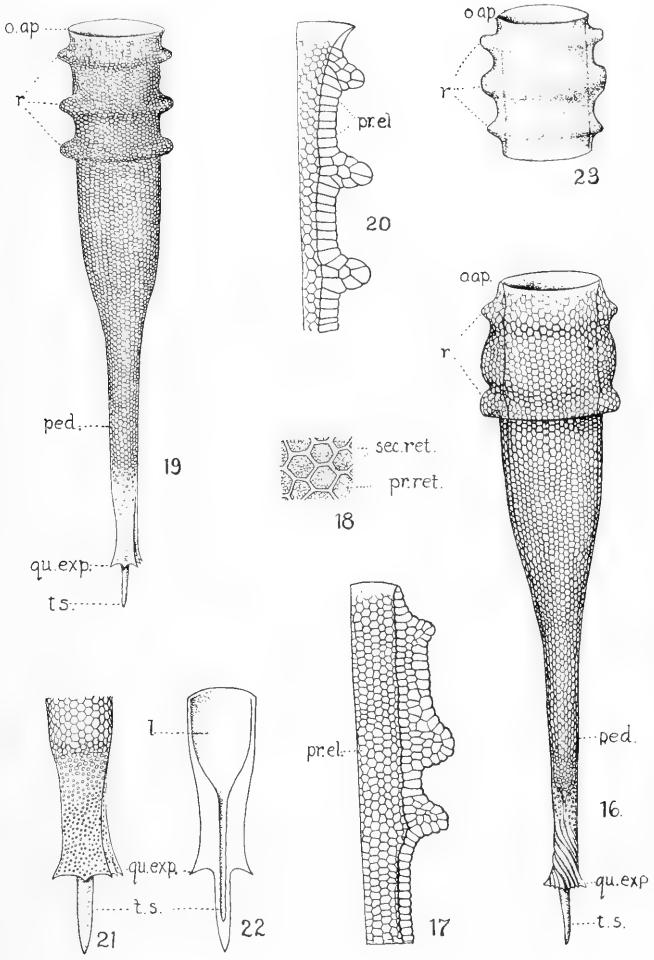
Fig. 21.—Posterior end of lorica of *C. pulchra*, ×500.

Fig. 22.—Optical section of same, showing lumen, ×500.

Fig. 23.—Anterior end of lorica of *C. pulchra*, viewed as a transparency. Lorica with modified central ring, ×250.

ABBREVIATIONS.

o. ap.—oral aperture.
ped.—pedicel.
pr. el.—prismatic elements.
pr. ret.—primary reticulation.
qu. ex.—quadrangular expansion.
r.—rings.
t. s.—terminal spine.
sec. ret.—secondary reticulation.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