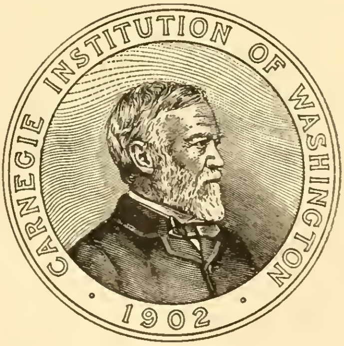
DEPARTMENT OF MARINE BIOLOGY
OF
CARNEGIE INSTITUTION OF WASHINGTON

ALFRED G. MAYER, DIRECTOR

PAPERS FROM THE TORTUGAS LABORATORY
OF THE
CARNEGIE INSTITUTION OF WASHINGTON

VOLUME V



WASHINGTON, D. C.
PUBLISHED BY THE CARNEGIE INSTITUTION OF WASHINGTON
1914

CARNEGIE INSTITUTION OF WASHINGTON

PUBLICATION NO. 182

3680

PRESS OF
THE NEW ERA PRINTING COMPANY
LANCASTER, PA.

CONTENTS.

I.

IN MEMORIAM.

George Harold Drew,

1881-1913.

One plate.

GEORGE HAROLD DREW

GEORGE HAROLD DREW.

(1881–1913.)

George Harold Drew, only son of George Drew, of Devonshire, England, was born on October 23, 1881, and died suddenly on January 29, 1913.

From early boyhood chemistry and microscopy fascinated him, and while yet a child he studied in a disused stable on his father's place, which was made to serve as a rough laboratory.

Until the age of ten he was taught by his mother, and then he was sent to New College, Eastbourne, Sussex. Being deeply interested in the scientific side of medicine, he entered Cambridge University, where he became a scholar of Christ's College, and gained the distinctions of Exhibitioner, Foundation Scholar, and Prizeman, afterwards becoming Schreiner University Scholar, and a student at Exeter Hospital. During his five years at Cambridge he took the entire medical course, but afterwards decided to devote his life to research, inclination leading him to choose the scientific side of his profession rather than to engage in its active practice.

After leaving Cambridge, he served for a year as University Scholar of St. Mary's Hospital, London, and subsequently, after working for a short time at the Port Erin Marine Laboratory, he went to Plymouth and associated himself with the Marine Biological Laboratory, wherein most of his scientific work was accomplished. He was one of those chosen by Captain Scott to serve upon the scientific staff of the British Antarctic Expedition, but he declined the honor, preferring not to break the continuity of his studies at Plymouth.

From 1910 until 1912 he held a Beit Memorial Fellowship for Medical Research in cancer; in the summer of 1912 he was appointed John Lucas Walker research student in the University of Cambridge, and on January 1, 1913, he became a Research Associate of the Department of Marine Biology of the Carnegie Institution of Washington.

His connection with the Carnegie Institution of Washington began in 1911, when he accompanied the expedition to Jamaica, afterwards studying at the Tortugas, and upon a second visit to America in 1912 he spent a month at the temporary laboratory established at Golding Cay, Andros Island, Bahamas.

He was to have been a member of the projected expedition to Torres Straits, Australia, in 1913, and his preparations were being matured at the time of his sudden death.

The saddest losses that the world sustains are often those it heeds the least, and all who knew him realize that this young man, with his keen insight for research, his broad culture, and well-rounded special training, was destined to become one of England's great men of science—a position which his rare personal charm would not only have graced, but would have rendered him powerful for advancing the intellectual welfare of his country.

In 1910 he carried out some interesting observations upon the reproduction and early development of the kelp (*Laminaria*) of the coast of Devonshire, proving that there is an alternation of generations in the life cycle of this seaweed; for the free-swimming sexual cells fuse in pairs and then settle down upon the bottom and develop into a chain of cells, any single cells of which may develop into a *Laminaria* plant.

His published works cover a period of only four years, yet in this brief time he was the author or joint author of fifteen papers.

His earliest paper, in 1909, is upon parasitic and other diseases of fish, in which he describes various forms of tumors and cancers.

This paper was followed by one of an experimental nature written in association with de Morgan as its joint author, and it was shown that, in *Pecten*, injurious bodies implanted in the tissues soon become surrounded by an agglutinated layer of blood-corpuscles and these are replaced by a mass of fibrous tissue which encapsules the foreign body very much as such bodies are incased by mesenchyme in injured vertebrates.

In 1911 Drew announced that, as a result of injury, cysts lined by columnar ciliated epithelium could be formed from the fibroblasts in *Pecten*. He also found that the blood corpuscles of Lamellibranchs are capable of ingesting and destroying bacteria, and that if the animal be wounded so that blood escapes, some of the corpuscles adhere to the cut surfaces and then send out slender processes which fuse with those from other corpuscles, thus forming a net-work the fibers of which finally contract and close the wound.

He also found that the repeated application of a strong solution of iodine to a circumscribed area of the skin of *Fundulus* produces an inflammatory tumor having some relation to certain abnormal growths seen in nature in fishes.

While at Plymouth the subject of the cause and nature of tumors and cancers engaged his major interest, and he did much histological work upon the fate or growth of transplanted tissues. His last work was upon the culture of living tissues from the frog and the dogfish in plasma outside the body of the animal. In this study he achieved decided success, having with his usual ingenuity devised an improved technique which enabled him to grow tissues upon microscope slides free from bacterial contamination. The paper describing these results was completed only a few days before he died and is published in the Journal of Pathology and Bacteriology, Cambridge.

Some of his most interesting work, however, was done while associated with the Department of Marine Biology of the Carnegie Institution of Washington.

In 1910 Sanford, and also Vaughan, published the conclusion that a considerable portion of the calcareous muds in the bays and sounds of southern Florida were precipitated out of the sea-water in some unknown manner. It remained for Drew, in 1911, to discover that there is in the warm surface waters of the West Indian and Florida region, and especially in the limestone mud itself, a bacillus which deprives the sea-water of its nitrogen, thus causing the calcium to combine with the dissolved carbon dioxide and to form the finely-divided limestone mud so characteristic of coral-reef regions. Drew isolated this bacillus and found that it became inactive in even moderately cold water, and thus it functions only in warm or tropical seas, thriving best at depths of less than 100 fathoms. In the surface waters of the Bahamas and Florida it is the most abundant marine bacillus.

Drew hoped to continue these studies and to extend them to the Pacific, for this calcium precipitation is an important factor, and has resulted in the formation of vast beds of limestone apparently far greater in bulk than that formed by corals.

The complex problem of the chemical balance of the constituents of sea-water and their solvent powers under various conditions was being enthusiastically considered by Drew, and had he lived it was the hope of this Laboratory that he might have had exceptional opportunities to continue these studies—for truly he was the exceptionally brilliant man, for the coming of whose like again the world must wait, we fear, for many years, for there are but few in each generation who are gifted with his rare genius for research.

Alfred Goldsborough Mayer.

BIBLIOGRAPHY.

1. Some notes on parasites and other diseases of fish, in Parasitology, vol. 2, No. 3, p. 193, 1909; also vol. 3, No. 1, p. 54, 1910. Also a review of the same in Journal Marine Biol. Association, Plymouth, vol. 9, No. 2, p. 246, 1911.
2. The reproduction and early development of *Laminaria digitata* and *Laminaria saccharina*, in Annals of Botany, vol. 24, p. 177, 1910. Also reviewed in Journal Marine Biol. Association, Plymouth, vol. 9, No. 2, p. 245, 1911.
3. Some points in the physiology of Lamellibranch blood-corpuscles, in Quart. Journal Microscop. Sci., vol. 54, pp. 605–622, 1910.
4. A table showing certain culture characteristics of some of the commonest bacteria found in the laboratory tanks at Plymouth, in Jour. Marine Biol. Association, vol. 9, No. 2, pp. 161–163, 1911.
5. The action of some denitrifying bacteria in tropical and temperate seas, and the bacterial precipitation of calcium carbonate in the sea, in Journal Marine Biol. Association, vol. 9, No. 2, pp. 142–155, 1911. Also in the Report of the Department of Marine Biology, Year Book of the Carnegie Institution of Washington, No. 10, pp. 136–141, 1911.
6. Some cases of new growths in fish, in Journal Marine Biol. Association, Plymouth, vol. 9, No. 3, pp. 281–287, 1 plate, 1912.
7. A note on some attempts to cause the formation of cytolysins and precipitins in certain invertebrates, in Jour. Hygiene, vol. 11, No. 2, 1911.
8. Experimental metaplasia. 1. The formation of columnar ciliated epithelium from fibroblasts in *Pecten*, in Journal of Experimental Zoology, vol. 10, pp. 349–374, 3 plates, 1911.

9. A note on the application of Giemsa's Romanowsky stain to the blood and tissues of marine invertebrates, in Parasitology, vol. 4, pp. 19–21, 1911.
10. An experimental investigation of the cytological changes produced in epithelial cells by long-continued irritation, in Journal of Pathology, vol. 17, 1912.
11. Report upon the formation of calcium carbonate through bacterial action in the tropical Atlantic, Report of the Department of Marine Biology, Year Book of the Carnegie Institution of Washington, No. 11, pp. 136–144, 1913.
12. On the culture in vitro of some tissues of the adult frog, in Journal of Pathology and Bacteriology, vol. 17, pp. 581–583, plates 44–46, 1913.
13. The origin and formation of fibrous tissues as a reaction to injury in *Pecten maximus*, by G. H. Drew and W. de Morgan, in Quart. Journal Microscop. Sci., vol. 55, pp. 595–610, plate 24, 1910. Also a review of the same in Journal of the Marine Biol. Association, vol. 9, No. 2, p. 595, 1911.
14. Note on the abnormal pigmentation of a whiting infested by trematode larvæ, by F. W. Gamble and G. H. Drew, in Journal Marine Biol. Assoc., vol. 9, No. 2, p. 243 1911.
15. On the pricipitation of calcium carbonate in the sea by marine bacteria, and on the action of denitrifying bacteria in tropical and temperate seas, in Papers from the Marine Biological Laboratory at Tortugas, Publication No. 182, Carnegie Institution of Washington, 1913.

II.

ON THE PRECIPITATION OF CALCIUM CARBONATE IN THE SEA BY MARINE BACTERIA, AND ON THE ACTION OF DENITRIFYING BACTERIA IN TROPICAL AND TEMPERATE SEAS.

BY G. HAROLD DREW.

Two maps and four figures.

TABLE OF CONTENTS.

ON THE PRECIPITATION OF CALCIUM CARBONATE IN THE SEA BY MARINE BACTERIA, AND ON THE ACTION OF DENITRIFYING BACTERIA IN TROPICAL AND TEMPERATE SEAS.

By G. Harold Drew.

INTRODUCTION.

The investigations described in this paper were made in the summers of 1911 and 1912 under the auspices of the Carnegie Institution of Washington. The original intention was to study the action of marine denitrifying bacteria in tropical seas. The discovery, during the course of the experiments, that these denitrifying bacteria also possess the power of precipitating calcium carbonate from soluble calcium salts present in sea-water has perhaps, by its geological significance, somewhat overshadowed the interest of the primary object of the work. The main contentions raised in this paper are:

(1) That in the seas of the American tropics bacteria exist which are actively precipitating calcium carbonate from the calcium salts present in solution in sea-water. It is suggested that this bacterial action has been a very considerable factor in the formation of chalk and many other varieties of sedimentary rock, chiefly or in part composed of calcium carbonate. It is also contended that the vast deposits of chalky mud now being formed to the west of the Bahamas and in the neighborhood of some of the Florida Keys are precipitated by bacterial agency and that a similar process plays an important part in the cementation of fragments of coral and other detritus into compact coralline rock.

(2) That the destruction of nitrates by bacterial action in the seas of the American tropics is far in excess of that occurring in temperate waters. Hence an explanation is afforded of the relative scarcity of plant life (and consequently of animal life) in tropical as compared to temperate seas, in accordance with the terms of Brandt's (2 and 3)[1] hypothesis.

Preliminary notes on this work have already been published in the Tortugas Laboratory Reports[2] for 1911 and 1912. The chronological sequence of the investigations will be followed in the account given here of the experimental work.

---

[1] The figures in parentheses refer to the bibliography, p. 45.

[2] Carnegie Institution of Washington, Year Book No. 10, 1911, pp. 136–141; Year Book No. 11, 1912, pp. 136–144.

GENERAL CONSIDERATIONS AND PREVIOUS WORK.

It is generally conceded that the plankton of tropical and subtropical seas is far less in quantity than that found in colder waters.[1] The zooplankton depends ultimately for its food on the phyto-plankton; hence any factor limiting the growth of the phyto-plankton which was capable of exercising its influence in tropical and not in temperate or arctic waters might offer an explanation of this phenomenon. It has been shown by various investigators that this factor is not temperature, light, or salinity, and it has been suggested that the explanation may lie in the relative deficiency, in tropical seas, of the nitrates or nitrogenous compounds so essential for all plant life. A matter of common observation in support of this view is the remarkable scarcity of algal growth in the shallow waters of tropical shores as compared with that in temperate regions, and the fact that in the tropics, wherever sewage or other nitrogenous waste is poured into the sea, a free growth of algæ is found.

There is at present no really reliable and accurate chemical method of estimating the combined nitrogen in sea-water, hence the above theory can not be directly put to the test. On the other hand, the existence of denitrifying bacteria in temperate waters has long been known, and it would seem a fair deduction that should this bacterial destruction of nitrates take place with greater intensity and completeness in tropical than temperate waters, an explanation of the relative scarcity of phyto-plankton in the former would be offered. This suggestion was first made by Brandt (3) in 1901, and is universally known as "Brandt's hypothesis." He enunciated it as follows:

> If the denitrifying bacteria of the sea, like the closely investigated denitrifying bacteria of the land, develop a strongly disturbing activity at higher temperatures, only a relatively small production (of phyto-plankton) would take place in the warm seas in spite of much more favorable conditions, according to the law of the minimum, owing to the great disturbance amongst the indispensable food substance; whilst, in the cold seas, more nitrogen compounds would be at the disposal of the producers owing to the retardation or suppression of the disturbing process. (From the published English translation.)

The presence of denitrifying bacteria has been demonstrated in Kiel Bay by Baur (1), along the Dutch coast by Gran (9), in the open waters of the North Sea and Baltic by Feitel (7) and Brandt (2), and in 1909 I identified several of the species described by Gran in samples of water obtained from the western part of the English Channel. All these denitrifying species have a higher temperature optimum than that of their natural environment and this is obviously a point strongly in favor of Brandt's hypothesis.

The chief difficulty in the way of putting the hypothesis directly to proof lies in the fact that at present no accurate method of determining the nitrate

---

[1] For the most recent work, and full discussion of this subject, see The Depths of the Ocean, by Murray and Hjort, p. 366 et seq., 1912. London.

contents of sea-water exists, and hence it is impossible to correlate quantitative plankton observations with direct analyses of the amount of combined nitrogen present in sea-water in different localities. Much valuable work on this subject has been done by Raben (15), but he states that his error in control experiments averages over 30 per cent. An exhaustive study (as yet unpublished) of all the methods of estimating combined nitrogen in sea-water as given by various investigators has been made by Mr. D. J. Matthews, hydrographer to the Marine Biological Association of the United Kingdom and to the Fishery Branch of the Department of Agriculture, etc., for Ireland, and he has come to the conclusion that the limits of error in all these methods are so large as to make them unsuitable for investigations such as these. Since chemical methods are at present inadequate to give evidence on this hypothetical deficiency of nitrates in warmer seas, it seemed of interest to investigate the distribution and relative activity of denitrifying bacteria in tropical waters in comparison to those found in temperate seas, and it was with this primary object that the present work was undertaken.

The previous researches most closely related to these investigations are those of Gran (9), who isolated a number of species of denitrifying bacteria from the inshore waters of the Dutch coast. He made use of solutions of nitrates, nitrites, or ammonium salts as the sole source of nitrogen in his culture media, which contained only a dilute solution of calcium malate as organic nutrient material for the bacteria. He classifies the bacteria into four groups, according to their reactions in pure cultures towards nitrates or nitrites.

1. Those which reduce nitrates and nitrites to free nitrogen without any ammonia formation.
2. Those which readily reduce nitrates to nitrites. The nitrite disappears slowly without perceptible formation of free nitrogen and some ammonia is formed.
3. Those which can not reduce nitrates to nitrites, but which are capable of slowly removing the nitrite without perceptible formation of free nitrogen. Though the nitrites are not reduced, yet they can serve as the sole source of nitrogen for the growth of the bacteria.
4. Those which can not reduce and are not capable of assimilating either nitrates or nitrites, but will flourish when ammonium salts are present.

In investigations on samples of water taken in the English Channel some 10 miles off Plymouth, I was able to recognize species belonging to the second group of Gran's classification, but could not detect the presence of species belonging to any of the other groups, and it would seem probable that these other groups are chiefly composed of littoral forms.

In fluid culture media inoculated with samples of sea-water and kept at a temperature of 28° C., Gran found that the formation of nitrite was detectible in from 1 to 2 days, and that eventually all the nitrate and nitrite was destroyed in the majority of cases, especially if the cultures were reinoculated at intervals. In my experiments I was able to obtain similar results in cultures kept at 30° C. after 8 days; in cultures kept at 15° C. the first formation of nitrite was detectible in from 5 to 6 days, but denitrification never proceeded beyond this stage.

Baur (1) showed that the optimum temperature for growth and denitrification of the species described by him lay between 20° and 25° C. when the bacteria were grown in fluid culture media containing peptone.

The most important work on the distribution of marine bacteria is that of Fischer (8) in 1886, 1889, and 1893, but he does not enter into the chemical activities of the species found, so that the observations do not throw much direct light on problems of the metabolism of the sea. The variations in the number of bacteria found in different surface samples from positions in mid-ocean are somewhat surprising and difficult to account for. Deeper samples were taken by means of a water-bottle made of brass, but in view of the now well-known bactericidal action of metals, and of copper in particular, I do not consider that any great value can be attached to these observations. With the exception of Fischer's work little seems to have been published on the general distribution of marine bacteria.

A point that has not yet been considered is the origin of the nitrate supply in the sea. Nitrates are absorbed by diatoms and the phyto-plankton in general, and are presumably built up into complex nitrogenous compounds within the plant. If these compounds, on the death of the plant, are broken up and the nitrogen again rendered available for use in the form of nitrates, a series of reactions must be gone through which may well be performed by bacterial agency, and this also applies to the waste nitrogenous products of animal metabolism. In addition, it has been shown that nitrates are actually decomposed by the denitrifying bacteria, which would thus tend to keep the nitrate concentration down to the level necessary for their own existence and would come into competition for this essential with other forms of plant life. If the bacteria are successful in decomposing nitrates to the extent of entirely removing the nitrogen from all chemical combination, as seems probable from the experiments in cultures, it follows that there must be some source of nitrates in order that the concentration in the sea may remain constant. The existence of nitrifying bacteria, which are capable of absorbing and combining with the free nitrogen of the air and eventually giving rise to nitrates, has been shown by Keding (10) and Keunter (11), but these have so far only been found on the bottom close to shore, or apparently living in symbiosis with algæ or plankton organisms. Similarly Thomsen (16) has demonstrated the presence on the bottom of inshore waters of bacteria which are capable of forming nitrites from ammonium salts, and others which can convert nitrites into nitrates. It would seem possible that similar bacteria having a nitrifying action remain to be discovered in the open sea.

The precipitation of calcium carbonate in the sea by bacterial agency is apparently a line of investigation that has not previously been suggested or followed. Both Baur (1) and Gran (9) made use of calcium salts in their culture solutions in order to obviate the great increase in alkalinity that resulted if potassium or sodium salts were used, but they have not called attention to, or apparently realized, the probable significance of this precipitation of calcium carbonate by bacterial agency as an important factor in the formation of various sedimentary calcareous rocks in tropical seas.

The subject of the precipitation of calcium carbonate in sea-water has been dealt with by Murray and Irvine (14) in 1889 and again by Murray (Sir John) and Hjort (13) in 1912, and they ascribe the precipitation to the interaction of ammonium carbonate, derived as an ultimate product of the decomposition of nitrogenous organic matter, with the calcium sulphate present in sea-water, according to the equation

$$(NH_4)_2CO_3 + CaSO_4 = CaCO_3 + (NH_4)_2SO_4$$

Expressed in the terms of the ionic hypothesis, this reaction can be explained by the statement that $CaCO_3$ must be precipitated when the product of the concentration of its ions Ca and CO_3 exceeds a certain limit; an increase in the concentration of CO_3 ions is produced by the advent of $(NH_4)_2CO_3$, which is partially ionized into NH_4 and CO_3, and hence the product of the concentrations of Ca and CO_3 ions is increased and $CaCO_3$ is thrown out of solution.

Though this reaction has been conclusively shown to occur under experimental conditions, where nitrogenous organic matter has been allowed to putrify for some time in sea-water, yet it is obvious that its effect must be purely local and must be confined to the immediate neighborhood of the decaying organic body which gives rise to the formation of $(NH_4)_2CO_3$.

In this paper the precipitation of $CaCO_3$ in an unorganized state alone is dealt with. The formation of the calcareous skeletons, tests, and shells of animals, and the skeletons and platelets of algæ, which play an immensely important part in the constitution of marine bottom-deposits, is beyond the scope of this work.

DESCRIPTION OF APPARATUS.

In 1911 the apparatus at my disposal was of a somewhat primitive nature, as it is difficult to know beforehand exactly what gear will be necessary in a new field of work. In 1912 a more complete outfit was available, and the Carnegie Institution's yacht *Anton Dohrn* was especially fitted for my requirements.

For deep-sea work the motor trawl winch was modified so as to carry fine sounding-wire, and a derrick was rigged aft, projecting over the stern of the boat, over which the wire was led. The motor winch is sunk below the level of the deck, a commendable arrangement, as it can be covered over with hatches when not in use and so affords great economy of deck space, and also has the advantage of bringing the weight of the winch nearer the water-line and avoiding the unstability that may be caused when a heavy winch is fixed on deck.

The sounding-wire was 2.2 mm. in diameter and consisted of four strands of eight wires each, made of high-tensile steel; the breaking strain was given as 400 pounds, but in practice I have no hesitation in saying that it far exceeded this figure. The wire was very difficult to kink, and did not show any tendency to untwist or permanently stretch under a tension of about 350 pounds; it proved in every way satisfactory.

For measuring the length of wire run out, one of the fathom-measuring sheaves made by the Telegraph Construction and Maintenance Company of London was used. This consisted of a sheave containing a steel wheel about 12 inches in diameter, grooved for and made especially to fit the wire; the length of wire run out is measured by the number of turns of the wheel indicated by a dial on the side of the sheave. The dial has two hands showing fathoms and hundreds of fathoms; the hands revolve backwards on winding in the wire, and so again register zero when the sounding is completed. The axle of the wheel revolves on simple bearings, avoiding thus the slight inaccuracy if ball bearings are employed.

Samples of the bottom were obtained with one of the "snapper rods" disengaging an iron 30-pound weight on touching the bottom. This consisted of two brass jaws closed by a strong spring, and kept apart by a trigger; on touching the bottom the trigger was released and the jaws closed on a sample of the bottom; at the same time the 30-pound weight, which was only held in position through the tension of its own weight, was disengaged as soon as the tension was relieved on touching the bottom, and so was left behind as the wire was reeled in.

In order to tell the depth at which bottom was sounded the wire was led through a pulley connected with a spring balance, which accordingly registered the tension of the wire. On touching the bottom the decrease in tension due to the release of the weight was shown on the dial of the balance. This arrangement was not satisfactory in rough weather, as the rolling of the yacht caused such varying tensions on the wire that it was not always possible to tell the exact depth at which the weight was disengaged.

For obtaining samples of water for bacterial analysis a special water-bottle was designed by Mr. D. J. Matthews. This apparatus is described in detail by Mr. Matthews (12) in vol. IX, No. 4, of the Journal of the Marine Biological Association of the United Kingdom, so only a brief account of it will be given here.

The apparatus employed by previous workers for obtaining samples of water from the deep sea for bacteriological examination has either consisted of some sort of water-bottle made of metal, or else of exhausted glass bulbs with a neck drawn out into a capillary tube which could be broken off at the depth from which a sample was desired. The use of exhausted glass bulbs presents considerable difficulties for depths as great as 800 fathoms; the bulbs must be strong and very thoroughly annealed, as otherwise the slight shock caused by breaking the capillary neck is liable under the great pressure to make the bulb fly into small fragments; another great disadvantage is the strong probability that the sudden reduction in pressure, to which the water is exposed as it enters the bulb, would immediately kill any bacteria in the water. The employment of a metal water-bottle seemed undesirable in view of the bactericidal action of metals. In order to settle this point some test experiments were made with various metals to see if a suitable one could be found. 100 c.c. of water from the laboratory tanks at Plymouth, diluted 1 in 100 with sterile sea-water, was exposed for 6 hours to the action of about 2 square inches of the various metals, with the following results:

Metal.	No. of plates.	No. of colonies of bacteria developing from 1 c.c. after plating on peptone agar, counted after 10 days.
Aluminium bronze...	1	0
" " ...	2	0
" " ...	3	0
Pure copper foil.....	1	1
" " "	2	0
" " "	3	0
Brass..............	1	0
"	2	0
"	3	1
Pure nickel.........	1	17
" "	2	12
" "	3	8
Silver (coins).......	1	3
"	2	2
"	3	4
Control experiment..	1	512
" " ..	2	560
" " ..	3	480

It is thus obvious that none of these metals are suitable for the work, and probably the only metal that could be used would be platinum, which would be prohibitive on account of the expense.

In order to overcome these difficulties, a water-bottle on a new principle was designed for me by Mr. Matthews. A purely diagrammatic representation of its method of working is shown in figure 1.

The container of the bottle consisted of a strong glass cylinder *B*, holding about 250 c.c.; this was closed at each end by thick rubber washers *W*, *W*, through the center of which a short piece of thin-walled rubber tubing passed, the tubing being sealed at the end within the cylinder. The washers were carried by the plates P_1 and P_2. The cylinder was carried in a skeleton frame, and by sending down two messengers along the sounding wire *S* it could be first opened and then closed at any required depth. The whole apparatus was first sterilized by steaming in a "Koch," and then the cylinder was completely filled with 95 per cent alcohol; the washers were kept tight on the ends of the cylinder by strong springs (not shown in the diagram) so that no leakage occurred and the various parts of the apparatus were in the position shown in figure 1, *A*. When the apparatus has been lowered to the required depth, the first messenger is sent down, this hitting the lever L_1, releasing the connecting rod C_1 and allowing the plate P_2 and the cylinder B to fall into the position shown in figure 1, B, the cylinder being prevented from falling on to P_2 by the check rod T, which falls through P_1 until caught by the knob at its extremity. The cylinder is thus opened at each end by the first messenger, and the alcohol being of lower specific gravity than sea-water, diffuses out almost instantaneously, causing an upward flow of water through the cylinder. On sending down the second messenger, which hits the lever L_2, the connecting rod C_2 was released, and by means of strong springs the plate P_1 was forced down on to the top of the cylinder, which at the same time fell on to the plate P_2, and thus the cylinder with its sample of water was tightly closed at each end by the rubber washers, the position of the parts being that shown in figure 1, C.

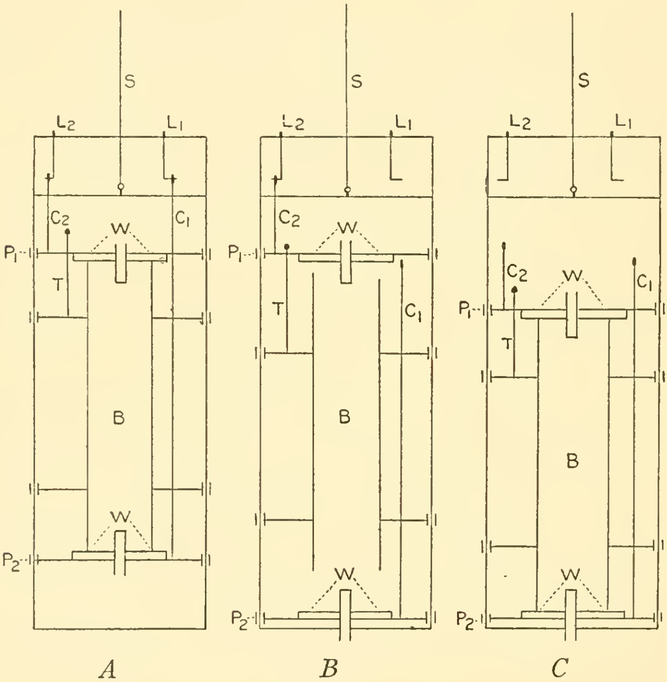


FIG. 1.

The washers with their attached pieces of thin rubber tubing had sufficient capability of bulging inwards to allow for the contraction of the alcohol due to the low temperature at any considerable depth, and to its compressibility being greater than that of sea-water; and similarly the expansion of the sample of water, as the apparatus was hauled up, was compensated for by the elasticity of the thin-walled rubber tubing. It is obvious that even had a slight amount of leakage occurred, a leakage inward during the descent of the apparatus would not vitiate the results, as bacteria would promptly be killed in the 95 per cent alcohol, and similarly on hauling up, the leakage, if any, would be outward, due to the expansion of the sample through the regularly increasing temperature and decreasing pressure, so that the sample would not be contaminated by any of the surface layers through which it was hauled. There was, however, no reason to suppose that any leakage occurred, and it appears that the expansibility of the rubber washers and tubing was sufficient to allow for the small changes in bulk of the fluids within the cylinder after the first sterilization by steaming. The action of the alcohol was relied on for sterilization between successive samples, and both experimentally and in practice this method was found to be absolutely safe, as all the marine bacteria are very readily killed by alcohol, and they do not form resistant spores.

After the collection of a sample it was siphoned off into a sterilized glass bottle by means of a sterilized length of rubber tubing; this method was considered preferable to any arrangement of taps leading from the collecting cylinder, owing to the difficulties of cleaning and sterilization which would be involved. Part of the sample was also siphoned off into bottles which were returned to Plymouth for analysis for salinity; these bottles had previously been thoroughly washed, rinsed with several changes of distilled water, and then dried in an oven; they were corked with rubber stoppers.

It was found in practice that this design of water-bottle worked extremely well and gave very little trouble. It is to be noted that the sample of water collected is only kept in contact with rubber and glass throughout, so that the bactericidal action of metals is avoided.

Surface samples of water were taken in wide-mouthed stoppered bottles, holding about 12 ounces; the samples were always taken from the bow of the boat when moving ahead, in order to avoid any possible contamination from the sides of the boat.

Some samples from depths up to 80 fathoms were collected off the Tortugas in 1911 in retort-shaped glass flasks of about 300 c.c. capacity, with narrow, recurved, and long-drawn-out necks. These were sterilized, exhausted, and sealed; they were then lowered in an apparatus in which the extremity of the neck could be broken off at any desired depth by sending a messenger down the sounding-wire, when the flasks became completely filled with water. After hauling up, a little water was shaken from the neck, and it was then sealed with the blowpipe. This method avoids risk of contamination from more superficial layers of water as the apparatus is drawn up, since the changes in pressure and temperature as it ascends tend to cause a continuous outflow through the narrow neck until the surface is reached.

A somewhat similar apparatus was used for obtaining deep samples from the station 70 miles west of Ushant, but the glass bulbs were smaller and the tube leading from them was bent at right angles to itself. Considerable difficulty was caused by the breaking of the tube owing to the force of the inrushing stream of water impinging on the wall where it was bent at right angles.

If this form of apparatus is used, all sharp angles in the inlet tube should be avoided, and it should be so arranged that the inrushing stream of water spreads itself in a fan-shaped manner over the sides of the bulb, but I do not consider that any form of exhausted glass flask is suitable even for depths as small as 80 fathoms.

In Jamaica no apparatus for obtaining deep samples was available, so the primitive method of lowering a sterilized stoppered bottle with a string tied to the stopper was employed. At the required depth the stopper was pulled out until the bottle was nearly full and then allowed to fall back in place. This method can only be used for very shallow depths, as the pressure of the water at greater depths makes it impossible to withdraw the stopper. A source of error is also introduced in that the inrushing water passes in close proximity to the stopper and its attachment, and may carry in bacteria which have adhered to them when passing through the surface layers.

Temperature records were obtained in the Bahamas by means of deep-sea reversing thermometers specially made by Messrs. Negretti & Zambra of London. They were tested up to a pressure of 3 tons to the square inch at the National Physical Laboratory at Teddington, England, and a table of temperature corrections was furnished for each instrument by the same institution. These reversing thermometers differ from ordinary thermometers in having a constriction and S-shaped dilatation immediately above the main bulb, with a somewhat large secondary bulb at the upper end of the stem. The graduations are reversed, so that the lowest temperature is marked near the top of the capillary portion. On turning the thermometer upside down, the mercury thread breaks at the constriction and fills the small bulb at the end of the capillary and also part of the capillary itself. The thermometer is read in the reversed position, and when certain corrections have been applied the temperature at which the thermometer was reversed is recorded. The effect of the pressure of the water is avoided by having the thermometer sealed in an outer glass case. The lower end of this case is partially filled with mercury, in which the bulb of the thermometer is immersed, thus allowing for rapid conduction of heat between the mercury in the thermometer bulb and the surrounding water. An auxiliary thermometer was sealed up in the same outer case as the reverser, so that the temperature at which the actual reading was taken could also be recorded. In order to calculate the correction that must be applied to the temperature registered by the reverser, three factors must be known:

(*a*) Temperature of thermometer at moment of reading.
(*b*) Kind of glass of which it is made.
(*c*) Volume (expressed in degrees of the stem) of the secondary bulb and the portion of the stem below the 0° graduation.

Of these *a* is given by the auxiliary thermometer, and *b* and *c* were engraved on the back of the stem of each reversing thermometer. All of the thermometers were made of the glass known as Jena^{er} 16 III, and the apparent dilatation of mercury in this glass is $\frac{1}{6300}$. The correction to be applied to the reading of the reverser is given by the formula $\frac{(V^\circ+T)(T-t)}{6{,}300}$, where T = the temperature registered by the reverser, t = the temperature shown by the auxiliary thermometer at the moment of reading, and V = the volume (expressed in degrees of the stem) of the secondary bulb and the portion of the stem below the 0° mark of the reverser.

The thermometers were mounted in pairs in simple metal cases, and were attached just below the water-bottle. They were suspended in a vertical position by a catch forming part of the water-bottle; this was released by the first messenger, when the thermometers fell by their own weight and so reversed, and were hauled up in this position. This simple arrangement proved quite as satisfactory as any of the more complicated reversing frames which are generally in use.

CULTURE MEDIA AND METHODS.

The culture media employed for isolating and counting the bacteria in plate cultures were the following.

I. Peptone agar: Peptone, 2.0 grams; potassium nitrate (KNO_3), 0.5 gram; sea-water, 1,000.0 c.c.; agar agar, 18.0 grams.

In the earlier work less agar was used, but eventually it was found more convenient to use a stiffer jelly, and this did not appear to appreciably hinder the growth of the bacteria.

II. Potassium malate agar: Potassium malate $\left(C_2H_3(OH)\Big\langle\begin{matrix}COOK\\COOK\end{matrix}\right)$, 1.0 gram; sodium phosphate (Na_2HPO_4, $12H_2O$), 0.25 gram; potassium nitrate (KNO_3), 0.5 gram; sea-water, 1,000.0 c.c.; agar agar, 12.0 grams.

The medium was only filtered through glass-wool, so that a very slight floccular precipitate of calcium phosphate was retained.

III. Peptone gelatin: Peptone, 2.0 grams; potassium nitrate (KNO_3), 0.5 gram; sea-water, 1,000.0 c.c.; gelatin, 150.0 grams.

This medium was used only at the Tortugas; it was necessary to keep it cooled with ice to about 20° C., as the temperature of the laboratory sometimes rose as high as 37° C. and gelatin media will not remain solid at these temperatures.

The following fluid media were used:

I. Gran's medium (*modified*): Potassium nitrate (KNO_3), 0.5 gram; sodium phosphate (Na_2HPO_4, $12H_2O$), 0.25 gram; calcium malate $\left(C_2H_3(OH)\Big\langle\begin{matrix}COO\\COO\end{matrix}\Big\rangle Ca\right)$, about 5.0 grams; sea-water, 1,000.0 c.c.

Calcium malate is only slightly soluble in water, so can be added in excess. Gran used distilled water and added 30 gm. sodium chloride per liter, but in these experiments sea-water has been used instead.

II. Calcium succinate medium: Calcium succinate $\left(C_2H_4\Big\langle\begin{matrix}COO\\COO\end{matrix}\Big\rangle Ca\right)$, 2.0 grams; potassium nitrate (KNO_3), 0.5 gram; sodium phosphate (Na_2HPO_4, $12H_2O$), 0.25 gram; sea-water, 1,000.0 c.c.

This medium was boiled and filtered before sterilization to remove the slight precipitate of calcium phosphate. It was found that this medium with the addition of the phosphate gave a more vigorous growth than if it was omitted.

III. Calcium acetate medium: Calcium acetate ($Ca(CH_3COO)_2$), 5.0 grams; sodium phosphate (Na_2HPO_4, $12H_2O$), 0.25 gram; potassium nitrate (KNO_3), 0.5 gram; sea-water, 1,000.0 c.c.

Boiled and filtered before sterilization to remove precipitate of phosphate.

IV. Peptone calcium acetate medium: Calcium acetate ($Ca(CH_3COO)_2$), 5.0 grams; peptone (Witte's), 0.2 gram; potassium nitrate (KNO_3), 0.5 gram; sea-water, 1,000.0 c.c.

Media II, III, and IV were also made up with the addition of 0.2 gm. of magnesium tartrate per 1,000 c.c.

The fluid media were made up in 1,500 c.c. resistance glass flasks, and 1,000 c.c. of medium were used for each culture.

For other purposes a simple solution of peptone in sea-water was employed (2 gm. to 1,000 c.c.), and media were also used consisting of this peptone solution with the addition of 0.5 per cent of various carbohydrates, such as cane sugar, dextrose, lævulose, mannite, lactose, etc., with sufficient neutral red solution to color them, in order to test the acid-forming properties of the bacteria in the presence of carbohydrates.

The ordinary "Koch" steam sterilizer and iron oven for dry-heat sterilization were used, and gasoline cooking stoves were found to be the most satisfactory source of heat. It was found an advantage to use Petri dishes with porous earthenware covers which enabled the water of condensation to evaporate partially; the evaporation could be checked at any time by covering the dishes with a bell jar lined with wet filter paper. It was usually found necessary to keep all cultures on tables with their feet standing in dishes of kerosene, in order to prevent the attacks of ants and other insects. In all other respects ordinary bacteriological routine was followed, and the methods need not be further particularized here.

The reduction of the nitrate to a nitrite in fluid culture media was tested for by the addition of 5 c.c. of 10 per cent sulphuric acid and 2 c.c. of a 1 per cent solution of metaphenylene diamine hydrochloride to 25 c.c. of the culture. The production of a brown coloration (due to the formation of Bismarck brown) is an indication of the presence of a nitrite, and is an extremely delicate reaction.

The diphenylamine and brucine sulphate reactions were also used when testing for the presence of nitrates.

The formation of ammonia was tested for by the addition of 5 c.c. of 10 per cent potassium hydrate and 5 c.c. of Nessler's reagent; the white precipitate formed on the addition of the potassium hydrate does not appreciably interfere with the test, though it renders it somewhat less delicate.

Under expeditionary conditions, and in the absence of the somewhat elaborate apparatus that would be necessary in order to estimate chemically the amount of denitrification in cultures, it was only possible to compare the rate of denitrification in different cultures by noting the time taken for the first appearance of the nitrite reaction and the time taken for all trace of nitrite or nitrate to disappear. It seems that the rate of denitrification in culture media inoculated with equal volumes of samples of sea-water must be a function of the number of bacteria in the sample, the temperature at which the cultures are grown, and the specific power of denitrification of the individual species of bacteria. Considering the rapid multiplication of bacteria when the food supply is plentiful, up to a maximum determined chiefly by the accumulation of the waste products of their own metabolism, it appears that the factor of the number of bacteria in the sample may be neglected within the limits of these experiments. For example, the number of bacteria in 1,000 c.c. of Gran's medium at the end of 24 hours would probably be much the same whether it were inoculated from a sample containing 8 or 16 bacteria per 1 c.c.; similarly it was a matter of experience that the first trace of nitrite formation was observable at about the same time, whether 5 or 10 c.c. of a given sample had been used for inoculation.

Consequently it would appear that for purposes of comparison, and within the limits of the experiments described, if the temperature be the same for the cultures compared, the rate of denitrification is a measure of the specific denitrifying power of the particular species of bacteria.

In the work on the bacterial precipitation of calcium carbonate, the precipitate (which was often so fine as to tend to remain in suspension) was usually obtained by centrifuging. It was either preserved in small bottles with some of the culture fluid, or else washed first with distilled water and then with absolute alcohol, and finally allowed to dry. These precipitates were sent to Dr. F. E. Wright, of the Geophysical Laboratory of the Carnegie Institution of Washington, who with great kindness reported on their mineralogical properties.

INVESTIGATION OF SAMPLES OF SEA-WATER TAKEN OFF PORT ROYAL, JAMAICA.

The work at Port Royal was done in May 1911, but was of a very preliminary nature. It was necessary to depend on a sailing-boat for obtaining the samples; yet, owing to the remarkable regularity with which an on-shore wind springs up every morning, but little difficulty was experienced from this cause. No apparatus for obtaining deep samples was available, but samples were taken from a depth of 6 fathoms by means of a bottle from which the stopper was pulled by a line and then allowed to fall back into place. A measurement of the rate of denitrification in fluid culture media inoculated with samples of sea-water was made, but isolation of the bacteria on solid media was not attempted. The following method was employed:

Samples of sea-water were collected in sterilized stoppered bottles from the surface and from depths of 3 and 6 fathoms from positions about 5 miles from shore, where, from a consideration of the wind and tide, the water was probably under truly oceanic conditions and unaffected by the neighboring land. 10 c.c. of these samples were added to 1,000 c.c. of Gran's medium. The cultures were kept in a moderate light and the temperature varied from 25° to 31.5° C. The average temperature during the growth of each culture was noted.

In a typical culture made from surface water, and for which the average temperature was 29° C., the first indication of the formation of a nitrite, as given by the metaphenylene diamine reaction, appeared after 27 hours; after 38 hours the brown color produced in this reaction was very intense, the culture became cloudy, and on testing with Nessler's reagent slight ammonia formation was apparent. After 48 hours the culture became very cloudy and a scum of bacterial growth developed; the nitrite and ammonia reactions remained unaltered. After 63 hours the nitrite reaction was somewhat less marked, the ammonia reaction was unaltered, and bubbles of gas began to appear. After 72 hours many bubbles of gas were being produced, and the nitrite and ammonia reactions were very slight. After 86 hours the bubbling had ceased, and no nitrite or ammonia was present in the culture. Testing the culture for nitrates by the brucine and diphenylamine reactions then showed that no nitrate was left in the solution.

In the absence of a gas-analysis apparatus the nature of the gas evolved could not be determined, but considering that it was non-inflammable, did not turn lime-water milky, and that the nitrate originally present had been destroyed, it seems strongly probable that this gas was pure nitrogen. Thus in 86 hours 0.5 gm. of potassium nitrate had been decomposed by bacterial growth. If a further 0.5 gm. of potassium nitrate were then added, it was rapidly decomposed, and this could be repeated many times until the other constituents of the culture medium were used up.

It was found that the rate of denitrification varied somewhat with the temperature, and that in cultures kept at a temperature of between 10° and 12° C. no growth or denitrification occurred. The denitrification was always more rapid in cultures from water taken from a depth of 3 or 6 fathoms than from the surface. It was also more rapid with samples taken from the thick muddy water of a mangrove swamp, where organic matter was plentiful.

The bacteria present in the cultures were very minute, actively motile bacilli with rounded ends.

An abstract of the behavior of a few of the cultures is given below.

1. Sample collected 5 miles south of Port Royal, wind southeast, force 4, tide rising. Sample taken from surface. 1,000 c.c. of Gran's medium was inoculated with 10 c.c. of sample.

After 20 hours a slight cloud developed in the culture and faint nitrite reactions were given.

After 36 hours a dense cloud developed in the culture and strong nitrite reactions were given.
After 60 hours a dense cloud and scum developed in the culture and strong nitrite and faint ammonia reactions were given.
After 70 hours a dense cloud, scum, and bubbles developed in the culture and faint nitrite and faint ammonia reactions were given.
After 84 hours culture was less cloudy, with much scum, no nitrite or nitrate reaction, very faint ammonia.
Average temperature at which the culture was grown, 30° C.

2. Sample collected from same spot under similar conditions, from a depth of 3 fathoms. 1,000 c.c. Gran's medium was inoculated with 10 c.c. of sample.
After 20 hours a slight cloud developed in the culture and faint nitrite reaction was given.
After 27 hours a denser cloud developed in the culture and strong nitrite and faint ammonia reactions were given.
After 38 hours a dense cloud and scum developed in the culture and strong nitrite and faint ammonia reactions were given.
After 48 hours a dense cloud and scum developed in the culture and moderate nitrite and faint ammonia reactions were given.
After 63 hours a moderate cloud, thick scum, and bubbles developed in the culture and faint nitrite and faint ammonia reactions were given.
After 72 hours a slight cloud and thick scum, no nitrite or nitrate, and very faint ammonia reaction.
Average temperature at which the culture was grown, 29° C.

3. Sample collected from a spot 6 miles south of Port Royal, wind ESE., force 4, high tide (slack). Taken from surface. 1,000 c.c. Gran's medium was inoculated with 10 c.c. of the sample.
After 20 hours a slight cloud developed in the culture, no nitrite reaction was given.
After 27 hours a slight cloud developed in the culture, faint nitrite reaction was given.
After 38 hours a dense cloud developed in the culture, strong nitrite and faint ammonia reactions were given.
After 48 hours a dense cloud and scum developed in the culture, strong nitrite and faint ammonia reactions were given.
After 63 hours a dense cloud and scum developed in the culture, moderate nitrite and faint ammonia reactions were given.
After 72 hours a moderate cloud, scum, and bubbles developed in the culture, very slight nitrite and faint ammonia reactions were given.
After 86 hours a moderate cloud and scum, no nitrite or nitrate and very faint ammonia reaction.
Average temperature at which the culture was grown, 29° C.

4. Sample taken from surface water of the large mangrove swamp lying northwest of Port Henderson. 1,000 c.c. of Gran's medium inoculated with 10 c.c. of sample.
After 20 hours no cloud or nitrite reaction.
After 24 hours slight cloud and slight nitrite reaction.
After 40 hours strong cloud and scum, strong nitrite and slight ammonia reaction.
After 75 hours cloud, scum, and bubbles, no nitrite or nitrate and slight ammonia reaction.
Average temperature at which the culture was kept, 30° C.

5. Subculture from culture (1). 1,000 c.c. Gran's medium inoculated with 5 c.c. of culture (1), and kept at a temperature of 10° C. to 12° C. by means of ice.
After 100 hours the culture was quite clear and gave no nitrite reaction. It was then removed from the ice and kept at the room temperature, which averaged 30° C.
After 107 hours a dense cloud developed in the culture and strong nitrite and faint ammonia reactions were given.
After 120 hours a dense cloud, scum, and bubbles developed in the culture and moderate nitrite and faint ammonia reactions were given.

After 131 hours a faint cloud, scum, and bubbles developed in the culture; very faint nitrite and faint ammonia reactions were given.

After 146 hours a faint cloud and scum, no nitrite or nitrate, and very slight ammonia reactions were given.

Twenty cultures were made from samples of water taken well out to sea from Port Royal, and the process of denitrification followed through with each. All gave very similar and consistent results, but the rate of denitrification decreased rapidly with the temperature at which the cultures were grown; thus at an average temperature of 27° C. the first trace of the nitrite reaction appeared after about 40 hours, and denitrification was complete after about 100 hours.

The results of precisely similar experiments that I made with samples of water taken from the English Channel near Plymouth in the autumn of 1909 showed that there the process of denitrification was very much slower, and was never complete at the room temperature (17° C.). The first trace of the formation of a nitrite in cultures in the modified Gran's medium, as detected by the metaphenylene diamine reaction, occurred about the fifth day, and a large proportion of the nitrite and nitrate always remained, even in the oldest cultures. In similar cultures incubated at 30° C., denitrification was complete by the eighth day at earliest, but uniformly consistent results were not obtained, as in some of the cultures complete denitrification was never obtained, even after several months.

It would thus appear that even under similar temperature conditions the marine bacteria in the seas off Jamaica are much more active in causing denitrification than those found in the English Channel, and since the rate of denitrification is a function of the temperature, it follows all the more that the destruction of nitrates by bacterial agency in the seas around Jamaica must be far in excess of that occurring in the cooler waters of the English Channel.

THE INVESTIGATION OF SAMPLES OF SEA-WATER TAKEN AROUND THE DRY TORTUGAS.

The Dry Tortugas consist of a group of eight small keys, the largest of which (Loggerhead Key) is only about three-quarters of a mile long by one-eighth of a mile wide. They are situated about 150 miles from the mainland of Florida, and form the extreme western end of the chain of the Florida Keys. The 100-fathom line lies some 30 miles to the south and southwest of the islands, and then trends round in a northwest direction; beyond the 100-fathom line the depth increases with moderate rapidity until depths of from 1,000 to 1,400 fathoms are reached. To the east, northeast, and north as far as the coast of Florida, the water is shallow, the soundings showing from 20 to 30 fathoms in most places. Beyond the 100-fathom line to the southward the influence of the Gulf Stream begins to make itself felt, though the region of maximum current velocity here lies nearer the coast of Cuba. The Tortugas Keys are of purely coral formation, consisting entirely of broken shell and coral sand, with no soil. The greatest elevations are the hurricane ridges, which are not more than 15 feet above sea-level, and during a hurricane the islands are sometimes completely submerged. There is no vegetation on the smaller keys, but Loggerhead Key, on which the Marine Biological Laboratory of the Carnegie Institution of Washington is situated, is partially covered with a growth of bushes and coarse grass. There is no fresh-water supply on the islands.

From these considerations it is obvious that the risk of contamination of samples of sea-water taken a few miles from the Keys through land bacteria is very small, and that such samples may be taken as being truly oceanic.

The motor yacht *Anton Dohrn* and smaller motor boats made the collection of samples an easy matter, and the well-equipped laboratory made possible fuller investigations than those attempted in Jamaica.

A number of cultures were made in Gran's medium under conditions exactly comparable to those made at Port Royal, and the rate at which the process of denitrification proceeded was observed. The results agreed almost exactly with those obtained at Port Royal, so need not be described in detail. It thus seems that the denitrifying power of the bacteria in the seas around the Tortugas is the same as that of those around Jamaica.

Cultures were also made on various solid media, and pure cultures of the various species of bacteria were isolated by plating in Petri dishes with peptone agar. Samples of surface water taken from various positions around Tortugas as far as possible removed from influence of the land, and collected on sunny days, gave an average count of 14 colonies per 1 c.c. of sample. Counts of several plates from the same locality, and from different localities, showed a somewhat remarkable agreement as to the number of colonies present, the highest count ever obtained being 20 and the lowest 8 per 1 c.c. Allowing for experimental error, this shows great uniformity in the distribution of bacteria in the sea around Tortugas.

The colonies appeared to be of two kinds when grown on peptone agar, one much more plentiful than the other. Subcultures made from these colonies in Gran's medium showed that the bacteria forming the most common type of colony produced an active denitrification, while the others grew very slowly in this medium and produced no denitrification.

The characteristics of the denitrifying form are as follows:

On the potassium malate, or peptone agar media, colonies are visible as minute white specks after 6 to 8 hours when the room temperature averages 29.5° C. After about 18 hours the colonies are well developed; they are white in color, circular but with finely irregular outline, and have a granular appearance. Superficial colonies are much elevated at first, but as growth proceeds they spread rapidly over the surface of the agar. Deep colonies remain small, circular, and discrete.

Growth is somewhat more rapid on peptone agar than on the potassium malate agar, and the older colonies develop a brownish tinge in the center when growing on the former medium. On gelatin peptone (5 per cent peptone in sea-water and kept at between 20° and 25° C. to insure the medium remaining solid), growth was very slow; in stab cultures growth proceeded slowly from the surface downwards, leaving a funnel-shaped depression of liquefied gelatin.

Acid formation occurs in dextrose, lævulose, mannite, and cane sugar, but not in lactose media.

Growth is inhibited at a temperature of 10° C., but takes place slowly at 15° C.

Growth is much retarded by exposure to bright sunlight, but the bacteria are not killed by a 10 hours' exposure.

The bacteria are facultative anaërobes, but growth under anaërobic conditions is very slow.

In Gran's medium growth is rapid, but no growth occurs if the potassium nitrate be omitted, or if the calcium malate be replaced by calcium carbonate. Growth in a pure solution of peptone in sea-water is very slight, but becomes abundant if potassium nitrate be added, when denitrification quickly ensues. The most rapid growth was produced in sea-water containing 2 per cent peptone, 1 per cent potassium malate, and 0.5 per cent potassium nitrate, and in this clear medium a slight floccular precipitate, presumably of calcium salts derived from the sea-water, was soon formed. Growth was also rapid at first in a solution of 5 per cent potassium malate and 0.5 per cent potassium nitrate in sea-water, but growth apparently ceased in this medium after a few days and denitrification was never complete; a slight precipitation occurred and the solution was found to have very definitely increased in alkalinity.

This bacterium does not appear to have been previously described, and I propose for it the name of *Bacterium calcis*, owing to its power of precipitating calcium carbonate from solutions of calcium salts. This point will be dealt with later in the paper.

The characteristics of the scarcer non-denitrifying form of bacterium found on the agar plates are as follows:

Growth on the potassium malate agar medium is very slow and indefinite. On peptone agar growth is somewhat slower than in the case of the denitrifying form. On the surface, circular cream-colored colonies are formed, having a brownish center; the edges are smooth and regular, and the colony remains discrete and does not tend to spread over the surface. The deep colonies are smaller and usually ovoid in shape, and of a somewhat darker color than those on the surface.

No growth was obtained on gelatin media.

Acid formation as shown by the neutral red reaction occurs in dextrose and lævulose, but not in cane sugar, lactose, or mannite media.

Growth takes place slowly at 10° C. No visible growth occurred at 0° C., but cultures were not killed by 24 hours' exposure to this temperature.

Growth is retarded by light, and cultures are killed by 4 hours' exposure to bright sunlight.

The bacterium is a strict aërobe.

Free growth takes place in Gran's medium, but develops much slower than in the case of the denitrifying form. No growth occurs if the potassium nitrate be omitted entirely, but takes place freely if a mere trace in excess of that normally present in the sea-water be added, though no denitrification results. Attempts were made to discover whether this bacterium had any nitrifying or denitrifying action in various culture media, but uniformly negative results were obtained. Nitrites were neither oxidized to nitrates nor reduced to ammonia or free nitrogen, and ammonia salts were unaffected. No growth was obtained in any culture medium that did not contain at least a trace of nitrates, so it was not practicable to ascertain whether the bacterium had a nitrifying action without the necessary facilities for quantitative work.

On one occasion samples were obtained from various depths up to 90 fathoms at a point near the Gulf Stream region, 25 miles south of Tortugas. Exhausted glass flasks with capillary necks which could be broken off at the required depth were used for the purpose.

These samples were plated in the peptone agar medium and counted, with the following average results:

Depth in fathoms.	Denitrifying orms (*Bacterium calcis*).	Non-denitrifying forms.	No. of colonies developing from 1 c.c. of sample.
0	9	2	11
10	25	4	29
40	2	2	4
60	5	3	8
90	5	6	11

These figures are probably not very reliable, especially for the greater depths, since it is possible that many of the bacteria were killed by the sudden reduction of pressure to which they were exposed as the water entered the exhausted bulb.

INVESTIGATION OF SAMPLES FROM A POINT 70 MILES WEST OF USHANT ISLAND, FRANCE.

This spot was chosen as it is sufficiently far out in the Atlantic to be largely removed from the influence of the English Channel water. The object was to investigate truly oceanic bacteria, and previous work in 1909 had shown that the bacterial flora of the Channel water was relatively very complicated, probably owing to the presence of littoral forms. The Marine Biological Association of the United Kingdom very kindly sent their steamship *Oithona* from Plymouth for this work, and gave me every facility both on board and in their laboratory. As in Tortugas, the deep samples were collected in exhausted glass flasks, and accordingly, as previously explained, the results obtained from the deep samples can not be considered to possess any very great degree of accuracy.

Attempts were made to plate the sample in peptone agar on board the boat, but the result was not satisfactory, as owing to the motion of the boat the jelly set in irregular waves and lumps. Consequently the samples were kept on ice, and cultures were made from them at Plymouth 24 hours after collection. It is clear that in future attempts to make plate cultures on board a small boat in rough weather, a very delicately swung table will be necessary, or else the roll-tube culture method must be employed.

Three plates on peptone agar were made from each sample, 1 c.c. of the sample being used for each plate. The plates were kept at the room temperature, averaging about 20° C., and the colonies were well developed after 48 hours; they appeared to be all of one kind. A count gave the following results:

Depth in fathoms.	No. of colonies developing from 1 c.c. of sample.
0	7
10	9
20	6
30	5
50	6
70	30
80	20

The increase in the number of colonies at 70 and 80 fathoms is somewhat remarkable, but no conclusions in this respect can be drawn from one series of observations.

The cultural characteristics of this bacterium are as follows:

On peptone agar, after about 36 hours at 20° C., the colonies are white in color, circular, with a finely serrated outline and a coarsely granular appearance. Superficial colonies grow very rapidly, and may spread as a whitish semi-transparent growth of irregular shape over the surface of the agar. The deep colonies remain small, globular, and discrete. In old agar cultures a brownish tinge is developed, and the color may diffuse through the substance of the agar. On gelatin peptone growth was rapid; in stab cultures growth proceeded from the surface downwards, leaving a funnel-shaped depression of liquefied gelatin, and eventually all the gelatin became liquefied.

Acid formation, as shown by the neutral-red reaction, took place in dextrose, mannite, and lævulose, but not in cane sugar or lactose media.

One thousand c.c. of Gran's medium, inoculated on board with 10 c.c. of a surface sample immediately after collection, and kept at an average temperature of about 20° C., showed the first trace of nitrite formation after 70 hours. After 84 hours a very strong nitrite reaction was obtained, and a slight ammonia reaction was given with Nessler's reagent. The process of denitrification, even after the lapse of weeks, did not extend beyond this, and no bubbles of gas were formed. Other experiments made with subcultures from agar and gelatin media gave similar results, so that it appears that this bacterium can not entirely break down nitrates at a temperature of 20° C. The optimum temperature for denitrification produced by this bacterium appears to be about 20° C., as the process was less rapid at average temperatures of 17° C. and 25° C. At a temperature of 32° C., rapid growth took place, but no denitrification resulted.

It should be noted that these temperature observations were only made with subcultures from colonies on peptone agar and peptone gelatin media, and there is reason to believe that the power of denitrification becomes diminished after cultivation on such media. Further and more accurate temperature experiments are required in which the culture medium is directly inoculated with freshly collected samples of water.

This bacterium appears to be closely related to the *Bacterium calcis*, its chief points of difference being:

1. Lesser denitrifying power and lower temperature optimum for denitrification.
2. More rapid growth on gelatin media.
3. Absence of acid formation in media containing cane sugar.

INVESTIGATION OF SAMPLES FROM MARQUESAS KEYS, AND EXPERIMENTAL PRECIPITATION OF CALCIUM CARBONATE BY BACTERIAL AGENCY.

The Marquesas Keys constitute a coral atoll which forms part of the long chain of keys separating the Gulf of Mexico from the Straits of Florida. Within the atoll the water is very shallow and the bottom consists of a fine chalky mud many feet deep. Samples of the water from the lagoon of the atoll were sent to me at Plymouth by post, and examined 14 days after collection.

On plating on peptone agar, an average of 800 colonies per 1 c.c. of the sample were obtained. These colonies appeared to be all of one species, and were identical in appearance and in all cultural characteristics with the *Bacterium calcis* previously described as occurring around the Tortugas.

A suspension of these bacteria from a culture on peptone agar was made in sterile sea-water, and a similar suspension containing roughly the same number of bacteria was made from a third subculture on peptone agar of the bacteria obtained from the station 70 miles west of Ushant. 1 c.c. of each of these suspensions was then added to 1,000 c.c. of the modified Gran's medium. Some of these cultures were kept at an average temperature of 20° C. and others at 32° C., with the following results:

At 20° C. cultures from Marquesas showed trace of nitrite after 45 hours.
At 20° C. cultures from Marquesas gave strong nitrite reaction after 53 hours.
At 20° C. cultures from 70 miles west of Ushant showed trace of nitrite after 140 hours.
At 20° C. cultures from 70 miles west of Ushant showed strong nitrite reaction after 162 hours.

In both cases a slight amount of ammonia was recognizable by Nessler's reagent when the nitrite reaction was strong, but decomposition of the nitrite did not proceed further even after 14 days.

At 32° C. cultures from the Marquesas showed trace of nitrite after 18 hours.
At 32° C. cultures from the Marquesas gave strong nitrite reaction after 22 hours.
At 32° C. cultures from 70 miles west of Ushant never gave nitrite or ammonia reaction.

The cultures from the Marquesas showed a slight amount of ammonia formation, but the decomposition of the nitrite did not proceed further.

From these experiments it appears that the bacteria from subcultures from the Marquesas have a much greater denitrifying power than those from subcultures from a point 70 miles west of Ushant, and that as the bacteria from the Marquesas appear to be of the same species as those investigated at the Dry Tortugas, their power of causing complete denitrification in Gran's medium has been lost by successive cultivations on peptone agar.

The presence of the thick layers of fine chalky mud within the Marquesas Keys, and elsewhere in many places near the Florida coast, led to a consideration of the possibility of its precipitation by bacterial agency.

Since these bacteria grow freely in Gran's medium, the calcium salt of a simple organic acid is a sufficient source of organic food for them, and it seems probable that they would thrive in sea-water containing the products of decomposing vegetable matter, provided that the nitrate supply and conditions of light and temperature were suitable. Such conditions should be especially well fulfilled by the drainage into the sea of a well-wooded country with a calcareous subsoil, and the soluble organic calcium salts would be precipitated as calcium carbonate by the action of the bacteria. In addition, the elimination of the acid radicle from the nitrate in the process of denitrification, by whatever stages it may occur, must leave the alkaline base free to destroy the normal equilibrium of the salts in sea-water, and by increasing the alkalinity would also result in the precipitation of calcium carbonate.

To test this theory cultures were made in a medium having the following composition:

Calcium succinate	2.5 grams
Potassium nitrate	0.5 gram
Sea-water	1,000.0 c.c.

Calcium succinate is soluble in these proportions and the medium is quite clear. Free growth was manifested by the cloudiness of the medium 48 hours after inoculation, and nitrite formation was apparent.

After 96 hours the medium appeared quite milky and this milkiness was due to the presence of exceedingly fine particles of a substance which was soluble in dilute hydrochloric acid with evolution of gas, and was presumably calcium carbonate. In some cultures these particles settled as a definite sediment, but in others the particles were so minute that they showed little tendency to settle and could only be separated with difficulty by centrifugalization. The conditions determining the size of the particles formed could not be ascertained, as the size varied in cultures which were apparently made and grown under identical conditions.

The addition to cultures in which the particles of calcium carbonate were so small as to remain in suspension of any foreign substance, such as finely powdered calcium sulphate or of larger particles of sand, resulted in the aggregation around them of the particles of calcium carbonate, forming a concretion around a central nucleus. These concretions were hard and of

CHART A

. . . . = 100 Fathom Line.

Chart Showing General Geographical Relations of the Western Bahama Island.

almost crystalline appearance under the microscope, and were soluble in dilute hydrochloric acid, with evolution of bubbles of a gas which, when the operation was performed on a microscopic slide, could be completely absorbed by running in a solution of sodium hydrate under the cover slip. Once this process of concretion has been initiated, it appears to progress independently of the presence of particles which act as nuclei, and a large concretion may often be found having a number of smaller concretions around it, or continued into a chain of small spheres, the whole presenting somewhat the arrangement shown by freely budding yeast cells. The deposition of this form of calcium carbonate also takes place on the sides of the flask, and more especially over any area where the glass is scratched or roughened.

From these results it would seem strongly probable that the layers of fine and unorganized chalky mud found in the Marquesas Keys are being precipitated by the action of the *Bacterium calcis*, and it would seem a reasonable suggestion that similar bacterial action may have played an important part in the formation of chalk and other limestone formations in geologic times. The formation of semi-crystalline concretions around a central nucleus at first seemed to suggest an explanation of the formation of oolite grains, but a mineralogical examination, very kindly made by Dr. Fred. E. Wright, showed that the concretions did not possess that laminated structure characteristic of oolite grains and that their crystalline structure was nearer that of calcite than aragonite.

SOME CONSIDERATIONS ON THE PHYSIOGRAPHY OF THE TONGUE OF THE OCEAN AND ANDROS ISLAND.

The position of the Tongue of the Ocean is shown in Chart A, which includes the greater part of the Bahama group and shows its position relative to Florida and Cuba. The Tongue consists of a long and narrow stretch of deep water, running in a NNW.–SSE. direction, and except at its northern end it is completely surrounded by shallows or land. On the west, for about three-fourths of its length, it is bounded by the coast of Andros Island; southwest of Andros it is separated from Santaren Channel by some 60 miles of shallow water lying over the Great Bahama Bank; to the south it is separated from the Old Bahama Channel by over 50 miles of shallows, averaging not more than 3 fathoms in depth; to the east it is separated from the deep water of Exuma Sound by from 20 to 40 miles of shallow water of from 2 to 3 fathoms in depth, and by the chain of islands and cays extending in a NNW. direction from Great Exuma Island. The mouth of the Tongue of the Ocean lies between New Providence Island on the east and the northern extremity of Andros Island on the west; it is here some 25 miles wide and it maintains this width for the greater part of its length as it stretches south. Between the southern extremity of Andros and Green Cay (see Chart A) it narrows to under 20 miles, but south of this point it expands eastward into an almost circular terminal basin of about 35 miles diameter. The total length is about 120 miles.

To the north, the Tongue of the Ocean is connected by a stretch of deep water, extending in a northeast direction, with the Providence NE. Channel and the Providence NW. Channel, leading respectively into the Atlantic and the Straits of Florida, and thus it is brought into direct connection with the two main divisions of the Gulf Stream.

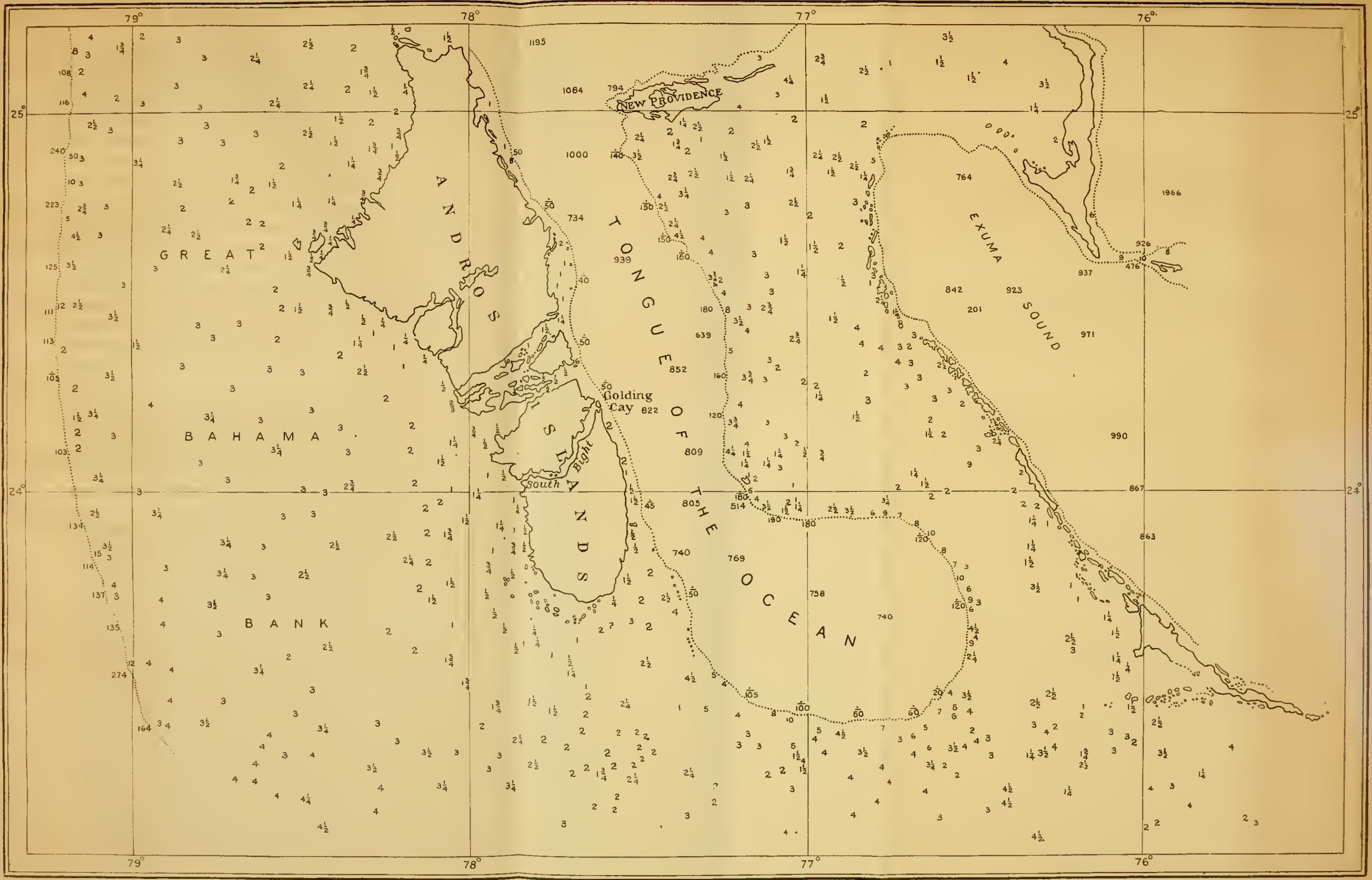
The soundings in this area are shown in Chart B. So far as observations go there seems to be a slight but regular upward gradient from a depth of 1,084 fathoms at the mouth to 740 fathoms in the southern terminal basin. Along the margins the gradient is extremely steep, and along the coast of Andros our observations showed that it was almost perpendicular at a distance of from one-fourth to one-half mile from the shore, but unfortunately no complete observations have been made from which this gradient could be calculated. When attempting to make soundings in this area, the sinker (a 30-pound conical iron weight) in every case was caught upon what was probably some projection on a submarine cliff, and it was impossible to free it; after several such attempts and loss of sinkers, the soundings were abandoned. The entrance to the Tongue by the Providence NE. Channel is of steadily increasing depth up to 2,200 fathoms at its junction with the still deeper water of the Atlantic; the Providence NW. Channel becomes shallower at its junction with the Straits of Florida, and between Great Isaac and the western end of Bahama Island is only between 200 and 300 fathoms in depth.

The surface water of the Tongue of the Ocean, except along the coast of Andros, is everywhere continuous with that overlying the thousands of square miles of shallows forming the Great Bahama Bank and the flats and cays lying to the north and west of the Exuma Islands, whereas the deeper water is only connected with the outer ocean by the comparatively narrow entrance between New Providence and the north of Andros, leading after a turn of about 90° into the Providence NE. and NW. Channels.

The laboratory from which this work was done was established at Golding Cay, at the eastern mouth of the South Bight of Andros; this position was especially suitable for the work, as by running out a few miles in a direction at right angles to the coast line the middle of the Tongue of the Ocean could soon be reached, and also the mud flats to the west of the island were readily accessible by water, as the South Bight runs right through the island to the west coast. In this region the tides are not strong, the average rise and fall being from 2 to 3 feet.

Much difficulty was experienced in getting any definite information as to the set of currents in the Tongue. Our local pilot stated that a current would set in a southerly direction for weeks at a time, and then without any apparent reason or change of wind would reverse and set in a northerly direction for several weeks; but such information derived from the negro natives can not be relied on. When taking observations on May 8, May 11, and May 23, we experienced a distinct southerly drift on each occasion,

CHART 8



. . . . = 100 Fathom Line.

Chart of Tongue of the Ocean and Adjacent Banks.

but the amount of this drift was not determined, and moreover the drift caused by the wind was an unknown factor. On May 8 the wind was SSE., of force 1 at 8^h30^m a.m. freshening to force 3 at 10^h30^m a.m. A rough estimate from the landfall on returning gave the drift of the boat as about 2 miles south during the 4 hours occupied in working the station; the boat had a large awning and exposed a considerable area to the wind and had drifted this distance against the wind, so it would seem that on that occasion there must have been a strong current setting south.

Andros Island consists of a limestone formation, the exact nature of which has been dealt with by Dr. T. Wayland Vaughan (17). The greater part of the island is very flat and is elevated only a few feet above sea-level; a few irregular undulations, probably not more than 100 feet high, are found, especially along the east coast. There is evidence to show that formerly the level of the land was much higher than at present, and signs of rapid erosion of the rock are everywhere obvious. One of the most remarkable features is the absence of soil, even in the well-wooded parts of the island, the trees and bushes growing directly out of crevices and holes in the rock and giving rise to practically no leaf-mold. In the numerous "pot-holes" which occur all over the island, a small deposit of black leaf-mold can be found, and these "pot-holes" are the favorite places for the cultivation of sugar cane and bananas. The erosive action of water on the rock is especially noticeable where the slow drainage from an inland swamp can be traced in its course to the sea; in such a locality the hard rock is eroded, honeycombed, and undermined to a most remarkable degree, even though the amount of drainage, except after the heaviest rains, can scarcely be more than a slow trickle. Erosion of the rock along the sea-coast, where it is exposed to the action of the sea-spray, is also very marked. From the occurrence of this erosion it is obvious that all the water draining from the land into the sea must contain a high proportion of calcium salts in solution.

Towards the west of the island the land is remarkably flat, and near the coast consists of white chalky mud which has partially dried and in places has formed a harder crust on the surface. These half-dried mud flats slope almost imperceptibly into the sea and are continuous with the submarine flats which extend some 60 miles off the west coast with an average depth of 2 to 3 fathoms. The mud forming these submerged flats is very soft, and near the coast it was easily possible to push a 12-foot sponge-pole down to its full length into it without touching any harder material. The surface layer of the mud for a depth of about 6 inches is of a creamy white color, but below that it is of a grayish tinge and has a slight odor of sulphureted hydrogen. Unfortunately there was no opportunity of obtaining information as to the real thickness of this layer of mud, nor of investigating more than the surface layers at any distance from the coast.

Microscopical examination showed that this mud was almost entirely composed of minute unorganized particles of calcium carbonate. Near the shore a good deal of organic matter was present, chiefly in the form of decaying mangrove roots. Farther out from the shore little organic matter was noticeable, but it was not possible to examine the deeper layers of the mud in these situations. The only organic matter that was seen consisted of the rootlets of a species of *Zostera*, found in occasional patches some miles off the coast.

BACTERIAL INVESTIGATIONS IN THE DEEP WATER OF THE TONGUE OF THE OCEAN.

Continued bad weather during the whole of our stay at Andros greatly added to the difficulties of this work, and on this account it was only found possible to work three stations. The last two were worked under the most disadvantageous conditions, the quick roll of the boat making the filling of the water-bottle with alcohol and the siphoning off of the sample under sterile conditions a matter of the greatest difficulty.

The first station worked was 6 miles due east of Golding Cay, the second 14 miles east of Golding Cay, and the third 10 miles ENE.¼E. of Golding Cay. The three stations were thus at the angles of a triangle which was nearly equilateral, the base being a little longer than the sides and running due east and west.

At the first station, worked on May 8, bottom was sounded at 822 fathoms. The sea was calm at first, with a SSE. swell, but became choppy later. The wind was SSE., force 0 to 1, at 8^h30^m a.m., freshening to about force 3 at 10^h30^m a.m. The sample of the bottom obtained by the snapper-rod was of a very stiff clay-like consistency, grayish white in color, and was composed of very minute unorganized particles of calcium carbonate containing a few pteropod and globigerina shells. The following temperatures, to which the necessary corrections have been applied, were recorded:

Depth.	Temperature.	Depth.	Temperature.
Fms.	*°C.*	*Fms.*	*°C.*
Surface	26.90	400	9.03 8.93 average = 8.98
10	25.90		
50	25.14	600	4.78 4.62 average = 4.70
100	22.00		
200	17.13	Bottom (822 fms.)	4.00 3.94 average = 3.97

These samples, without previous dilution, were plated in peptone agar, 1 c.c. of the sample being used for each plate. The agar was cooled to just under 40° C. before plating. It is very necessary that this temperature should not be exceeded, as many marine bacteria are very sensitive to heat; the use of agar at as high a temperature as 45° C. will cause the death of a large proportion of the bacteria, though in the process of plating they can be exposed to this temperature only for a very short time. The cultures were kept in the dark at the room temperature (averaging about 28° C.) and at the end of 24 hours a free growth of colonies was apparent. At the end of 48 hours the plates were counted with the following results:

Depth (in fathoms).	No. of colonies developing from 1 c.c. of sample, and remarks.
822 (bottom)	0
822 (bottom)	3
822 (bottom)	1
600	17
600	14
400	15
400	16
200	1,760 Very much overcrowded; indications of presence of many more colonies undeveloped from overcrowding.
200	1,500
100	Uncountable owing to overcrowding.
100	Do.
50	Do.
50	Do.
10	Do.
10	Do.
Surface	Do.
Do	Do.

From these counts it is apparent that the number of bacteria falls off at some point between 200 and 400 fathoms.

The second station was worked on May 11 at a point 14 miles due east of Golding Cay. The sea was calm at first, and the wind ENE., force 1, but later in the day a heavy swell set in and the wind freshened to about force 4; eventually the weather became so bad that it was impossible to work, and the station had to be abandoned before it was completed. Bottom was sounded at 890 fathoms, but there was some stray on the wire, so that the true depth was probably about 825 fathoms, as shown by the chart. The bottom consisted of fine white calcareous ooze; no remains of pteropods were seen, but some globigerina shells were present. The following temperatures were recorded:

Depth.	Temperature.	Depth.	Temperature.
Fms.	°C.	*Fms.*	°C.
Surface	26.30	300	14.37 14.27 average = 14.32
10	26.40	400	9.86 9.73 average = 9.79
50	24.89	Bottom	4.17 4.13 average = 4.15
100	22.63		
200	17.42		

Samples down to a depth of 200 fathoms were diluted 1 in 100 with sterilized sea-water before plating. The following results were obtained after 48 hours' growth:

Depth.	No. of colonies developing from 1 c.c. of sample.
Fms.	
Surface	16,200
10	13,100
50	14,000
100	14,000
200	15,000
300	14
400	12

The figures given represent the mean of the number of colonies developing in the two plates that were made from each sample. It is here apparent that the number of bacteria per 1 c.c. falls off very rapidly between 200 and 300 fathoms.

The third station was worked on May 23 at a point 10 miles ENE.½E. of Golding Cay. The wind was east, of about force 4. As it had been blowing for the previous ten days without intermission, the sea was so rough that it was only possible to work when steaming slowly ahead into the wind. This resulted in the production of a great deal of stray on the sounding-wire, so that the number of fathoms of wire run out is greater than the actual depth at which the samples were taken; these differences will be large for the more superficial samples, but small at greater depths, as the wire strays in a curve whose gradient becomes very steep a little below the surface under these conditions.

The following temperatures were recorded:

Length of wire run out.	Temperature.	Length of wire run out.	Temperature.
Fms.	°C.	*Fms.*	°C.
Surface	27.10	250	14.97 15.00 average=14.98
20	26.50		
100	22.80	350	10.85 10.84 average=10.85
160	18.83		

At this point the station had to be abandoned, owing to the bad weather. The samples down to 160 fathoms were diluted 1 in 100 with sterilized sea-water before plating in peptone agar; the remaining two were plated undiluted. At the end of 48 hours the following counts were made, representing the mean of the number of colonies in the two plates made from each sample:

Length of wire run out.	No. of colonies developing from 1 c.c. of sample.
Fms.	
Surface	15,000
20	15,500
100	13,700
160	13.300
250	14,300
350	16

The colonies developing in all the cultures were only of two kinds, the *Bacterium calcis* and the non-denitrifying species already described. The non-denitrifying species formed a relatively small proportion of the total, and were not found at all in cultures made from samples taken below 250 fathoms. As they appear to be comparatively inactive chemically, and as nothing is at present known concerning the part played by them in the metabolism of the sea, they will not be further considered here.

A consideration of these results obtained in the Tongue of the Ocean shows that the waters down to a depth of somewhere about 300 fathoms in April 1912 contained an enormously larger number of bacteria than the water in the neighborhood of Tortugas in June 1911. The number of bacteria falls off from about 14,000 to about 12 per 1 c.c. between depths of 250 and 350 fathoms; the temperature at 250 fathoms was about 15° C. and at 350 fathoms about 11° C., and it was shown in June 1911 at Tortugas that *B. calcis* will grow slowly at 15° C., but that growth is totally inhibited at 10° C. It would thus seem that the observed distribution of the bacteria agrees fairly with what might be expected from the temperature conditions.

As regards these observations on the occurrence of bacteria in small numbers at depths below 350 fathoms, the possibility of experimental error must be considered; a leakage into the water-bottle of 0.25 c.c., as it was being hauled up through the last 300 fathoms, would account for the number found, and there are also many possible sources of error in the process of siphoning off the sample and making the cultures where a permanent laboratory is not available. It is possible that the water below 350 fathoms was really sterile, though if so the constancy of the results obtained is curious if ascribed to experimental error. In any case, the small number of bacteria found at depths below 350 fathoms can play no part in the metabolism of the sea, since it has been shown that *B. calcis* is incapable of growth at the temperatures obtaining at these depths.

The much greater abundance of bacteria in the surface waters of the Tongue of the Ocean than in the waters around Tortugas may perhaps be accounted for by the fact that in the Tongue of the Ocean by far the greater part of the surface water must flow over the immense chalky mud flats and shallows which bound it in most directions and, as will presently be shown, these mud flats are phenomenally rich in bacteria and are probably still being deposited by bacterial agency.

HYDROGRAPHIC OBSERVATIONS IN THE TONGUE OF THE OCEAN.

The samples of water taken for hydrographic investigations were analyzed by Mr. D. J. Matthews at Plymouth. With great kindness he calculated the results, and from his notes the following observations and conclusions are drawn.

The samples were analyzed for salinity in comparison with the standard sea-water supplied by the Central Laboratory of the Conseil International pour l'Exploration de la Mer, and hence the results are strictly comparable with all other analyses published under the auspices of this International Council. The following results were obtained:

Depth.	At first station, 6 miles east of Golding Cay.				
	Temp.	Cl 0/00	S 0/00	σ_0	σ_t
Fms.	*°C.*	*P.ct.*	*P.ct.*		
0	26.90	20.06	36.24	29.12	23.70
10	25.90	20.46	36.96	29.71	24.57
50	25.14	20.43	36.91	29.66	24.76
100	22.00	20.28	36.64	29.45	25.48
200	17.13	20.08	36.27	29.15	26.48
400	8.98	19.58	35.37	28.43	27.43
600	4.70	19.49	35.21	28.30	27.90
822	3.97	19.367	34.98	28.11	27.79

Note.—The original surface sample was lost, owing to breakage of the bottle in transit to England. The analysis was made on a sample taken 3 days later at the same spot.

In this table Cl 0/00 means the weight of chlorine in grams found in 1,000 grams of sea-water. S 0/00 means the salinity, or total weight of salt in grams found in 1,000 grams of sea-water. σ_0 represents the specific gravity of the sample at 0° C., and σ_t represents the specific gravity of the sample at the temperature t at which it was collected, with no correction for pressure.

At the second station, 13.5 miles east of Golding Cay, the following results were obtained:

Depth.	Temp.	Cl ⁰/₀₀	S ⁰/₀₀	σ_0	σ_t
Fms.	°*C.*	*P.ct.*	*P.ct.*		
0	26.30	20.25	36.58	29.40	24.15
10	26.40	20.33	36.73	29.52	24.24
50	24.89	20.395	36.84	29.61	24.78
100	22.63	20.36	36.78	29.56	25.42
200	17.42	20.12	36.35	29.21	26.47
300	14.32	19.81	35.79	28.76	26.75
400	9.79	19.56	35.34	28.40	27.27
890	4.15	(No sample, bottle did not work.)			

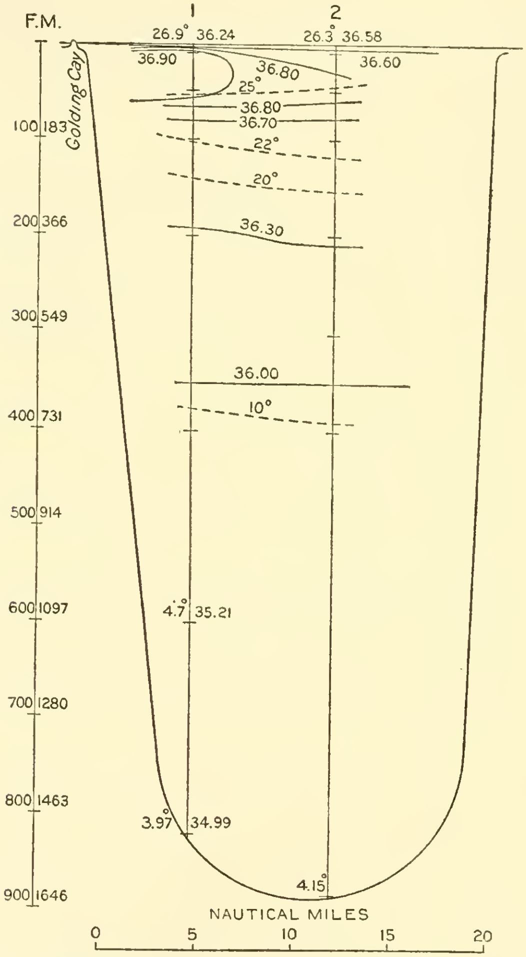


FIG. 2.—Section across the Tongue of the Ocean from Golding Cay, Andros Island, showing salinities and temperatures.

Owing to the uncertainty of the depths at the third station, due to the bad weather and consequent stray on the wire, it was decided not to include these observations in a consideration of the hydrographic conditions, and to make what deductions were possible from the results obtained at the two stations given.

Figure 2 shows the vertical distribution of layers of different salinities at the two stations in diagrammatic form.

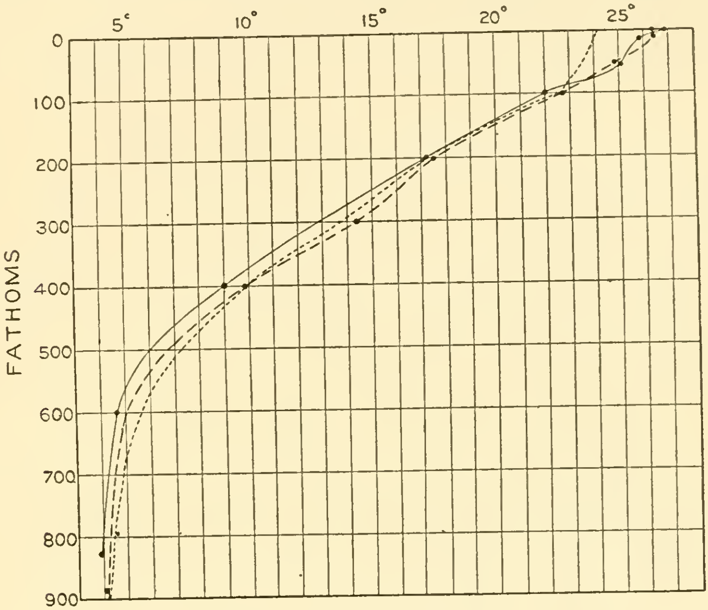


FIG. 3.—Temperature curves.
Continuous line = Station 1.
Broken line = Station 2.
Dotted line = *Challenger* Station No. 27.

The curves in figure 3 show the vertical distribution of temperatures at the two stations, and also give the temperatures obtained by *Challenger* Station No. 27 in 22° 49′ N., 65° 19′ W. March 28, 1873, where the depth was 2,960 fathoms. It is interesting to note that the actual reading at 200 fathoms at the latter station, 17.22° C., agrees more closely with the temperatures in the Tongue of the Ocean than that taken from the smoothed curve, which was 18.17° C.

The curves in figure 4 show the vertical distribution of salinities at the two stations, and also the salinities obtained by the *Michael Sars* in 37° 12′ N., 48° 30′ W., on June 25, 1910.

From these tables and diagrams it can be seen that the surface salinity increases from west to east very rapidly, 0.34 per cent in 7.5 miles, but the surface temperature is fairly uniform, between 26° C. and 27° C.

At both stations the salinity increases downwards to a maximum probably lying between 10 fathoms and 50 fathoms, but more rapidly at Station I, so that from 10 fathoms to 50 fathoms the salinity decreases from west to east.

Below 100 fathoms the conditions are closely similar at both stations, as far as the observations go; the salinity decreases fairly rapidly to 400 fathoms and then more slowly to the bottom.

The temperatures decrease rapidly and uniformly from the surface to about 500 fathoms, then more slowly to the bottom.

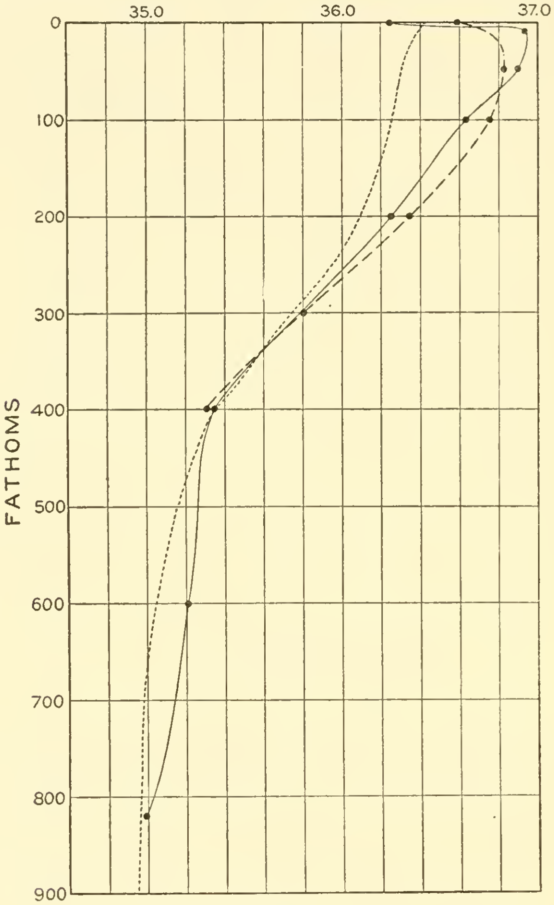


FIG. 4.—Salinity curves.
Continuous line = Station 1.
Broken line = Station 2.
Dotted line = *Michael Sars* Station No. 65.

There is practically no thermocline (German "sprungschicht") in the temperature at any depth and only a poorly marked one, confined to the upper stratum, in salinity.

The absence of a temperature thermocline is remarkable (see the curves for the two stations, and the two from the *Michael Sars* and the German South Pole Expedition, drawn for comparison).

In general, below about 250 fathoms the temperatures and salinities agree with the nearest stations of the *Michael Sars* in the open Atlantic;

above this depth they are higher, and differ from them and the open ocean north of the belt of calms, in the absence of a temperature thermocline, and in the maximum salinity being found below the surface. The latter points either to a considerable local supply of fresh water or to a current of lower salinity from either the Florida stream or the region of equatorial calms. Unfortunately we have no reliable salinity observations for the two latter.

With regard to the accuracy of the work, Mr. Matthews makes the following remarks:

THE ACCURACY OF THE OBSERVATIONS.

a. *Salinity.*—The method of taking the samples from the water-bottle was rather inconvenient, as a siphon was used; the samples were very small, but well preserved. The water-bottle itself might have leaked or closed at the wrong depth, as was the case with earlier models.[1] That this was not so is shown by

(1) The sharp fall in the number of bacteria at between 200 and 300 fathoms.

(2) The close agreement of the salinities at 400 fathoms, the greatest depth at which they were taken on both stations. Station I gave 35.37; Station II, 35.34.

(3) The close agreement between the bottom salinity at Station I, 34.98 at 822 fathoms, and the salinity found at the same depth at the nearest position at which we have modern observations—i. e., *Michael Sars* Station 65, in 37° 12′ N., 48° 30′ W., June 1910; according to the curve this is about 34.96.

b. *Temperatures.*—The National Physical Laboratory correction was given to 0.1° only, but the readings below 15° are comparable among themselves to 0.05° or possibly less. The curves of temperature for the two stations agree well in shape below 300 fathoms, but the temperature on Station II is generally slightly higher than on Station I, as a rule by an amount corresponding to a difference of depth of about 20 to 25 fathoms.

Below 200 fathoms the curves for both stations agree very closely with that for *Michael Sars* Station 64, in 34° 44′ N., 47° 52′ W.

It is almost certain from the above considerations that the results are only incorrect by the experimental errors in measuring the depth, in determining the salinity (0.01° at most), and by perhaps 0.1° C. of temperature.

These observations are sufficient to show that the Tongue of the Ocean is an area of considerable interest from a hydrographic point of view, and it is much to be regretted that the continued bad weather during our stay made it impossible to obtain more observations and samples.

BACTERIAL INVESTIGATION OF THE CHALKY MUD FLATS WHICH ARE BEING DEPOSITED TO THE WEST OF ANDROS ISLAND.

Samples of the mud were taken from the western entrance of South Bight (see Chart B), and from points 2 and 3 miles out from the shore; practically identical results were obtained from all these localities. The sample at the mouth of the bight was taken in about 4 feet of water, that 2 miles out in 7 feet, and that 3 miles out in 8 feet. The samples were necessarily taken from the surface of the mud.

---

[1] The water-bottle only failed once, at about 890 fathoms at Station II.

For bacterial examination, one part of this mud was shaken up with three parts of sterilized sea-water; this was allowed to settle for 15 minutes, and then the clearer surface layer was diluted 1 in 1,000,000 with sterilized sea-water. The diluted fluid was plated in peptone agar, 1 c.c. being used for each of the plates. The count of a number of plates after 48 hours gave 40 colonies as an average, and thus the mud itself must contain 40 × 4 × 1,000,000 = 160,000,000 bacteria per 1 c.c. The actual number in the mud possibly exceeds this figure, since a large proportion of the bacteria would probably settle with the larger particles after the first dilution.

The bacteria found in these cultures were nearly all the *B. calcis;* only occasionally were a few colonies of the non-denitrifying species seen.

A sample of the water taken from the surface at a spot 3 miles out from the western entrance of South Bight gave a count of 35,000 colonies per 1 c.c., the great majority of these being *B. calcis.*

Subcultures of *B. calcis* were made in Gran's medium, and in the calcium succinate, calcium acetate, and peptone calcium acetate media, whose composition has already been given. Denitrification in all these media was rapid and eventually complete, and was accompanied by the precipitation of calcium carbonate. In the last three media, which contained no solid matter and were quite clear and transparent before inoculation, this precipitation was manifested after 12 hours by the formation of a thick white cloud in the fluid, readily distinguishable from the cloudiness produced merely by bacterial growth. The development of this precipitate continued rapidly during the first 48 hours, but in many cases it was composed of such fine particles that they showed little tendency to settle to the bottom of the flask; in other cases larger particles were formed and a sediment similar in appearance to the chalky mud of the mud flats was produced. The exact conditions determining the size of the particles precipitated could not be ascertained, as the size varied largely in cultures made at the same time, in the same media, and kept apparently under the same conditions. The addition of magnesium tartrate in small quantities (0.2 gram per 1,000 c.c.) to the culture media seemed to induce the precipitation of larger particles, but it did not appreciably affect the rate of growth of the bacteria. In some of the older cultures that had been kept for a week or more, the sides of the flasks were coated with a thin layer consisting of extremely minute rhombohedral crystals of calcium carbonate. Occasionally these crystals formed around small bubbles that had remained near the surface of the fluid, the weight of the crystals eventually caused the bubbles to sink, and then the contained gas became dissolved; in this way a number of small, hollow spheres were formed, their walls consisting of minute crystals of calcium carbonate. The formation of these curious bodies occurred especially readily in the calcium succinate medium to which 0.2 gm. of magnesium tartrate per liter had been added. The deposition of calcium carbonate in a distinctly crystalline form was only noted in old cultures, and then it was in an amount relatively extremely small when compared to the precipitate of unorganized and amorphous calcium carbonate.

Specimens of the precipitates from some of the culture media were sent to Dr. Fred. E. Wright, of the Geophysical Laboratory of the Carnegie Institution of Washington, who described them as follows:

> *Preparation I:* Precipitate from medium composed of calcium acetate 5.0 grams, potassium nitrate 0.5 gram, peptone (Witte's) 0.2 gram, sea-water 1,000.0 c.c., filtered and sterilized, contains two substances: (1) Fine grains of a strongly birefracting, apparently uniaxial, optically negative substance and with refractive index about 1.66. This is probably calcite. The grains are isolated, and no evidence of spherulitic crystallization was observed. On treatment with very dilute hydrochloric acid a noticeable evolution of carbon dioxide took place. (2) Scattered through the preparation are fine needles of a weakly birefracting substance of refractive index of about 1.525; extinction angle large. These needles are evidently selenite (hydrated calcium sulphate).
>
> *Preparation II:* Precipitate from medium composed of calcium succinate 2.0 grams, magnesium tartrate 0.2 gram, potassium nitrate 0.5 gram, sea-water 1,000.0 c.c., consists largely of a cryptocrystalline aggregate of a weakly birefracting substance, whose refractive index is about 1.52 to 1.53. This substance proved too fine for further determination. Scattered through this substance are rounded and irregular patches of a second cryptocrystalline substance of strong birefringence, which gives off CO_2 when treated with dilute hydrochloric acid, and is probably calcite.
>
> *Preparation III:* Precipitate from a medium composed of calcium acetate 5.0 grams, sodium phosphate ($Na_2HPO_4 12H_2O$) 0.25 gram, potassium nitrate 0.5 gram, sea-water 1,000.0 c.c., is again very fine-grained and consists (1) in large measure of minute grains of a substance which agrees with calcite in its optical properties in so far as they could be determined. On immersion in dilute HCl a distinct evolution of CO_2 gas was observed. (2) Of a substance whose grains are somewhat coarser than the calcite grains, their birefringence being medium to weak; refractive index about 1.525; biaxial and apparently optically positive; probably selenite, but not crystallized in the usual manner.

The small quantity of hydrated calcium sulphate present in these precipitates is undoubtedly derived from that in solution in the sea-water with which the media were made up, but the reason of its precipitation is difficult to explain, since no such precipitation occurred in culture media kept uninoculated under similar conditions as control experiments. It would therefore appear that this deposition of calcium sulphate along with the calcium carbonate must in some indirect way be the result of bacterial action, and it would seem a possible suggestion that the odor of sulphureted hydrogen noticeable in the deeper layers of the mud flats might be due to the reduction of the calcium sulphate to a sulphide, and subsequent decomposition of the sulphide.

These observations have shown that on the chalky mud flats of the Great Bahama Bank the *B. calcis* is found in enormous numbers, and also that this bacterium is capable of precipitating calcium carbonate from fluid media containing soluble calcium salts. It would seem a fair deduction that these mud flats, consisting of fine unorganized particles of calcium carbonate, have been precipitated by the action of the *B. calcis* on the soluble calcium salts carried into the sea by drainage from the land, where extensive and rapid weathering of the limestone rock is in progress.

CONCLUSION.

The observations so far available are too few, and the area they cover too small, to attempt to make any broad generalization at present. However, it can be stated with a fair degree of certainty that the very extensive chalky mud flats forming the Great Bahama Bank and those which are found in places in the neighborhood of the Florida Keys are now being precipitated by the action of the *Bacterium calcis* on the calcium salts present in solution in sea-water. From this the suggestion is obvious that the *Bacterium calcis*, or other bacteria having a similar action, may have been an important factor in the formation of various chalk strata, in addition to the part played by the shells of foraminifera and other organisms in the formation of these rocks. Dr. T. Wayland Vaughan has also suggested that the Miami oolite and other oolitic rocks may owe their origin to the occurrence of some diagenic change in the precipitate of very finely divided particles of calcium carbonate produced in this way by bacterial action. If this view as to the formation of chalk and oolite rocks is correct, it would seem probable that these strata must have been deposited in comparatively shallow seas whose temperature approximated to that of tropical seas at the present time.

It has also been shown that bacterial denitrification is far more rapid and complete in the tropical seas around Jamaica, Tortugas, and Andros than in the temperate waters of the Bay of Biscay and the English Channel, and hence an explanation is provided of the relative scarcity of plankton and algal growth in the former localities, in accordance with the terms of Brandt's hypothesis.

The distribution of the bacteria, both as to numbers and species, has been shown to vary at different localities and at different depths, but there are at present too few observations to enable any conclusions or generalizations to be drawn.

As it now stands, the investigation can at most be considered to offer a mere indication of the part played by bacterial growth in the metabolism of the sea. To obtain a real insight into the question, it would be necessary to make more extensive bacterial and chemical observations in tropical, temperate, and arctic waters, to study the bacteriology of other areas where calcium carbonate is being precipitated from the sea, and to make further investigations in the laboratory into the chemistry of the reactions that can be brought about by various species of marine bacteria.

LITERATURE.

1. Baur, E. 1901. Ueber zwei denitrifizierende Bakterien aus der Ostsee. Wiss. Meeresunters., vol. vi. Kiel.
2. Brandt, K. 1905. On the production and the conditions of production in the sea. Conseil Internat. Rapp. et Proc. Verb., vol. iii.
3. ——— 1904. Ueber die Bedeutung der Stickstoffverbindungen für die Produktion im Meere. Botan. Centralblatt, vol. xvi.
4. Drew, G. Harold. 1911. Report of preliminary investigations on the marine denitrifying bacteria. Year Book No. 10, Carnegie Institution of Washington.
5. ——— 1911. The action of some denitrifying bacteria in tropical and temperate seas, and the bacterial precipitation of calcium carbonate in the sea. Jour. Marine Biolog. Assoc. of the U. K., vol. ix, No. 2.
6. ——— 1912. Report of investigations on marine bacteria carried on at Andros Island, Bahamas, British West Indies, in April 1912. Year Book No. 11, Carnegie Institution of Washington.
7. Feitel, R. 1903. Beiträge zur Kenntnis denitrifizierender Meeresbakterien. Wiss. Meeresunters., vol. vii. Kiel.
8. Fischer, B. 1894. Die Bakterien des Meeres. German Plankton Expedition.
9. Gran, H. H. 1901. Studien über Meeresbakterien, I. Bergens Museums, Nr. 10. Aarbog.
10. Keding, M. 1906. Weitere Untersuchungen über stickstoffbindende Bakterien. Wiss. Meeresunters., vol. ix. Kiel.
11. Kentner, J. 1905. Ueber das Vorkommen und Verbreitung stickstoffbindende Bakterien im Meere. Wiss. Meeresunters., vol. viii. Kiel.
12. Matthews, D. J. 1913. Deep-sea Bacteriological Water-bottle. Jour. Marine Biolog. Assoc. of the U. K., vol. ix, No. 4.
13. Murray, J., and J. Hjort. 1912. The depths of the ocean. London,
14. Murray, J., and R. Irvine. 1889. On coral reefs and other carbonate of lime formations in modern seas. Proc. Royal Soc. of Edinburgh, vol. xvii.
15. Raben, E. 1905. Ueber quantitative Bestimmung von Stickstoffverbindungen im Meerwasser. Wiss. Meeresunters., vol. viii. Kiel.
16. Thomsen, P. 1910. Ueber das Vorkommen von Nitrobakterien im Meere. Wiss. Meeresunters., vol. xi. Kiel.
17. Vaughan, T. Wayland. 1912. Carnegie Institution of Washington, Year Book No. 11, pp. 153–162.

III.

PRELIMINARY REMARKS ON THE GEOLOGY OF THE BAHAMAS, WITH SPECIAL REFERENCE TO THE ORIGIN OF THE BAHAMAN AND FLORIDIAN OOLITES.

By THOMAS WAYLAND VAUGHAN,
Geologist in charge of Coastal Plain Investigations, U. S. Geological Survey.

PRELIMINARY REMARKS ON THE GEOLOGY OF THE BAHAMAS, WITH SPECIAL REFERENCE TO THE ORIGIN OF THE BAHAMAN AND FLORIDIAN OOLITES.[1]

By Thomas Wayland Vaughan.

At Doctor Mayer's request the following preliminary statement on certain aspects of Bahaman geology and on the origin of the Bahaman and Floridian oolites is submitted as a companion paper to that of Mr. Drew, whose untimely death is both a source of great sorrow to his friends and a heavy loss to science. As Drew's investigations have proven an essential step in the solution of the problem of the origin of the extensive oolitic limestone formations of Florida and the Bahamas, it is fitting that an account of the processes by which they originate should accompany his posthumous memoir. Although the investigation of the rock specimens and bottom samples obtained in the Bahamas and Florida from April to July 1912 is not complete, certain definite and some tentative conclusions have been reached which may here be appropriately stated.

The Bahama Islands and their accompanying shoals occupy a triangular area which lies east of Florida and north of the islands of Cuba and Haiti. The northwest corner of the triangle is in latitude 27° 35′ N., longitude 79° 2′ W., about 40 miles north of Jupiter Inlet on the Florida coast. The southeast corner is Turks Islands, north of Haiti, in latitude 21° 20′ N. and longitude 71° 5′ W. The western side is a nearly north-and-south line from Little Bahama Bank to about latitude 25° 30′, whence the boundary bends into a south-of-east direction. The islands either occur on one of two large banks, the Little Bahama and the Great Bahama Banks, or they rise to the southeast of the latter bank as isolated eminences separated by water as much as 1,000 fathoms in depth.

The shoalest water in the bottom of New Providence Channel between Little and Great Bahama Banks is 253 fathoms in depth; that in the Straits of Florida, between the former bank and the Florida coast, off Jupiter Inlet, is 341 fathoms deep; between the latter bank and Florida the depth is 422 fathoms. The Great Bahama Bank is separated from Cuba by the Old Bahama Channel, which ranges from 276 to 296 fathoms in depth. This bank is indented by two bodies of deep water. The first of these, the Tongue

---

[1] The investigations, the results of which are here presented, were conducted under the joint auspices of the Department of Marine Biology of the Carnegie Institution of Washington and the United States Geological Survey. The former organization furnished opportunities for field work, while the latter authorized the prosecution of the investigation as a part of my official duties, and furnished facilities for laboratory studies in Washington.

of the Ocean, is sack-shaped and lies east of Andros Island and west of the bank, on the northern end of which is New Providence Island. Its depth ranges from 795 to 1,200 fathoms. The second indentation, Exuma Sound, is eastward from the Tongue of the Ocean, across the bank and keys extending southward from New Providence Island. This sound is purse-shaped and exceeds 1,000 fathoms in depth. Water 1,000 fathoms in depth is close to the eastern shore of the Bahamas as far north as Elbow Cay on Little Bahama Bank. Eastward of the 1,000-fathom curve the bottom rapidly descends to a depth between 2,000 and 3,000 fathoms. The Bahama Islands are subaerial protuberants above the nearly level, slightly submerged surfaces of extensive plateaus which on one or more sides rise precipitously from oceanic depths.

The water from Gun Key to Northwest Passage, a distance of 67 knots, is only 7 to 12 feet in depth, while the bottom southeast of New Providence Island ranges from awash to 12 or 18 feet below water-level. New Providence Island is mostly a platform from sea-level to 20 feet in elevation, with several east and west ridges standing above it; the highest of these, Nassau Ridge, rises to an altitude of about 100 feet. Andros Island has a similar physiography, a nearly level platform ranging in height from sea-level to 20 feet above that datum plane. Along its eastern front, lying near the shore, is a series of interrupted hills that range in elevation from 20 to 60, and perhaps in some instances to 100, feet. West of the coastal hills the surface is low, usually less than 10 feet in elevation, while much of the areas along the west front is affected by the tides. The Barrier Reef of Andros stands on the seaward edge of a shallow, submarine platform, at a distance of one-half mile to 2 miles off shore. The slope of the bottom seaward of the reef is comparatively rapid; between the reef and the shore the depth ranges from 1 to 2 fathoms. The platform between the reef and the shore is composed of hard lime rock, the surface of which is indented by numerous submarine pits. The deepest of the holes, locally known as "blue holes," sounded was 36 feet deep. As the general aspect of these holes is similar to the abundant subaerial pot-holes, locally known as "banana holes," formed by solution of the limestone, they are evidence of subsidence.

The general country rock of the Bahamas is oolite. The sea bottom from Gun Key to Northwest Passage, New Providence Island, and Andros Island is all or mostly composed of oolite, precisely similar to that of southern Florida. The material forming the ridge at Nassau has been wind-blown, and evidently is a dune accumulation. Many or all of the ridges rising higher than 20 or 30 feet above sea-level have been formed of wind-blown material, of which oolite is an important constituent, but the oolite of most or all the lower areas is of marine origin and has not been subjected to æolian action.

The finely divided calcium carbonate oozes in the shoal waters of Florida and the Bahamas have long attracted attention. Louis Agassiz, as early as 1851, noted them, as did Captain Hunt, Alexander Agassiz, and others.

Dall, so far as I am aware, was the first to suggest that "much of the limy deposit of the area behind the reefs and defended by them is probably the result of the deposition of lime originally in solution and precipitated by chemical action rather than of mechanically transported sediment."[1] Later, Samuel Sanford became convinced that the flocculent oozes in some of the Florida bays and sounds were chemically precipitated, and so expressed himself.[2] The most careful study as yet made of the shoal-water bottom deposits of south Florida was the one initiated by me in 1908 and conducted in conjunction with George C. Matson.[3]

This investigation led to the conviction that the flocculent, so-called amorphous, calcium carbonate is neither of detrital nor of organic origin, and therefore must be a chemical precipitate. In 1911, G. H. Drew came to the Tortugas Laboratory for the purpose of studying denitrifying bacteria. As he discovered that ammonia was a product of the metabolism of these organisms he was led to conduct experiments to ascertain the effect they might have in precipitating calcium carbonate. They were found to be active in Florida; and investigations he subsequently made in the Bahamas showed 160,000,000 of these bacteria to the cubic centimeter of surface mud on the west side of Andros Island. Drew says:[4]

> A consideration of these observations shows firstly that *B. calcis* is found in enormous numbers in the chalky mud flats of the Great Bahama Bank, and secondly that this bacterium is capable of precipitating calcium carbonate from fluid media containing soluble calcium salts. It would seem a fair deduction that these mud flats have been precipitated by the action of *B. calcis* on the soluble calcium salts carried into the sea by drainage from the land, where extensive and rapid weathering of the limestone rock is in progress.

Drew has shown what we may be confident is the major agency in producing the precipitation of the calcium carbonate ooze.

Every geologist who has studied the Florida oolites, except Alexander Agassiz, has considered them marine deposits; and Louis Agassiz, Sanford, and myself considered them associated with or derived from the fine calcareous muds. My opinion[5] was more definitely expressed than those of the other investigators.

Rainey, as early as 1858, showed, in a remarkable book entitled "On the mode of formation of shells of animals, of bone, and of several other structures, by a process of molecular coalescence, demonstrated in certain artificially formed products," that calcium carbonate precipitated from water-soluble salts of calcium in a viscid solution form spherulites and not crystals. In 1871, Harting, in a memoir, "Recherches de morphologie synthétique sur la production artificielle de quelques formations calcaires organiques,"[6] showed that calcium carbonate precipitated from a solution of a water-soluble calcium salt by the addition of the carbonate of potassium

---

[1] U. S. Geological Survey Bull. No. 84, p. 101. 1892.

[2] Second Annual Report Florida Geological Survey, p. 228. 1910.

[3] A contribution to the geologic history of the Floridian Plateau. Carnegie Institution of Washington Pub. No. 133, pp. 114–145. 1910.

[4] Carnegie Institution of Washington, Year Book No. 11, p. 144. 1912.

[5] Carnegie Institution of Washington Pub. No. 133, pp. 173–177. 1910.

[6] Verh. Kon. Akad. Wetensk., Amsterdam, vol. 13, pp. 84, 4 pls. 1871.

or sodium is at first of gelatinous consistency and later aggregates into spherulites.

In 1903, G. Linck published, in an article entitled "Die Bildung der Oolithe und Rogensteine,"[1] accounts of a series of important experiments he conducted on the precipitation of calcium carbonate from sea-water by the addition of alkaline carbonates, and in 1909 another contribution from him, "Ueber die Bildung der Oolithe und Rogensteine," appeared in the Jenaische Zeitschrift für Wissenschaft, vol. 45, pp. 267–278. According to Linck's experiments calcium carbonate precipitated from sea-water at a temperature of 17° C. to 40° C., by adding an alkaline carbonate, is aragonite and aggregates into spherulites, the diameters of which range from 0.02 to 0.2 mm. Murray and Irvine have shown that calcium carbonate precipitated from sea-water by an alkaline carbonate at a temperature of 34° F. is calcite, at 47° F. is a mixture of calcite and aragonite, at 80° and over is aragonite.[2]

Drew in 1912 published the following statement regarding the calcium carbonate precipitated[3] in a culture from a sample of water from Marquesas Lagoon:

> To such a culture a trace of very finely powdered hydrated calcium sulphate was added. This resulted in the formation of a precipitate, which, on microscopical examination, could be seen to consist of finely laminated concretions, some of which appeared to have a particle of calcium sulphate or sand as a nucleus. The concretions were soluble in dilute hydrochloric acid with evolution of carbon dioxide. These concretions bear a resemblance to those of some oolitic limestones, and the experiment suggests the manner in which such oolites may have been formed.

These references, although they lay no claim to completeness, are clear evidence that calcium carbonate, particularly aragonite, when precipitated from a water-soluble calcium salt by the addition of an alkaline carbonate, is at first of gelatinous consistency and later aggregates into spherulites.[4]

As I did not observe oolite grains in the muds when collected in the field, I was led to the opinion that oolitization was the result of secondary changes after precipitation and directed my attention to ascertaining if such supposed changes were taking place.[5]

Bahaman shoal-water bottom muds were collected through South Bight and off the west shore of Andros; and other samples were collected in Florida. As has been stated, these flocculent oozes when collected were not observed to contain oolite grains; however, such grains may have been present and may have escaped attention. All the Bahaman muds when examined at the end of November did contain oolite. Besides oolite grains, finely divided particles less than 0.001 mm. in diameter, some fragmental

---

[1] Neues Jahrb. für Min. Beilage, Bd. 16, pp. 495–513.

[2] Proc. Roy. Sci. Edin., vol. 17, pp. 79–109. 1890.

[3] Carnegie Institution of Washington, Year Book No. 10, p. 141. 1911.

[4] Without making a special diversion to go into the subject, it may be mentioned that spherulites or oolites of calcium malate and calcium phosphate are well known, and that the occurrence of spherulites of barium carbonate and strontium carbonate have been recorded. It is therefore established that a number of salts of the calcium group of elements may assume a spherulitic form.

[5] Carnegie Institution of Washington, Year Book No. 11, pp. 155, 157, 158. 1913.

calcium carbonate, alcyonarian spicules, shoal-water foraminifera, and other micro-organisms were present.[1]

Dr. Fred. Eugene Wright has examined some of the bottom samples for me and reports that the particles large enough for ascertaining their optical properties are calcite, but the fine material can not be optically determined. A series of the muds and several powdered specimens of Pleistocene oolites from Florida and the Bahamas were tested with the cobalt nitrate reaction; and as all of these upon heating gave the purple color characteristic of aragonite, this form of calcium carbonate was shown also to be present. The muds and the Pleistocene oolites, therefore, are composed of a mixture of aragonite and calcite.

The grains of the Bahama and Florida oolites range in size from 0.10 to 0.80 mm., and occasionally a grain perhaps exceeds 1 mm. in diameter. The spherulites or spheroid aggregates in the muds range from 0.004 or 0.006 mm. to oolite grains of ordinary size.

In order to test the growth of the grains, samples of a number of muds were strained through No. 10 bolting-cloth, which has a mesh of about 0.13 mm. in diameter, and the fine material that passed through the bolting-cloth was put into bottles containing sea-water. These bottles were permitted to stand from about November 25 until the first week in March, over three months, when a small portion of each sample was again strained through No. 10 bolting-cloth, and the portion retained on the cloth studied. The formation of oolite grains was found to be in progress in every sample, and numerous grains had apparently grown to such a size as to preclude their passing through the mesh of bolting-cloth. The grains showed the usual forms of oolite grains: spheroids, ovoids, and ellipsoids. The larger grains had smaller diameters of 0.17 mm.; longer diameters up to 0.23 mm. Those newly formed are soft and easily crushed by any kind of pressure. The experiments indicate increase both in number and in size of grains.

The precipitated calcium carbonate may segregate around a variety of nuclei, for instance, spherulites or round aggregates formed of the precipitated material, small grains of sands, shells of foraminifera, and gas bubbles.[2]

Although there is need for additional study of the factors that accelerate, retard, or inhibit the formation of spherulites and initial round aggregates and the subsequent growth of the grains, the empirical facts in the process of the formation of the Floridian and Bahaman oolites are clear. They are as follows:

1. Denitrifying bacteria are very active in the shoal waters of both regions and are precipitating enormous quantities of calcium carbonate which is largely aragonite.
2. This chemically precipitated calcium carbonate may form spherulites or small balls which by accretion may become oolite grains of the usual size, or it may accumulate around a variety of nuclei to build such grains.

---

[1] The investigation of these muds is still in progress [June 1913] and will not be finished for some months, The completed results will appear in a subsequent publication.

[2] See the papers by Linck, Drew, and Vaughan, already cited.

The deduction may be made that all marine oolites, originally composed of calcium carbonate, of whatever geologic age, may confidently be attributed to this process.

Two other important deductions may be made from the knowledge of this process, viz:

1. Neither the Bahamas nor the oolitic keys of southern Florida are coral islands, but they have been formed by this other process. Elevated coral rock is exceedingly scarce in the Bahamas and the Recent reef of Andros is comparatively insignificant as a constructional geologic agent. The material composing the land masses and much or most of the submarine platforms of the Bahamas is thus removed from the category of "coral rock" and the living reef reduced to a subordinate ratio as a builder of limestone.

2. Drew's studies (unfortunately incomplete) of the distribution of denitrifying bacteria have shown them to be most prevalent in the shoal waters of the tropics. They therefore conform to the temperature relations enunciated by Murray[1] for the distribution of lime-secreting organisms. By combining the results of Drew and Murray, the deduction seems warranted that great limestone formations, whether they be composed of organic or of chemically precipitated calcium carbonate, were laid down in waters of which at least the surface temperatures were warm, if not actually tropical.

This brief paper may be closed with the following statement and tentative outline of the geologic history of the Bahamas, with special reference to the eastern part of Andros Island:

The presence of oolite containing Pleistocene marine fossils above sea-level indicates elevation in the Bahamas; the presence of submerged solution pot-holes, not filled with sediment, indicates that the last movement was downward.

TENTATIVE OUTLINE OF THE PLEISTOCENE AND RECENT GEOLOGIC HISTORY OF THE BAHAMAS, AND ESPECIALLY OF ANDROS ISLAND.

(1) During Pleistocene, perhaps earlier Pleistocene time, numerous shallow submarine banks existed, on which calcium carbonate was chemically precipitated mostly as aragonite, and this was converted into oolite.

(2) This submergence was followed by uplift with the production by marine erosion of a platform and a margining shore cliff, and the formation of shore dunes paralleling the windward sea-front.

(3) Apparently there was further uplift and pot-holes were subaerially formed by solution on the platform between the dunes and the sea-front. At this time the land on the east side of Andros Island stood about 40 feet higher than now.

(4) The last event was a subsidence of about 40 feet, admitting the sea back to the edge of the previously cut low scarp, and the present barrier reef developed on the off-shore margin of the submerged platform.

---

[1] Natural Science, vol. 2, pp. 25–27. 1897.

IV.

THE BUILDING OF THE MARQUESAS AND TORTUGAS ATOLLS AND A SKETCH OF THE GEOLOGIC HISTORY OF THE FLORIDA REEF TRACT.

BY THOMAS WAYLAND VAUGHAN,
Geologist in charge of Coastal Plain Investigations, U. S. Geological Survey,

IV.

THE BUILDING OF THE MARQUESAS AND TORTUGAS ATOLLS AND A SKETCH OF THE GEOLOGIC HISTORY OF THE FLORIDA REEF TRACT.

By Thomas Wayland Vaughan.

INTRODUCTION.

The following brief article is supplementary to my paper "A contribution to the geologic history of the Floridian Plateau,"[1] in which it is stated that "the geologic history of the Marquesas and Tortugas is reserved for future consideration." The study of the geology and the geologic processes of the Florida reef tract, and especially of the Tortugas and the Marquesas, has been continued since 1910. During the field season of 1913 Mr. R. B. Dole, of the U. S. Geological Survey, undertook a special investigation of the solvent effect, by virtue of the content of carbon dioxide, of sea-water flowing into and out of Tortugas Lagoon. As the various lines of investigation have given definite results, the principal factors in the formation of the Marquesas and Tortugas atolls and their inclosed lagoons now seem clear, although some details still require elucidation. It is now also possible to outline with a feeling of confidence the salient geologic episodes in the history of the entire Florida reef tract and to institute comparisons with other coral-reef areas. As this paper is only a preliminary statement, it is intended subsequently to publish a more comprehensive discussion of the different problems here treated in a cursory manner.

BUILDING OF THE MARQUESAS AND TORTUGAS ATOLLS.

An inspection of the charts of the U. S. Coast and Geodetic Survey, No. 1252 for the Marquesas and No. 471*a* for the Tortugas, will show a striking similarity in the configuration of both, for in each banks or keys surround a central depression and in each there are major entrances in the southeast, southwest, and northwest quadrants. The Tortugas, however, are of a more elliptical form than the Marquesas, the axis of the ellipse extending from northeast to southwest. The Marquesas lagoon is only 1 to 15 feet in depth, while that of the Tortugas is from 7 to 13 fathoms. In both the principal key or bank slightly under water extends from the southeast

---

[1] Carnegie Institution of Washington, Pub. 133, pp. 99–185, 15 pls. 1910.

to the northwest entrance, or is on the east, northeast, and north sides. The keys and banks between the southeast and southwest passages and between the southwest and northwest passages are minor as compared with the larger one mentioned. It may also be pointed out that the Marquesas occur just west of Boca Grande Channel, and that the Tortugas lie just west of Rebecca Channel.

That the Marquesas were formed through the agency of waves and currents operating under proper conditions has been evident for some time, but the processes by which the Tortugas were built were less clear. It was thought possible that submarine solution had been efficacious in the latter, while it was apparent that it was ineffective in the former. In order to answer the question for the Tortugas, two lines of inquiry were undertaken. One of these was the examination of the bottom of the Tortugas Lagoon, to discover whether or not sediment is there accumulating; the other was to ascertain by chemical examination whether or not there was any excess of carbon dioxide in the water flowing into the lagoon and whether there was any difference in the quantity of carbonates in the outflowing and inflowing water. The latter investigation was undertaken by Mr. R. B. Dole. The bottom samples collected at numerous localities in the Tortugas established that the bottom in the channel between Garden Key and Bush Key, in Bird Key Harbor, and in the lagoon channels west and east of White Shoal and north of that shoal is formed of soft calcareous mud, largely of the kind Drew showed to be precipitated by denitrifying bacteria. The examination showed conclusively that sedimentation predominates over the removal of material, perhaps except where currents may corrade the sides or bottoms of the channels along which they flow. The conditions in the Tortugas lagoon are similar to those in the bays and sounds behind the Florida keys and to those in Marquesas Lagoon, in all of which filling by deposition is progressing.

The specimens examined by Mr. Dole were collected twice a day on the principal flowing and ebbing tides for nearly a lunar period, from May 20 to June 15, near buoy No. C3, in Southwest Channel, off the southern end of White Shoal. Mr. Dole's results are summarized on page 74 of this publication. They show that none of the water, neither that flowing into nor that flowing out of the lagoon, contains any dissolved free carbon dioxide, that all the carbon dioxide in the water is present in the carbonate or bicarbonate form, and that the inflowing water possesses no power to dissolve calcium carbonate by virtue of its content of carbon dioxide, as its capacity for the solution of lime has been exhausted before flowing into the lagoon. The chemical investigations of the waters and the study of the bottom deposits gave mutually confirmatory results, that the water flowing through the Tortugas Lagoon does not dissolve calcium carbonate and that the lagoon has not been formed by solution.

As two kinds of phenomena observed in the Tortugas might be considered to afford evidence in favor of solution, both will be briefly discussed.

One is the frequent occurrence of submerged coral heads, the interiors of which have been removed, leaving a partially inclosing skeletal shell covered by living polyps. Some of these heads have a suggestive resemblance to atolls, but the resemblance is only superficial. The excavation of the interior is to be explained by the upper surface of the envelope of living tissue having been damaged in some way, thus giving an opportunity for boring organisms of great variety to begin and prosecute their work of disintegrating the skeleton. Waves and currents wash out the broken-up material, forming a cavity which is bounded by a shell of substance whose outer surface is covered by living polyps. The other phenomena that might be attributed to solution are the overhanging projections along the steep, submarine cliffs or rock pinnacles which in places occur on the sides of channels. Since these stand against the sides of the currents it is probable that submarine scour, corrasion, has been a factor in producing them; and subaerial modification deserves consideration, as will later appear. As the dynamic agencies have been more and more thoroughly studied, the necessity for referring any phenomena observed in the Tortugas to submarine solution has been eliminated, and the conclusion definitely reached that such solution produces no geologic effects of importance.

As the production of the Marquesas and Tortugas atolls with their inclosed lagoons by solution is eliminated, other factors, especially waves and currents, will be considered. There are two current-shaped physiographic forms to which it is desired particularly to call attention—these are current-shaped crescents and current-shaped linear ridges. With reference to crescents it may be said that if an obstruction lies across the line of direction of a constant current, the current shears to each side and will drift detrital material in such directions as to form a crescentic accumulation, the bow of the crescent facing the current, while the horns of the crescent will curve before the current. An eddy may be produced in the space between the horns of the crescent, and a deposit may be formed there.[1]

Crescentic sand-dunes and crescentic keys are both well known. Should there be no cross obstruction, currents both aerial and aqueous will form linear ridges, under conditions which induce dropping material. Both linear sand-dunes and linear submarine banks are well known. Of current-transported detritus, crescentic accumulations lie across the main direction of the current, while linear ridges lie along its direction.

The currents of the Florida keys are of three kinds: wind-formed currents, which are accompanied by waves; the Florida counter current; and tidal currents. The winds at Key West, where accurate records have been kept, prevailingly range in direction from northeast to southeast, those from the east predominating over those from any other direction. Both the Marquesas and the Tortugas lie within the tract of the Florida counter current, which moves in general toward the west. The directions of the

---

[1] Dr. A. G. Mayer called my attention to the occurrence of this eddy.

wind-formed currents and the counter current are concordant and they therefore cooperate. The tidal impulse, however, is roughly from north to south and the direction of tidal currents is therefore transverse to the other currents.

The principal arcs of the rims of both the Marquesas and the Tortugas, *i. e.*, those from the southeast to the northwest entrance, are bowed toward the east, against the prevailing direction of the wind and that of the counter current, while the northern limb of the arc in each instance trails with these currents. These arcs therefore satisfy the requirements of wave and current-shaped arcs.

The southern sides of both the Marquesas and Tortugas are broken by southeast and southwest passages. These breaks are probably to be attributed to cross-tidal currents. Also both the Marquesas and Tortugas have a northwest passage. The explanation of this is probably as follows: In the Tortugas, although the data on currents are inexact, the available evidence indicates a stronger tidal inflow than outflow, much of the water of the receding tides not passing through the lagoon but around the outside of its rim. The water coming into the lagoon would tend to be driven toward the west by the winds, and would consequently find its outlet in the northwest quadrant.

In the Marquesas, the land area west of the southeast passage follows a line that would be expected of the southeast horn of a crescent formed under conditions of wind and currents known to prevail there. The formation of the bank and the small keys on it on the west side of the lagoon is more obscure. Perhaps they were formed by winds and accompanying waves that come, especially during hurricanes, from the west and by a current eddy produced to the leeward of the bow of the crescent.

The main agencies whereby the principal arc of the rim of the Tortugas was formed seem definitely known, but those building other parts of the rim are still somewhat vague. Between what is known as Five-foot Channel and Southwest Passage are holes, some of which are 6 fathoms or more in depth. It is evident from the distribution of these holes that once there were several channels trending more or less from southwest to northeast and approximately following the course of tidal flow, the channels bounded by banks elongate in the same direction. Detritus carried westward by waves and currents has filled parts of the channels and broken them up into holes, some series of which may still be recognized.

Loggerhead Key, as well as the bank on which it stands, is elongate from southwest to northeast and has each of its ends somewhat curved toward the west. The general direction of the bank is approximately along that of tidal flow, but it is not an unmodified linear ridge coinciding in direction with that of one current, for it is evident that the prevailing run of the waves before the wind, and perhaps the counter current acting at its southern end, have curved its ends westward. The effect of waves running before the wind in shaping a key was studied in detail on Loggerhead Key, where both the north and south horns of the key curve before the prevailing easterly winds. A reversal of a part of the horn of the north end of the key was observed during a swell from the northwest. During this reversal of the direction of the run of the waves, a reversed crescent was formed at the end of the spit, the bow of the crescent being toward the current while the horns curved before it. The more indurated beach rock on each side of Loggerhead Key slopes toward the sea, showing that the key is wave-built, on the surface at least. In this connection it may be said that a current too weak to pick up and carry detritus will, when agitation has lifted particles above the bottom, appreciably move them in the direction of the current. Loggerhead Key stands on the lee side of the lagoon, where waves from the east would be weaker than on the windward side, and where waves from the west would exert their full force. The following is offered as an hypothesis for the formation of the bank on which this key stands: It is largely or mostly a detrital ridge, formed in a partial eddy on the leeward side of the lagoon, mainly along the direction of flow of the stronger tidal currents. Wave agitation from the east and west has facilitated the movements of detritus and has built the sloping beach rock on both the lagoon and the sea sides. The stronger winds from the east have given a slight westward curvature to the extremities of the bank.

Before leaving the discussion of Loggerhead Bank and Key, attention will be directed to changes that have occurred since October 1910, when the last severe hurricane visited this region. Since that time the waves have acted with only slight cessation on the eastern side of the key and have cut away the eastern side of its northern end, while building has taken place on the western side; thus the outline of the northern end of the key has shifted westward. Accurate measurements of some of these changes have been kept but will not be given here.

Besides the banks and keys forming the perimeter of the Tortugas, there are also shoals and some small keys in the lagoon. Some of the shoals, White Shoal for example, lie along the direction of flow of the major tidal currents, although with their ends slightly curving toward the west; others are isolated rocks. That some of the latter may be coral masses is suggested by an experience on Garden Key, where all large rocks examined proved to be dead coral heads.

The rocks composing both Marquesas and Tortugas are known only from superficial examination. The foundation of the Marquesas may be oolite, similar to that found on Boca Grande Key, as some of the bottom samples from them were found to contain hard oolite grains. The keys, however, are composed of calcareous detritus, of which *Halimeda* is an important constituent. There is no important coral growth around the Marquesas. The keys of the Tortugas are mostly composed of the comminuted remains of a considerable variety of organisms that secrete calcium carbonate, mollusca, corals, nullipores, echinoids, etc. The corals here, in contradistinction to the Marquesas, are important. Coral reefs, patches, or heads occur along the west side of Loggerhead bank throughout its entire length and around both its southern and northern ends. Bush Key Reef, southwest of Southeast Passage, is luxuriant, and outer reef patches occur northward of Southeast Passage. Reef corals also occur at many places along the sides of channels within the lagoon. Other species of corals, not so large and massive as those on the reefs proper, live on the shallow flats, where not overwhelmed with detritus. Although it has not been practicable to make for the Tortugas a quantitative estimate of the proportions of material contributed by the different kinds of organisms, corals are rather surely the most important. The Marquesas, therefore, are composed of calcareous detritus mostly of other than coral origin; while the Tortugas are composed of calcareous material, of complex origin but largely due to the activity of corals.

The foregoing remarks may be summarized as follows: (1) Submarine solution has not been instrumental in the formation of the Marquesas or the Tortugas lagoon; (2) the atoll rings are constructional phenomena and were shaped by prevailing currents, those caused by winds, the Florida counter current, and tidal currents. The detrital material on which these agencies have worked in the Marquesas is mostly not of coral origin; while in the Tortugas, although of complex composition,[1] it is largely composed of coral débris.

The relative ages of the Marquesas and Tortugas atolls and their relations to oscillation of water-level will now be briefly considered, and in this connection further attention will be given to the probable relations of corals to the formation of the latter atoll. The Marquesas rim is composed of unconsolidated detrital material and evidently requires no oscillation of water-level for its formation. No indication of change of level during or since the building of the rim around the lagoon was observed.

Such a structure as the Tortugas would scarcely be built in the Florida region through material derived from reef corals without change in depth, as the depth of water in the lagoon, 13 fathoms, and outside the atoll rim, 13 fathoms or more, is greater than that in which the Florida reef species are known to flourish.[2] Other evidence, to be adduced in giving an account of the coastal oscillation, renders it reasonably certain that the Tortugas were initially outlined during subsidence.[3] Certain facts indicate that the history of the Tortugas is more complicated than that of the Marquesas.

---

[1] The following literature is cited in this connection:

Vaughan Cornish. On the formation of sand dunes. Geog. Jour. vol. 9, pp. 278-309. 1897.

C. Hedley and T. Griffith-Taylor. Corals of the Great Barrier, Queensland, a study of their structure, life-distribution, and relation to mainland physiography. Austral. Assoc. Adv. Sci. Adelaide meeting, 17 pp., 3 pls. 1907.

F. Wood-Jones. Coral and atolls. London. Lovell Reeve & Co. Ltd. (especially chapters XII and XIII, pp. 253-277). 1910.

James Bryce. South America observations and impressions. New York, Macmillan Co. 1912. [Pp. 58, 59 give a good description of crescentic sand-dunes, "the convex of the crescent always facing the wind," on the great inner plateau of Peru.]

[2] In the following discussion of oscillation the terms "uplift," "depression," and "subsidence" are used with reference to land, but it is recognized that oscillation may be due to negative or positive movement of sea-level independent of crustal movement.

[3] The wells bored on Key Vaca by the Florida East Coast Railway, under the supervision of Samuel Sanford, showed the thickness of the elevated coral reef rock to be 105 feet (= 17½ fathoms), indicating that the Pleistocene barrier reef was formed under conditions of subsidence, similar to those postulated for the initial building of the Tortugas rim.

Most or all of the material above sea-level in the Tortugas is unconsolidated, except an outer crust of some of the beach rock, as observed on Loggerhead Key. Extending beneath the sea-level, however, to a depth of 8 feet or more, is beach rock that appears more indurated. Harder rock was also observed at a depth of 3 or 4 feet under water on Southwest and Northeast keys, the subaerial portions of both have been cut away by wave action, and in places submarine cliffs of hard rock, which has been undercut and overhangs the sides of the channels, are evident at depths of over 20 feet. The presence of an older formation for the living reef corals is clear. It seems probable that this rock was subaerially indurated and then depressed. The probability of this subsidence will be further discussed in a succeeding paragraph, wherein the later movements of the Florida coast line will be more fully considered. It appears that the Tortugas atoll with its inclosed lagoon was outlined previous to the present development of the coral reefs of that area, that it was elevated about 50 feet, and that there has been a subsequent (the latest) depression; the land after the oscillation perhaps lacked 10 or 15 feet of being depressed to its former level, thus leaving the keys standing somewhat higher than before.

It has already been stated that the skeletal remains of corals are not only an important constituent of the Tortugas rocks, but are rather surely the most important contributor to its composition. Whether or not the various keys, banks, and isolated rocks were outlined by coral reefs may not be ascertained, but as coral reefs obey the laws of current-moved detritus, in many instances being the principal single source of the detritus, a positive answer to this question is not essential for the validity of the explanation here presented for the building of the Tortugas. Hedley and Taylor say in their paper on the Great Barrier, referred to in the footnote on page 62:

> The growth of an individual reef is shown to proceed in a regular cycle. If the reef reaches the surface with its axis along the wind, then its shape endures; but if across the wind, then its extremities are produced backward, forming first a crescent, later a horseshoe, and lastly an oval, thus inclosing a lagoon.

SKETCH OF THE GEOLOGIC HISTORY OF THE FLORIDA REEF TRACT.

The probability of elevation and subsidence in the Tortugas area leads to a consideration of evidence from which the later movements of the Florida coast line have been inferred and of conditions antecedent to the development of the living Florida barrier reef. That the last important movement of the Florida east coast was downward from Jacksonville to San Augustine is attested by the submerged channel of the mouth of St. Johns River and the submarine fresh-water springs off San Augustine. Late depression of the west coast is positively shown not only by the forms of Tampa Bay and Charlotte Harbor, but also by submerged channels off shore in that region. As the channels off this coast, however, appear not to affect the 10-fathom curve the depression was probably not so great as 60 feet. The very ragged character of the coast line from Cape Romano to the head of Florida Bay, with its salients, reentrants, and almost numberless small islands lying near shore, as Ten Thousand Islands, separated by an interlocking maze of channels, suggests that the southern end of the peninsula to its very tip has undergone subsidence at no distant date. On keys west of Bahia Honda Sanford noted holes, which, at a distance of a quarter of a mile or more from shore, connect with underground passages containing salt water; and on more easterly keys formed of elevated coral reef rock he observed free openings or cavities that extend to a depth as great as 30 feet below sea-level. The evidence is clear that the keys participated in the uplift and subsequent depression that affected the mainland and that at one time they stood more than 30 feet higher with reference to sea-level than they now do. This uplift and the subsequent depression, according to all available evidence, extended to the Tortugas.

The highest points to which the elevated reef extends are on Windleys Island and Plantation Key, where elevations of 18 feet are attained. Supposing these points to have been at sea-level, an uplift with reference to sea-level, of somewhat more than 48 feet, must have taken place since the elevated reef was formed.

The evidence presented shows that the platform, on the outer edge of which the present barrier reef of Florida is principally growing, has geologically, just antecedent to its present relations to sea-level, stood 30 feet or more higher. It is on this shelf, the last oscillatory movement of which was one of depression, that the living reefs of the Florida barrier have established themselves and have grown. However, although the last earth movement has been downward, the net result of the last oscillation, *i. e.*, uplift followed by subsidence, has been to bring the surface of the submarine shelf nearer to the surface of the sea. Although the building of the platform seaward of the Pleistocene barrier reef needs further study, it is known that the base of the Pleistocene reef is about 100 feet below sea-level. As the reef would not have begun to grow in a marked depression, it is probable that the water seaward of it was not shallower than that at its base. The maximum depth of Hawk Channel is about 7 fathoms, while in places the living barrier reaches the surface of the sea. Therefore, since the initiation of the Pleistocene reef the bottom seaward of it has been built up to a thickness ranging from 70 to 100 feet. As the question, how much of this material may be Pleistocene, can not now be answered, it is not known whether or not the living reef has Pleistocene corals beneath it. However these questions may ultimately be answered, it is clear that both addition of material (upbuilding) and uplift have contributed to raising the surface of the basement of the Recent reef, notwithstanding that the last oscillatory movement carried the land surface downward. The hydrographic charts (see particularly U. S. Coast and Geodetic Chart No. 165, Hillsboro Inlet and Fowey Rocks) clearly show the northward extension of the reef platform beyond the limits of the living reefs, which are merely superimposed on a platform whose existence antedates their own.

The conditions under which the Pleistocene barrier reef was formed may be reconstructed by using the results obtained from the recent geologic investigations on the Florida mainland and the records of the wells bored by the Florida East Coast Railway on Key Vaca. Pliocene deposition was followed by uplift, the ensuing Pleistocene deposits being laid down on the eroded surface of those preceding. The Pleistocene reef, which is 105 feet thick, was therefore formed on a subsiding sea-bottom succeeding the uplift at the end of Pliocene time.

The oscillations of southern Florida with reference to coral reefs may be tabularly expressed as follows:

Oscillations of Southern Florida.

Recent.........	Depression (modern) reefs.
Pleistocene......	Uplift.
	Depression (Pleistocene reefs, parts of which now stand as much as 18 feet above sea-level).
	Uplift.
Pliocene........	Depression (some reef corals but no well-developed reefs).

The results of the recent investigations by Sanford, Drew, Dole, and myself have revealed the salient facts in the geologic history of the tract of the Florida keys and reefs, except the immediate foundation rock of the living barrier reef. Great progress was made by clearly showing the process by which the oolites were formed and by proving that the atoll rims of the Marquesas and Tortugas are not due to the solution of an interior mass of limestone but to constructional geologic processes. The hypothesis that Biscayne Bay was formed by marine solution is also definitely disproven.

This history may be summarized as follows: Pliocene deposition was followed by uplift, which was succeeded by depression; during this Pleistocene subsidence along a curve from the eastern side of Biscayne Bay, first trending southward and then bending westward, a barrier coral reef flourished, separated by a channel from the main bank on which the Miami oolite was forming or had formed in strongly agitated waters. West of the coral reef, on an extensive flat in shoal water, the Key West oolite was formed, while still farther to the westward the Tortugas were outlined under the influence of winds and currents. This period of events was succeeded by the elevation of the entire key region to more than 50 feet above its previous level. This uplift was succeeded by one of depression, lowering the surface 30 feet or more, establishing practically the same relation of the sea-level to land that now prevails. Subsequent to the beginning of this last depression the present barrier reef has developed seaward of the keys on a platform already prepared for it, the Marquesas have been formed by winds and currents, and coral reefs have reestablished themselves in the Tortugas.

COMPARISONS OF THE FLORIDA REEF TRACT WITH SOME OTHER CORAL REEF AREAS.

In order to compare the relations of the barrier reef of Florida with the last change of sea-level in Cuba and in Andros Island, Bahamas, the following statements will be made: Hayes, Vaughan, and Spencer[1] have shown, as is evidenced by the pouch-shaped harbors of the Cuban coast and filled channels, such as the submerged filled channel in Havana Harbor, that the last movement of the Cuban coast has been downward with reference to sea-level. As an account of the Cuban reefs would be out of place here, reference is made to that published by A. Agassiz.[2] The platform on which the Cuban reefs grow has been brought to its present position by subsidence. The great barrier reef of Andros Island, Bahamas, as I have shown,[3] occupies the outer edge of a depressed platform. Therefore the Floridian, Andros, and Cuban reefs all have a similar relation to the oscillation of sea-level, as in each instance there has been elevation antecedent to depression which has brought the platforms on which the reefs stand into their present positions.

There is, however, in one important respect, a difference between the relations of the Recent reefs of Florida, Andros Island, Bahamas, and of those of Cuba to Pleistocene oscillation. The oscillations in Florida and Andros Island have taken place without notable differential crustal movements; while in Cuba there was notable deformation accompanying the oscillations. The Pleistocene terraces rise in height toward the eastern end of Cuba in Oriente Province, where altitudes of about 600 feet are attained near Cape Maisí; while in Santa Clara, Matanzas, and Havana provinces terraces on the north side are distinct and rise in several steps to heights of about 200 feet, but are absent or indistinct on the southern side.[4] These facts show that there has been pronounced tilting in late Pleistocene time. In Barbados Pleistocene reefs extend to 1,000 feet in elevation.

By working out the salient features in the development of the Florida reefs and instituting comparisons with the West Indies a basis has been supplied for explaining certain puzzling relations of the reefs in the Tropical Pacific. A. Agassiz discovered that in the Paumotuan atolls the Recent corals were growing as a thin crust on an older limestone foundation. His explanation of the formation of the atolls by the destruction of the interior of a limestone mass must be discarded, as they were certainly not formed in that manner but by constructional agencies. There was evidently a period of atoll formation in the Paumotus previous to the growth of the Recent corals, which have established themselves on an atoll basement already prepared for them. A great development of Pleistocene (and perhaps late Tertiary) coral reefs in the tropical Pacific has been proven in the most convincing way.

---

[1] Report on a geological reconnaissance of Cuba, made under the direction of General Leonard Wood, Military Governor, 1901. Report of the Military Governor for 1901.

[2] Bull. Mus. Comp. Zool., vol. 26, pp. 133–136. 1894.

[3] Carn. Inst. Wash. Year Book, No. 11, p. 154, 1912; Carn. Inst. Wash. Pub. 182, page 50, 1913.

[4] Hayes, Vaughan, and Spencer, Geological reconnaissance of Cuba, pp. 18–20.

There is abundant evidence of differential crustal movement in the tropical Pacific similar to that indicated for the West Indies. E. C. Andrews[1] and C. Elschner[2] have both described warping or tilting, the former for the Fijis, the latter for the Pacific more or less in general. Agassiz described an elevated atoll, Makatea, in the Paumotus, and Andrews has given a detailed description of the elevated atoll of Mango, Fijis. The old reefs have been subjected to differentiated earth movement, so that in certain places old atolls, such as Rangiroa and others in the Paumotus, now stand at or near sea-level, while other atolls have been uplifted to heights as great as 230 feet in Makatea and 600 feet in Tuvuthá, Fijis. In other areas there has been depression, Bora-Bora, for instance, as Dana, P. Marshall, and more recently W. M. Davis, have shown.

In conclusion it will be said regarding the Pacific coral reefs: (1) Atolls are not formed by solution, but by constructional geologic agencies; (2) there was in the tropical Pacific a great development of Pleistocene and perhaps late Tertiary reefs which have subsequent to their formation been subjected to extensive differential crustal movement; (3) these deformed older reefs are frequently the basement of the Recent reefs. Although important contributions have already been made to the study of Pleistocene and Recent oscillation and deformation in the Tropical Pacific, there is great need for more extensive and more detailed investigations of this phase of the coral-reef problem in order to ascertain more accurately the relations of the older to the Recent reef series.

---

[1] Notes on the limestones and general geology of the Fiji Islands; Bull. Mus. Comp. Zool., vol. 38, pp. 27–30. 1900.

[2] Corallogene Posphat-Inseln Austral-Oceaniens, pp. 15–19, Lübeck. 1913.

V.

SOME CHEMICAL CHARACTERISTICS OF SEA-WATER AT TORTUGAS AND AROUND BISCAYNE BAY, FLORIDA.

By R. B. DOLE,
Chemist U. S. Geological Survey.

One Map.

SOME CHEMICAL CHARACTERISTICS OF SEA-WATER AT TORTUGAS AND AROUND BISCAYNE BAY, FLORIDA.

By R. B. Dole.

INTRODUCTION.

The chemical tests at Tortugas were performed by the writer in June 1913, in the Marine Biological Laboratory, Tortugas, Florida, for the primary purpose of ascertaining what soluble effect, if any, carbon dioxide in sea-water might have on coral and other deposits of calcium carbonate. The tests of waters from Biscayne Bay were made to ascertain the differences in concentration of sea-water in the bay and the diluting effect of Miami River. The samples for the latter work were collected by the writer June 23, 1913, and they were examined during the summer by E. C. Bain, junior chemist, U. S. Geological Survey.

DETERMINATION OF CARBON DIOXIDE.

To 100 c.c. of the sample, in a Nessler tube measuring 17.5 cm. to the graduating mark, 10 drops of 1 per cent phenolphthalein was added and the solution was titrated to an acid reaction by means of N/20 sulphuric acid. This is the usual procedure for estimation of normal carbonates in water. The result of the titration has been calculated to "carbon dioxide (CO_2) present as carbonate (CO_3)" by means of the formula $A = 22Q/d$, in which A represents milligrams per liter of carbon dioxide, Q the number of cubic centimeters of N/20 sulphuric acid required, and d the density of the water.

A sufficient excess of N/20 sulphuric acid was added to 200 c.c. of the sample in a Jena flask and the solution was gently boiled long enough to drive off carbon dioxide, after which the total quantity of acid consumed was determined by titrating the excess with barium hydrate in presence of phenolphthalein. This procedure was followed by Fox[1] and others in determining the alkalinity of sea-water. The "carbon dioxide (CO_2) present as bicarbonate (HCO_3)" was computed by means of the formula $B = 11(Q' - 4Q)/d$, in which B represents milligrams per liter of carbon dioxide, and Q' the total quantity of acid required. The result of the second titration has also been expressed as "total alkalinity in equivalent OH" in order to afford comparison with the results of certain other analysts. This calculation has been made by the formula $C = 4.275Q'/d$, in which C represents the equivalent alkalinity in milligrams per liter of the hydroxyl radicle (OH).

---

[1] Fox, C. J. J., On the coefficients of absorption of the atmospheric gases in distilled water and sea-water. Conseil permanent international de la mer, pub. de circonstance 44. February 1909.

DETERMINATION OF CHLORINE.

Chlorine was estimated by means of the salinity outfit supplied by the Copenhagen laboratory of the Conseil permanent international de la mer. This apparatus was obtained through the courtesy of the United States Bureau of Fisheries. The procedure is an adaptation of the usual method of estimating chlorine by titrating with silver nitrate in presence of potassium chromate. An essential feature is a sealed tube of standard sea-water whose content of chlorine has been very carefully determined. This water is used for comparison and the apparatus is so constructed and calibrated as to insure maximum accuracy. Standardized burette No. 8, measuring about 1.5 mm. between graduations, and pipette No. 3, having a capacity of 15.04 c.c., were used. Standard sea-water P_7 2/2, 1912, with a chlorine content of 19.386 grams per kilogram, was titrated frequently during the tests at Tortugas. In the later tests comparison was made indirectly with the same standard by means of a large sample of sea-water from Tortugas that had been titrated several times. Knudsen's correction (*k*) has been applied to the titrations[1] and salinity (*S*) has been computed by means of his formula,[1] in which Cl represents grams per kilogram of chlorine: $S = 0.030 + 1.805 \text{ Cl}$.

SPECIFIC GRAVITY.

Density was determined by comparison in 10 c.c. weighing flasks with distilled water at 25° C. Knudsen's values[1] for $\rho_{17.5}$ were used for computing density ($S^{17.5}_{17.5}$) as follows $S^{17.5}_{17.5} = 1 + \rho\frac{17.5}{1,000}$, where $\rho_{17.5} = 1.00129 (0.1245 + \sigma_0 - 0.0595\sigma_0 + 0.000155\sigma_0^2)$ and $\sigma_0 = -0.069 + 1.4708 \text{ Cl} - 0.001570\text{Cl}^2 + 0.0000398 \text{ Cl}^3$. Part of the relatively slight difference between determined and computed figures for sea-water around Biscayne Bay may be attributed to difference of standard; that is, by the determined value the sea-water is compared with distilled water at 25° C., while by the calculated value the specific gravity of the sea-water at 17.5° is referred to distilled water of the same temperature.

SEA-WATERS AT TORTUGAS.

It is believed that solution of calcium carbonate by carbon dioxide in sea-water, if such action takes place, would be shown by regular differences in condition of carbon dioxide in the ebb and flood waters passing out of and into the lagoon surrounded by the shoals and keys of the Tortugas. Accordingly, samples of sea-water were collected twice a day from the middle of Southwest Channel about a mile southeast of Loggerhead Key; these were taken in bottles provided with washered caps that could be clamped down to prevent escape of gases and the samples were kept on ice until they were examined. Those collected from June 11 to 16, inclusive, were tested immediately, and though those taken before the former date had been stored for several days the tests do not indicate that the delay in examination had any appreciable effect on their composition.

---

[1] Knudsen, Martin, Hydrographical tables. Copenhagen, 1901.

TABLE 1.—*Salinity and Carbon-Dioxide Content of Sea-Water from Southwest Channel, Tortugas, Florida.*

Date 1913.	Condition of tide.	Chlorine (Cl).	Salinity (S).	N/20 acid required to neutralize 100 c.c. in the cold (Q).	N/20 acid required to neutralize 200 c.c. after boiling (Q').	Carbon dioxide (CO_2).			Total alkalinity expressed in equivalent OH.	Calculated specific gravity $\left(S\frac{17.5}{17.5}\right)$.
						Present as carbonate (CO_3).	Present as bicarbonate (HCO_3).	Total.		
		Grams per Kgm.		c.c.	c.c.	Grams per kilogram.				
May 20	Ebbing	19.91	35.97	0.80	9.66	0.018	0.069	0.087	0.0402	1.02748
21	Flowing	19.93	36.00	.92	9.58	.020	.063	.083	.0399	1.02750
	Nearly slack	19.94	36.02	.68	9.54	.015	.073	.088	.0398	1.02752
22	Nearly full	19.94	36.02	.79	9.63	.017	.069	.086	.0402	1.02752
	Ebbing	19.92	35.99	.89	9.88	.020	.068	.088	.0411	1.02749
23	Flowing	19.93	36.00	.96	9.70	.020	.062	.082	.0404	1.02750
	Ebbing	19.91	35.97	.93	9.80	.020	.065	.085	.0408	1.02748
24	Flowing	19.88	35.91	.76	10.07	.017	.075	.092	.0419	1.02743
	Ebbing[1]	19.85	35.86	.51	9.48	.011	.080	.091	.0395	1.02739
25	Flowing	19.89	35.93	.80	10.32	.018	.076	.094	.0430	1.02745
	Ebbing	19.93	36.00	.51	10.26	.011	.088	.099	.0427	1.02750
26	Flowing	......	....	......	......	......	......	......	....	....
	Ebbing	19.92	35.99	.58	9.46	.013	.076	.089	.0394	1.02749
27	Nearly slack	19.93	36.00	.62	9.49	.014	.075	.089	.0396	1.02750
	Ebbing	19.92	35.99	.72	9.50	.016	.071	.087	.0396	1.02749
28	Flowing	19.93	36.00	.70	9.75	.015	.074	.089	.0406	1.02750
	Ebbing	19.93	36.00	.75	9.36	.016	.068	.084	.0390	1.02750
29	Ebbing	19.94	36.02	.75	9.72	.016	.072	.088	.0405	1.02752
	Flowing	19.93	36.00	.83	9.68	.018	.068	.086	.0403	1.02750
30	Ebbing	19.93	36.00	.82	9.28	.018	.064	.082	.0387	1.02750
	Flowing	19.96	36.06	.92	9.53	.020	.062	.082	.0396	1.02754
31	Ebbing	19.94	36.02	.79	9.57	.017	.069	.086	.0399	1.02752
	Flowing	19.94	36.02	.86	9.51	.019	.065	.084	.0396	1.02752
June 1	Ebbing	19.95	36.04	.99	9.41	.021	.059	.080	.0392	1.02753
	Flowing	19.97	36.08	.94	9.44	.020	.060	.080	.0394	1.02756
2	Ebbing	19.95	36.04	.82	9.37	.018	.065	.083	.0391	1.02753
	Flowing	19.94	36.02	.88	9.43	.019	.063	.082	.0393	1.02752
3	Ebbing	19.94	36.02	.80	10.21	.018	.075	.093	.0425	1.02752
	Flowing	19.96	36.06	.70	9.45	.015	.071	.086	.0394	1.02754
4	Ebbing	19.96	36.06	.89	9.34	.020	.062	.082	.0389	1.02754
	Flowing	19.95	36.04	1.04	9.72	.022	.060	.082	.0405	1.02753
5	Ebbing	19.97	36.08	.77	9.54	.017	.069	.086	.0398	1.02756
	Flowing	[2]19.50	[2]35.23	.80	9.93	.018	.072	.090	.0413	1.02691
6	Flowing	19.95	36.04	.75	9.45	.016	.069	.085	.0394	1.02753
	Ebbing	19.95	36.04	.85	9.59	.019	.066	.085	.0400	1.02753
7	Flowing	19.93	36.00	.79	9.45	.017	.067	.084	.0394	1.02750
	Ebbing	19.94	36.02	.77	9.45	.017	.068	.085	.0394	1.02752
8	Flowing	19.95	36.04	.79	9.64	.017	.069	.086	.0402	1.02753
	Ebbing	19.95	36.04	.81	9.55	.018	.067	.085	.0398	1.02753
9	Ebbing	19.95	36.04	.77	9.46	.017	.070	.087	.0394	1.02753
	Flowing	19.96	36.06	.73	9.46	.016	.068	.084	.0394	1.02754
10	Flowing	19.94	36.02	.61	9.55	.013	.076	.089	.0398	1.02752
	Ebbing	19.94	36.02	.54	9.52	.012	.079	.091	.0397	1.02752
11	Flowing	19.98	36.09	.58	9.43	.013	.076	.089	.0393	1.02757
	Ebbing	19.98	36.09	.94	9.54	.020	.062	.082	.0398	1.02757
12	Nearly slack	19.96	36.06	.80	9.86	.018	.071	.089	.0410	1.02754
	Flowing	19.97	36.08	.80	9.44	.018	.067	.085	.0394	1.02756
13	Ebbing	19.92	35.99	.74	9.49	.016	.070	.086	.0396	1.02749
	Flowing	19.92	35.99	.77	9.23	.017	.066	.083	.0385	1.02749
14	Ebbing	19.93	36.00	.88	9.41	.019	.063	.082	.0392	1.02750
	Flowing	19.93	36.00	.77	10.04	.017	.075	.092	.0418	1.02750
15	Ebbing	19.85	35.86	.71	9.33	.016	.069	.085	.0389	1.02739
	Flowing	19.86	35.88	.80	9.56	.018	.068	.086	.0399	1.02741
16	Ebbing	19.91	35.97	.68	9.42	.015	.072	.087	.0392	1.02748
Highest ebbing		19.98	36.09	.....	......	.021	.088	.099	.0427	1.02757
Lowest ebbing		19.85	35.86	......	......	.011	.059	.080	.0387	1.02739
Average ebbing		19.932	36.01	......	......	.017	.070	.087	.0399	1.02750
Average deviation ebbing		±.02	....	......	......	±.002	±.004	±.003	....	....
Highest flowing		19.98	36.09	......	......	.022	.076	.094	.0430	1.02757
Lowest flowing		19.86	35.88	......	......	.013	.060	.080	.0385	1.02691
Average flowing		19.936	36.01	......	......	.018	.068	.086	.0401	1.02749
Average deviation flowing		±.02	....	......	.....	±.002	±.004	±.002	....	....
Highest entire series		19.98	36.09	......	......	.022	.088	.099	.0430	1.02757
Lowest entire series		19.85	35.86	......	......	.011	.059	.080	.0385	1.02691
Average entire series		19.934	36.01	......	......	.017	.069	.086	.0400	1.02750
Average deviation entire series		±.02	....	......	......	±.002	±.004	±.003	±.0008	....
Composite flowing		....	....	.72	9.53	.016	.071	.087	.0399	....
Composite ebbing		....	....	.65	9.60	.014	.075	.089	.0400	....

[1] After heavy shower lasting one hour.

[2] Two determinations; omitted from summary.

SALINITY.

The data in table 1 show that there is no significant or regular difference in chemical composition of the incoming and the outgoing tide. The average chlorine content of the flood water is 19.936 grams per kilogram and the maximum range is only 0.12 gram per kilogram, while the content of the slack water is 19.932 grams per kilogram with a maximum range of 0.13 gram per kilogram. The close agreement of these averages, the narrow range of the values, and the insignificant differences between daily tide contents indicate that there was no essential difference in concentration of the waters during the period in which the samples were collected. These results, with those in table 2, show, however, that the salinity of the sea-water at Tortugas is slightly greater than that of average ocean-water. This greater concentration is doubtless due to high rate of evaporation in the comparatively shallow water.

TABLE 2.—*Chlorine Content and Salinity of Sea-Water at Tortugas, Florida.*

[Grams per kilogram.]

Source.	Date.	Chlorine.	Salinity.
Off Loggerhead Key[1]	1910.	19.60	35.41
Reef, Loggerhead Key[2]	June 1912	19.95	36.04
Southwest Channel[3]	Average for May and June 1913	19.93	36.01
Do.[2]	June 1912	19.99	36.11
Wharf, Fort Jefferson[2]	Do.	19.99	36.11
Off Garden Key[3]	May 25, 1913	19.84	35.84
Do.[3]	June 14, 1913	19.96	36.06
Moat, Fort Jefferson[2]	June 1912	20.09	36.29
Do.[3]	During rain, Jan. 27, 1913.	19.61	35.43
Do.[3]	After rain, Jan. 27, 1913	19.60	35.41
Do.[3]	During rain, Feb. 27, 1913	19.83	35.82
Do.[3]	After rain, Feb. 27, 1913	17.79	32.14
Do.[3]	May 25, 1913	19.67	35.53
Do.[3]	June 14, 1913	19.83	35.82
Do.[3]	June 15, 1913	19.19	34.67
Content of ocean water[4]		19.386	35.02

[1] Computed from report of analysis by G. Steiger, of the U. S. Geological Survey Laboratory; published in The Data of Geochemistry, by F. W. Clarke, Bull. U. S. Geological Survey, 491, p. 113, 1911.
[2] Tested at the Plymouth (England) laboratory.
[3] Tested by R. B. Dole.
[4] Standard P_7 2/2, 1912.

ALKALINITY.

The average alkalinity of water from the Southwest Channel, 0.0400 OH gram per kilogram, is that given by Allen and others for normal sea-water.[1] The average alkalinity of the flood water, 0.0401, and that of the slack water, 0.0399, differ from each other much less than the average deviation of individual observations (±0.0008), and agree with the estimates of alkalinity of the composite flood- and slack-tide samples recorded in the last two lines of table 1. The alkalinity of these waters seems to be practically the same as that of normal sea-water.

The average total content of carbon dioxide of the incoming water is essentially that of the outgoing water, and though the recorded values differ somewhat from day to day the range is not very great or very significant; there is no regular excess of the values of one set over the other. Though the probable error of individual determinations, about 0.0020 gram per

---

[1] Allen, E. J., and E. W. Nelson. On the artificial culture of marine plankton organisms. Quart. Journ. Micros. Science, vol. 55, pt. 2, June 1910.

kilogram, is less than some of the differences, the variations are about what might be expected in a series of examinations of a flowing water.

The quantity of acid required to neutralize the cold sea-water in presence of phenolphthalein proves conclusively that *"free" carbon dioxide, in the ordinary acceptance of that term in America, is not present.* Consequently, the inflowing waters at Tortugas would have no soluble action on deposits of calcium carbonate by virtue of the carbon dioxide they contain. One-half the carbon dioxide in equilibrium as the bicarbonate radicle (HCO_3) is commonly termed the "half-bound" carbon dioxide and that quantity is probably the carbon dioxide referred to as "free" by some writers on the composition of sea-water. So far as can be ascertained from the literature the carbonate radicle (CO_3), but not the free acid, is always present in sea-water; or, as Dittmar expressed it in his computation of hypothetical combinations, the carbon dioxide is more than sufficient to complete the formation of the carbonate but considerably less than is required to form the bicarbonate.[1] Dittmar reports[2] the average alkalinity of 130 samples of ocean water as 54.70 milligrams per liter of CO_2, meaning thereby the combined carbon dioxide (total minus the half-bound acid); the corresponding figure computed from the results at Tortugas is 52.5 milligrams per liter.

Briefly, it may be stated that the condition and the quantity of carbon dioxide in the water entering Tortugas Harbor do not appear to be essentially different from those of the escaping water or normal sea-water. *The inflowing water has no apparent action on deposits of calcium carbonate by virtue of its content of carbon dioxide.*

SEA-WATER AROUND BISCAYNE BAY.

HYDROGRAPHY.

Biscayne Bay ranges from 3 to 8 miles in width and extends north and south of the mouth of Miami River, though lying mostly south of it. It is bounded on the east by low keys and reefs, through which there are numerous narrow channels. It is very shallow, being for the greater part only 8 to 12 feet deep. Featherbed Bank, a shoal, cuts off the northern part of the bay, and coral banks covered with sand extend from Ragged Keys to Key Biscayne. Miami River is a small stream, discharging only about 400 second-feet at the time of sampling.

COMPOSITION OF THE WATER OF MIAMI RIVER.

No analyses of water from Miami River above tidal influence are available, but as it receives drainage from the Everglades its water is doubtless similar in concentration and composition to that of Lake Okeechobee and Fort Lauderdale Canal, analyses of which are quoted in Table 1. These are analyses of calcium-carbonate waters of low mineral content carrying considerable organic matter. Normally Miami River may be expected to contain a small amount of free carbon dioxide and no carbonate (CO_3).

---

[1] Quoted by Fox, C. J. J. Conseil permanent international de la mer, pub. de circonstance 44. February 1909.

[2] Dittmar, William. The alkalinity of ocean water. Report of the voyage of *H. M. S. Challenger* 1873-76, vol. 1, p. 124.

TABLE 3.—*Composition of Drainage from the Florida Everglades.*[1]

[Milligrams per liter.]

	North New River Canal, at lock 6 miles above Fort Lauderdale.	Lake Okeechobee, 3 miles north of Ritta Island.
Total solids at 180° C.	130	183
Total solids at dull red heat	126	143
Organic and volatile matter	4	40
Silica (SiO_2)	8.2	8.2
Iron (Fe)	.03	.03
Calcium (Ca)	26	31
Magnesium (Mg)	6.7	7.0
Sodium (Na)	19	16
Potassium (K)	2.0	2.0
Carbonate radicle (CO_3)	.0	4.8
Bicarbonate radicle (HCO_3)	94	104
Sulphate radicle (SO_4)	4.1	7.3
Chlorine (Cl)	26	28
Nitrate radicle (NO_3)	.1	.1
Color	32	41

[1] Samples collected in June 1913, by R. B. Dole; analyzed by W. T. Read.

TESTS OF BAY WATERS.

Samples were collected in or just outside Biscayne Bay at the points shown on the accompanying map and the chemical tests of them are recorded in table 4.

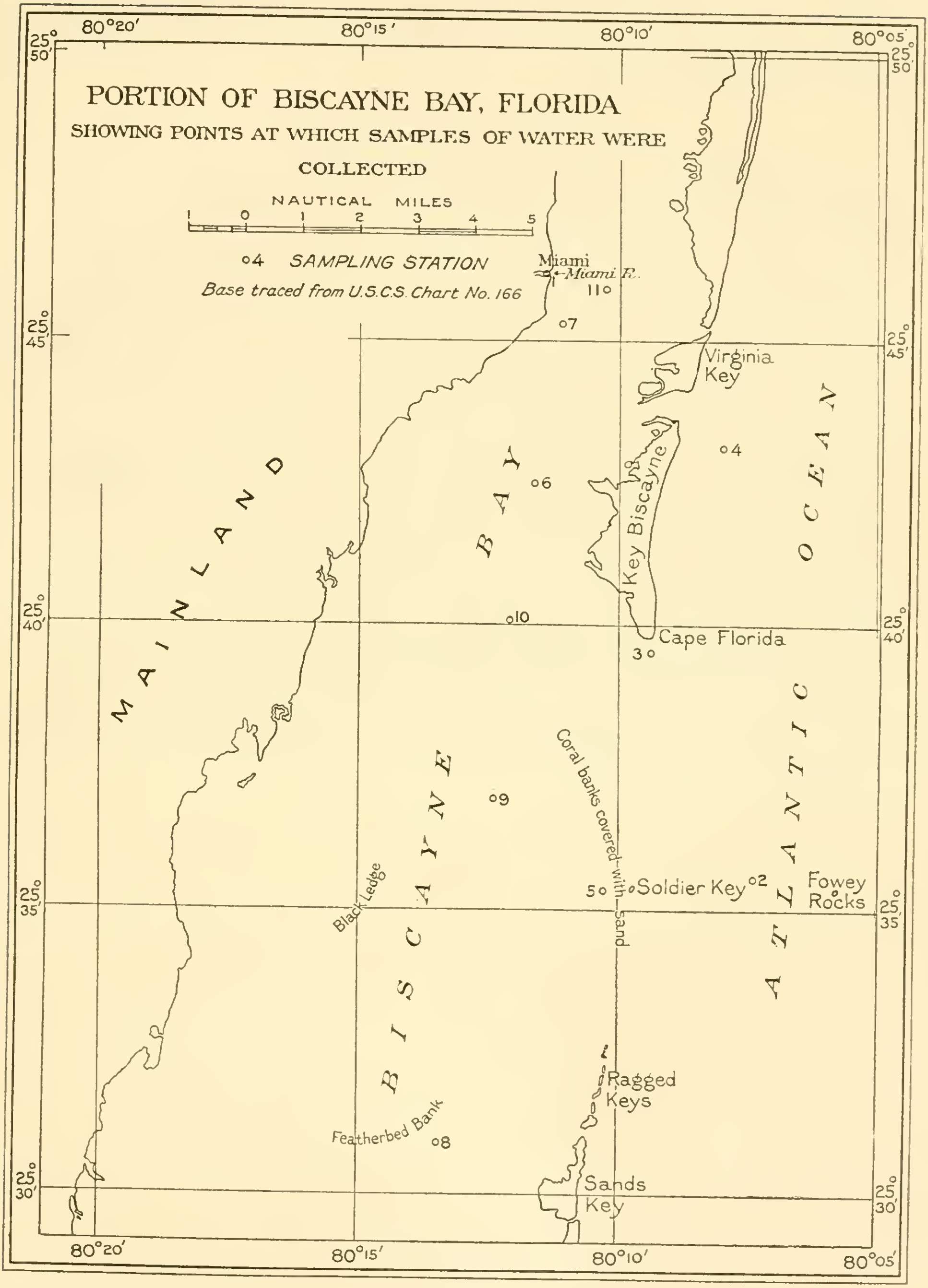
TABLE 4.—*Some Chemical Characteristics of Sea-Water Around Biscayne Bay, Florida.*

[Samples collected June 23, 1913, by R. B. Dole; analyses by E. C. Bain.]

No.	Location.	Temp. of water.	Time.	Carbon dioxide (CO_2) present as carbonate (CO_3).	Carbon dioxide (CO_2) present as bicarbonate (HCO_3).	Total alkalinity in equivalent OH.	Chlorine.	Calculated salinity.	Specific gravity calculated (17.5°).	Specific gravity determined (25°).
		° C.		Grams per kilogram.						
1	Mouth Miami River inside bar near Royal Palm dock	26.3	4^h30^m a.m.	Tr.	0.232	0.078	1.42	2.59	1.0020	1.0023
11	1.5 miles east of Miami at 11 ft. depth in government channel north of Virginia Key	27.3	2 00 p.m.	0.022	.068	.043	14.73	26.62	1.0203	1.0197
7	Off Cormorant Point (tide ebbing)	26.6	4 45 a.m.	.018	.091	.049	13.35	24.13	1.0184	1.0184
6	1 mile west of west point of Key Biscayne near inside P & O marker	27.2	5 30	.013	.083	.043	16.80	30.35	1.0232	1.0228
10	0.25 mile west of Old Man Beacon	26.0	6 00	.023	.064	.043	18.79	33.95	1.0259	1.0256
9	3 miles northeast of Black Ledge	27.3	7 00	.026	.047	.038	20.33	36.73	1.0281	....
5	0.5 mile west of Soldier Key	27.0	9 00	.018	.064	.039	20.28	36.64	1.0280	1.0279
8	In channel through Featherbed Bank	26.4	8 00	.018	.037	.028	20.28	36.64	1.0280	1.0278
2	1.5 miles west of Fowey Rocks Light, outside bay	26.9	11 00	.026	.083	.053	19.93	36.00	1.0275	1.0270
3	In channel south of Key Biscayne and 0.5 mile south of Old Florida Cape Light, outside bay	27.2	11 45	.026	.033	.032	19.83	35.82	1.0274	....
4	At red buoy outside bar across entrance to Bear Cut, a mile southeast of Virginia Key; outside bay	27.7	1 15 p.m.	.026	.055	.042	19.99	36.11	1.0276	1.0274

DETERMINED AND CALCULATED DENSITIES.

No particular importance can be given to the relatively slight differences between the determined and calculated densities, especially in view of the absence of several duplicate determinations on each sample. On the other hand, the fairly close agreement of the estimates indicates that the density of sea-water, even when largely diluted by river water, may be used in


PORTION OF BISCAYNE BAY, FLORIDA
SHOWING POINTS AT WHICH SAMPLES OF WATER WERE COLLECTED
NAUTICAL MILES
1 0 1 2 3 4 5
o4 SAMPLING STATION
Base traced from U.S.C.S. Chart No. 166
80°20′
80°15′
80°10′
80°05′
25° 50′
25° 45′
25° 40′
25° 35′
25° 30′
Miami
Miami R.
11
7
Virginia Key
4
6
Key Biscayne
10
Cape Florida
3
MAINLAND
BAY
BISCAYNE
ATLANTIC OCEAN
Coral banks covered with sand
9
Black Ledge
5
Soldier Key
2
Fowey Rocks
Ragged Keys
Featherbed Bank
8
Sands Key

place of the directly determined density in computation of the chemical analysis. Obviously, however, the relation could not be depended upon for inland saline solutions, which vary greatly in the percentage composition of their anhydrous residues.

DIFFERENCE IN CONCENTRATION.

The salinities of the three samples taken outside the reefs (2, 3, and 4) agree closely with each other and with the salinity of gulf water at Tortugas, Florida (36.01), which is somewhat greater than that of standard ocean water (35.02). The water in the south part of the bay is somewhat more concentrated, samples Nos. 9, 5, and 8 having salinities of 36.73, 36.64, and 36.64, respectively. This evidence that the water in this part of the bay is concentrated by evaporation during its retention in the shallows serves further to indicate that circulation there is not very rapid and that the greater bulk of the water inside the keys is not thoroughly mixed or shifted by the tides. The inside samples only as far south as Old Man Beacon give evidence of dilution by fresh water; therefore it may be concluded that, at least at the time these samples were collected, the effect of Miami River on the water of the bay did not extend south of Soldier Key nor outside the keys. Sample 1 has a salinity obviously higher than the pure water of Miami River alone may be expected to have, and represents admixture with bay water; carbonates are absent from it, but bicarbonates are much higher than in the normal drainage from the Everglades and may be attributed to reaction of the carbon dioxide that the river water carries. In all other samples normal carbonates are present as in sea-water and *free carbon dioxide is entirely absent*, but there are wide differences in the alkalinity from point to point.

VI.

OBSERVATIONS UPON THE GROWTH-RATE AND OECOLOGY OF GORGONIANS.

BY LEWIS R. CARY,

Instructor in Biology, Princeton University.

Two plates.

OBSERVATIONS UPON THE GROWTH-RATE AND OECOLOGY OF GORGONIANS.

By Lewis R. Cary.

The following account includes the record of observations, extending over a period of three years, upon the growth-rate of three species of gorgonians under the natural environmental conditions found on the reefs about Dry Tortugas, Florida. The œcological data have been secured in the same periods of observation and are supplemented by observations made at Montego Bay, Jamaica.

RATE OF GROWTH OF GORGONIANS.

The records of the growth-rate of *Gorgonia flabellum* and *Plexaura flexuosa* are for specimens occurring on the reefs immediately surrounding Loggerhead Key, the location of the Tortugas laboratory. All of the specimens have been allowed to remain in their original place of attachment except those shown in the accompanying plates, the measurements of which are given in table 2. These were cemented to tiles in order that they could be more easily photographed from time to time to afford a visual as well as a linear record of their growth.

Table 1.

Specimen No.	Gorgonia flabellum.					
	Height.				Increase from—	
	June 1910.	Jan. 1911.	June 1911.	Aug. 1912.	1910–11.	1911–12.
	mm.	*mm.*	*mm.*	*mm.*	*p. ct.*	*p. ct.*
1	[1]100	135	150	gone	50	....
2	[1]100	138	150	155	50	3.33
3	[1]70	100	145	183	107.14	26.20
4	300	....	300	374	10	10.30
5	150	....	219	245	46.38	12.38

Specimen No.	Plexaura flexuosa.					
	Height.				Increase from—	
	June 1910.	Jan. 1911.	July 1911.	Aug. 1912.	1910–11.	1911–12.
	mm.	*mm.*	*mm.*	*mm.*	*p. ct.*	*p. ct.*
1	80	105	135	175	68.77	29.62
2	150	....	155	210	3.3	35.48
3	50	65	83	101	66.66	21.68
4	245	....	269	287	9.7	6.69
5	115	150	163	183	41.39	12.27

---

[1] These specimens had been exposed to the air for a long time during an exceptionally low tide on June 6, 1910, so that the height given in the table does not represent the actual growth since attachment, but the amount living at that time.

The most complete records of the growth of specimens of *G. flabellum* and *P. flexuosa* among my data are those for some specimens growing upon a single coral head (*Orbicella annularis*) some 12 feet in diameter, situated about 200 yards west from the laboratory upon a shallow reef. Table 1 shows the growth-record for the period since June 1910, and gives the original size and the change in height of the same specimens of gorgonians after 7 months, 1 year, and 2 years from the time of first measurement; with the percentage of increase in height for the 2 years.

Similar records of individuals of the same species growing upon tiles, photographs of which constitute a part of this report, are shown in table 2.

TABLE 2.—*Heights of gorgonians attached to tiles to show growth in a year.*

Tile and species.		July 1911.	Aug. 1912.	Per cent increase.
		mm.	*mm.*	
Tile 1	G. flabellum	65	148	127.69
	P. flexuosa	130	150	15.38
Tile 2	P. flexuosa (*a*)	145	175	20.62
	P. flexuosa (*b*)	70	120	70.43
Tile 3.	G. flabellum	41	124	202.43

All of the specimens recorded in table 2 were selected without any special reference to size, as at that time no data were at hand to afford the basis for a correlation between size and age. Small (young) individuals of either of the above-listed species were so rarely found on the reefs during the period of observation in June 1910 or July 1912 that, although the specimens on any of the reefs studied could be readily arranged into a series of groups, each containing individuals of about the same size, the relation in respect to age among the several groups could not be determined with certainty.

The study of the same areas of reef in August 1912 showed the presence of a considerable number of small specimens of both species. On the coral head west of the laboratory there was found on August 21, 1912, seven specimens of *P. flexuosa*, which had become attached, or at least had become noticeable, since July 23, 1911. The length of these specimens, in order of magnitude, was 25 mm., 26 mm., 31 mm., 32 mm., 42 mm., 42 mm., and 46 mm., respectively. Beside these there was found a single young specimen 3 mm. in length, which consisted of only two calyces and polyps. The identification of this specimen as *P. flexuosa*, which is based upon the character of the spicules and that of the orifice of the calyx, is at best uncertain. The specific identity of the specimen is of considerable interest in connection with other data bearing on the time and duration of the breeding season, as will be pointed out in the section of this paper dealing with œcology.

On a shallow reef east of Loggerhead Key, where measurements of all gorgonians had been made yearly since 1910, there were found 15 specimens of *P. flexuosa* less than 50 mm. in length. These were not of a recognizable size, if present, when the measurements were made over the same area in July 1911.

Upon the last-mentioned reef 26 specimens of *G. flabellum*, less than 65 mm. in height, were also found, which were not recognizable when the measurements were made in July 1911.

On the basis of these observations, in conjunction with the records given in tables 1 and 2, it becomes possible to make the records complete for at least two years in the case of *G. flabellum* (fig. 8, plate 2). Observations after another year's growth will, moreover, fill in the stages to complete the record for six years.

All specimens of *G. flabellum* and of *P. flexuosa*, on a reef east of Loggerhead Key, were measured in July 1911 and again in August 1912. Most of the individuals, as already mentioned, fall into natural "size groups," which for convenience have been designated as follows: Group 1, 0 to 75 mm.; group 2, 75 to 150 mm.; group 3, 150 to 300 mm.; group 4, 300 to 450 mm.; group 5, 450 to 600 mm.; group 6, 600 + mm. As shown in table 3, the percentage of individuals in groups 1 and 2 varied markedly in the two seasons, while the number of the larger specimens was proportionately similar for the two years.

TABLE 3.—*Size groupings as shown by measurements of all individuals on a single shallow reef.*

Species and date.	Group 1.	Group 2.	Group 3.	Group 4.	Group 5.	Group 6.
	p. ct.	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*	*p. ct.*
G. flabellum, 1911............	0	7.35	36.76	30.88	16.17	8.82
G. flabellum, 1912............	15.4	10.61	29.70	22.02	18.45	3.59
P. flexuosa, 1911.............	0.62	8.06	45.16	37.09	6.54	0.62
P. flexuosa, 1912.............	8.33	17.77	44.44	23.88	5.00	0.55

The observations upon the breeding season and the attachment of the planulæ are intimately connected with those in relation to the absence of small (young) specimens of gorgonians during the seasons of 1910 and 1911. In June 1910 almost every colony of *P. flexuosa* examined was carrying mature eggs which could be stimulated to development by the use of chemicals which are ordinarily efficacious in bringing about artificial parthenogenesis. None of the planulæ among those to be obtained in the tow net could with certainty be identified as those of this species, nor could any of the colonies be kept long enough in aquaria to secure planulæ. The evidence from artificial parthenogenesis is, however, enough to establish the fact that the breeding season was in progress at that time.

In July 1911 some of the colonies of *P. flexuosa* contained ripe eggs, but the greater number were without apparent gonads. Late in August 1912 not a single specimen was found in which gonads were recognizable, although more individuals were examined to determine this point than in either of the other years. The breeding-season for *P. flexuosa* is, then, apparently at its height in June. The number of individuals with ripe sexual products diminishes rapidly through July, while by the latter part of August the breeding season is over for any given year. On August 21, 1912, a young specimen, probably of *P. flexuosa*, was found, the size of which (3 mm. in height) was such that it would have been overlooked had it not been growing in a location where its color was in striking contrast to the background of white coral.

To apply these facts to the observed scarcity of yearling specimens in 1911, which was a general occurrence over all of the reefs visited in the regions about Tortugas, it is necessary to take into account a severe hurricane which occurred on October 16, 1910. The destruction of adult gorgonians by this storm is known to have been very severe upon certain reefs and the amount of débris moved over the bottom in shallow water was very great, which in itself would account for the destruction of the very young specimens at that time. In July 1911 there would be no easily recognizable young which had set during the same season, and only very rarely had any of those from the set of the year before been able to survive the destructive effects of the hurricane. In August 1912, on the other hand, young specimens of several gorgonians, besides the two above discussed, were found upon every considerable reef examined. This would seem to show that the setting of a considerable number of young was the usual occurrence. That the number of young found during the past season on the reefs, which had been carefully examined each season for three years, may be greater than would ordinarily be found might be inferred from the breeding habits of some other sedentary invertebrates, especially the Mollusca, where after a season, when for any cause the set is below normal, an especially heavy set is to be expected the following year.

ATTACHMENT OF PLANULÆ.

Vaughan's observations on the attachment of coral planulæ[1] show that for effective attachment they must settle in a place protected from too rapid currents and wave-action, where the bottom is rough, and where other more rapidly growing organisms are least likely to obtain a foothold.

For the effective attachment of the planulæ of the gorgonians studied the roughness of the bottom, *i. e.*, the presence of small depressions or cracks into which the planulæ could settle, appears to be the most important factor. In every instance the one-year old specimen had its base in a depression. Frequently the depth of the point of attachment below the surface of the rock was more than half the length of the colony. The single (very small) specimen found, when it consisted of only one or two calyces, was entirely below the level of the surface of the coral head to which it was attached. Many of the adult colonies have their point of attachment at the bottom of a crack of considerable depth, so that, on the basis of the observed growth for a year, they must have remained below the general level of the bottom until more than one year old. In the later growth of the gorgonian colony its non-polyp-bearing basal portion spreads beyond the

---

[1] Carnegie Institution of Washington Year Book No. 10, pp. 151–152.

limits of the crack over the bottom, so that its apparent height is not measured from its original point of attachment.

On the shallow reefs, where the gorgonians are most abundant, the amount of algæ, bryozoons, and other incrusting organisms appears to vary only slightly during the different seasons of the year. In no observed instance did these organisms seem to form a mass dense enough to exclude a sufficient amount of water for the well-being of the young gorgonian colony. Frequently the fronds of algæ extend beyond the free ends of the gorgonian colony, but the specimens found in such locations appear, to judge from comparative measurements, to have suffered no harm from being so closely surrounded.

In comparison with the young coral polyp the gorgonian colony has an obvious advantage in that its most rapid growth is perpendicular to the surface of the substratum, which would keep the most rapidly growing part in a position favorable for the securing of food and oxygen.

On the sea-bottom, away from the shallow reefs, gorgonians are generally found as scattered specimens or in groups of at most only a few individuals. These colonies will almost invariably be found to be attached to some irregular mass of rock which affords the protecting cavity necessary for the permanent attachment of the young gorgonian.

DESTRUCTIVE AGENTS.

Of the destructive agents to which the gorgonians are subjected the wave-action during severe storms is apparently by far the most important. The wave-action developed by the ordinary northeast trade-winds during the winter months is of sufficient force to cause the destruction of many colonies which have a comparatively weak attachment. The tendency for any colony to be torn away will increase from year to year as its surface area becomes increasingly larger.

An opportunity to study wave-action at its maximum severity was afforded the writer in January 1911, and later, in July of the same year, when the observations made during the first visit were confirmed and extended to a much greater area. The hasty observation made in January shows that, as the result of the hurricane of the previous October, there had been a great destruction of gorgonians on the reefs about Tortugas. On the east shore of Loggerhead Key, the only one visited at that time, many specimens of some five or six species of gorgonians were found thrown up on the beach along its entire length. At that time no estimate of the number cast up was made nor was the area visited sufficient to give conclusive evidence of the proportion of colonies carried from their natural location. In July 1911 the observations on these points were extended to cover a large area of shore-line and submerged reef.

At one point on the inside of the east reef, near Bush Key, the gorgonian skeletons were counted over a strip of beach 112 yards in length, where there was a windrow, perhaps a yard wide, made up of these skeletons. The number of skeletons in a linear yard (it was practically a square yard) averages 75.7 for ten counts made at approximately equal distances through the above-mentioned distance, or nearly 8,500 colonies for the whole area. This area showed very clearly that the most destructive part of the storm came from nearly northeast. On the outside of the reef, in the direction indicated by the wash of the storm, only two living colonies of gorgonians were found for as far off-shore as the water was sufficiently shallow to allow one to wade about over the reef. Gorgonians were growing abundantly over this area when it was visited in 1910, so the destruction had been almost complete. That the great number of the colonies found in the windrow on the beach had come from this shallow-water area was shown by the fact that in deeper water on the outer portion of the reef there was little evidence of the lessening of the number of colonies below the normal number for such locations; the colonies here are always comparatively scattered, never forming dense "thickets," as they do on the reefs in shallow water. The very shallow water on the outside of the reefs contained a considerable number of skeletons of *Gorgonia flabellum* and *Plexaura flexuosa*, which had been broken off from their supports and carried away from their original location while still attached to a good-sized piece of coral rock. Apparently these specimens had reached their present location at a time when the wave-action had become insufficient to carry them over the crest of the reef onto the beach on the lagoon side. By far the larger number of specimens on the beach, on the lagoon side of the reef, were still attached to a piece of coral rock, usually of small size. In almost every instance the skeleton shows that the colony was complete when washed on shore. Any physical injury undergone had not been to the extent of having branches broken off or, in the case of *G. flabellum*, having suffered any tearing of the blade-like portion of the colony.

On the east side of Loggerhead Key, where the greatest force of the storm came across comparatively shallow water, the reef just mentioned being about 3 miles distant, most of the specimens, when examined in January 1911, had the usual spicule-bearing tissues present, although considerably macerated in many instances. None of these colonies showed any considerable amount of injury, such as the loss of branches or the tearing of the living tissue from the skeleton.

None of the common gorgonians of the Tortugas region can be kept alive for any considerable time after they have been broken off from their natural support and allowed to fall over into a horizontal position. When such a colony is put into a live-car, where most of the other marine invertebrates and practically all of the sedentary Cœlenterates can be kept alive for an indefinite period, it will be only two or three days before maceration sets in. It seems apparent, therefore, that the greatest destruction by storms comes from the tearing of the gorgonian colonies from their natural supports rather than from any laceration of the tissues.

On the reef where the measurements previously mentioned were made, a considerable number of colonies were carried away during the storm. Of the remaining colonies, many were found in January 1911 which had suffered laceration to a considerable extent. The most common injury observed was a destruction of the living tissues of the colony, such as would result from twisting a specimen in one's hand while holding it firmly by each end. The loss of branches in the branched forms, or the tearing of the skeleton of the leaf-like portion of *G. flabellum*, was a very unusual occurrence. The injuries caused by the twisting from the wave-action were quite evenly distributed among the different species growing on this reef. Such injuries often involve as much as half the total surface-area of each colony. In all large colonies, of whatever species, the injury was greatest over the basal portion, while the outer end or branches were usually uninjured. At the time of the examination in January 1911 there had been comparatively little ingrowth of new tissue over the denuded areas, so that the extent of the injury to any colony could be readily determined.

When the same specimens were re-examined in July 1911, in at least 50 per cent of the specimens noted as injured at the time of the earlier observations, the reparation had been so complete that there was no longer any evidence of injury. In all of the colonies where the injury consisted in the removal of living tissue from about the base of the skeleton, there was yet an area where the skeleton was exposed. In all cases where the injury was of this nature there was no evidence of any growth of the living tissue down over the naked skeleton. The exposed skeleton was usually covered with a dense growth of algæ, bryozoa, or hydroids, so that there seemed to be no probability that it would again be covered with the normal tissues.

The examination of the same individuals in August 1912 showed comparatively little change since the previous summer. In some instances the cœnenchyma had grown down over the naked skeleton for some little distance, but usually the basal portions of the skeleton were, just as at the last examination, covered with algæ, incrusting bryozoa, etc.

The leaving exposed of areas of the skeleton near the base of the colony may have a causal relation to the fact that, on all of the shallow reefs, gorgonians are found which are to a greater or less extent covered by an overgrowth of *Millepora alcicornis*. In most cases the *Millepora* surrounds what was really the basal portion only of a gorgonian skeleton. Not at all uncommonly, however, a colony of *Millepora* is found which covers a skeleton of *Gorgonia flabellum*, in which the mesh-work of the skeleton of the "leaf" could be made out in all its details. Frequently the relation between the height and width of the colony, as well as the characters of its outline, showed that the *Gorgonia* had not suffered any disintegration before being covered by the *Millepora*. As in a small number of instances the *Millepora* was observed growing up about the naked skeleton at the base of the *Gorgonia* colony, and as the complete naked skeleton of such a colony is very rarely found in its natural attachment on the reef, it seems almost certain that the *Millepora* must have, on account of its more rapid growth, covered over and destroyed the living tissue of the colony.

A skeleton thus incrusted with *Millepora*, which was complete in structural detail in July 1911, had by August 1912 been reduced to about one-third of its original height. Nothing of the *Gorgonia* skeleton beyond the stouter branches remained. The whole of the "leaf" had been broken down, presumably by the weight of the incrusting *Millepora*.

The previously mentioned hurricane was, as had been pointed out in dealing with the growth-records, sufficiently prolonged to destroy almost every young gorgonian which had become attached during the breeding-season of that year. No evidence could be secured to determine whether the destruction took place by an actual washing of the colonies from their attachment or by the shifting of the easily movable material—algæ, sediment, shells, and even quite large fragments of coral rock—which by filling up all cracks in the surface of the reef would have been sufficient to smother the small individuals.

Gorgonians growing upon the shallow reefs are, with more or less regularity, subjected to exposure to the air. In summer the uncommonly low spring-tides (when the low full-moon tide comes in the late afternoon) most frequently come on calm days, when the exposure is most destructive. On June 6 and 8, 1910, and again on July 23, 1911, all of the shallow reefs were exposed for a space of time sufficient to destroy the superficial tissues of most corals and gorgonians which grew on the highest part of the reefs. While all of the species of gorgonians studied suffered to a greater or less extent, the injuries were most severe in the case of *G. flabellum* and *G. acerosa*. Frequently there resulted the death of the distal half of the colony which, within a few days after its exposure to the air, would slough off from the uninjured proximal part. *Plexaura* and *Eunecia* were much less frequently injured, the latter in only two observed instances, and then only after prolonged exposure. The ability of the two last-mentioned forms to withstand the exposure is at least correlated with, if not dependent upon, the thickness and toughness of the cœnenchyma into which the polyps may be retracted when the colony is exposed.

In all observed instances of injury from exposure to the air the uninjured portions of the colony showed no ill effects from the injury of the distal portion and their growth was at least as rapid as in an uninjured specimen.

REGENERATION EXPERIMENTS.

The injuries occurring in nature are so variable and are besides so entirely uncontrollable that a series of experiments was undertaken in order to secure more definite data concerning the capacity for regeneration in these animals. All of the experiments here described were extensive in nature, usually involving skeleton and cœnenchyma as well as the polyps. In short, they were made to simulate the injuries to which the gorgonians are subjected under natural conditions on the reefs.

Table 4 shows the nature and extent of the operations performed upon the gorgonians used in the regeneration experiments and the extent of recovery at different times after the operations.

Table 4.

Species and specimen Nos.	Operation June 1911.	Recovery.		
		January 1911.	July 1911.	August 1912.
G. flabellum:				
No. 1....	One-half cut from each leaf (longitudinally).	Healed, no regeneration.	No lateral growth....	No change.
No. 2....	Split lengthwise into 5 pieces.	Edges healed........	0.25 inch lateral growth.	0.5 inch lateral growth.
No. 3....	Circular pieces cut from leaf.	Edges healed........	0.25 inch in growth...	Spaces nearly filled with new tissue.
No. 4....	Cut back one-half (6 in. remaining).	Healed over; had grown to 7.5 inches.	9.5 inches long, distal end of leaf rounded.	12.25 inches long.
P. flexuosa:				
No. 1....	Side branches cut off, central ones slabbed on one side, exposing the skeleton.	Had healed over the cut places; new polyps appearing in the scar-tissue.	Polyps now cover all stripped areas. New branches (8) have come in on stumps of cut branches.	No change.
No. 2....	Cut back from 11 inches to 6 inches.	Ends of branches healed over. Now 7.25 in. high.	Now 10 inches high...	13 inches high.
G. acerosa...	One side of all branches trimmed and slabbed.	No new branches. Scar-tissue covers all wounds. No polyps on scar-tissue of larger branches.	Polyps have appeared in scar-tissue on all smaller branches but not on any of the larger branches.	No change.

Pieces of the regenerating branches of *G. acerosa* were preserved when the reefs were visited in January 1911 and sections of this material cut and studied. In this species there is always found a complete layer of cœnenchyma over a denuded area which remains free from polyps for some time. The entodermal canals keep pace with the formation of the other tissues, but it is only after a considerable time that the bud-like swellings of the canal, which mark the points of origin of new polyps, make their appearance. They always follow the same sequence as that shown in the formation of new tissue over a denuded area, appearing first at the periphery of the wound nearest to the uninjured polyps. The formation of new skeletal tissue at the cut ends of the branches takes place very slowly at first. After the new rod of skeletal tissue has reached a diameter equal to that of the older portion the elongation of the branch takes place rapidly. If the living tissue be removed from about the base of the colony, there is, so far as my observations go, little down-growth of the tissues from the cut surface over the naked skeleton.

EXPLANATION OF PLATES.

The disks to which the specimens photographed are attached are 8 inches in diameter. While the reduction is not exact in every instance, the diameter of most of the disks in the reproductions is about 2 inches, making the specimens approximately 0.25 natural size.

PLATE 1.

1. Tile 1. A, *Plexaura flexuosa;* B, *Gorgonia flabellum;* C, *Eunecia* sp. Photographed August 1911.
2. Tile 1. Specimens same as above. Photographed August 1912.
3. Tile 2. A and B, two specimens of *Plexaura flexuosa.* Photographed August 1911.
4. Tile 2. Same as in figure 3. Photographed August 1912.
5. Tile 3. A, *Eunecia* sp.; B, *Gorgonia flabellum.* Photographed August 1911.
6. Tile 3. Same. Photographed August 1912.

PLATE 2.

7. Tile 8. A, *Eunecia* sp.; B, *Plexaura flexuosa;* C, *Eunecia* sp. Photographed August 1911.
8. Tile 8. Specimens as in figure 1. Photographed August 1912.
9. Tile 7. A, *Plexaura flexuosa;* B, *Eunecia* sp.; C, *Gorgonia flabellum.* Photographed August 1912. See figure 13.
10. Tile 15. A, *Eunecia* sp.; one year old, B, *Gorgonia flabellum,* one year old. Photographed August 1912.
11. Specimen of *Plexaura flexuosa,* one year old; 0.5 natural size. Photographed August 1912.
12. Tile 16. One-year old specimens of *Plexaura flexuosa.* Photographed August 1912.
13. Tile 7. Specimens as in figure 9. Photographed August 1911.
14. Tile 18. A, One-year old specimen, and B, a two-year old specimen of ***Gorgonia flabellum.*** Photographed August 1912.

1

2

3

5

4

6

7

8

9

10

11

12

13

14

VII.

GROWTH-CHANGES IN BRITTLE STARS.

By HUBERT LYMAN CLARK.

Three plates.

GROWTH-CHANGES IN BRITTLE-STARS.

By Hubert Lyman Clark.

INTRODUCTION.

Although the systematic work of Ljungman, Lütken, Lyman, and Kœhler, which has brought to light hundreds of species of brittle-stars, has been of a very high quality, the real interrelationships of the genera and families within the group are still virtually unknown. Indeed the definitions of most of the families and of many of the genera are so hazy as to be exasperating, and the more one studies the system at present in use the more assured one becomes that it is artificial and unnatural. The first step towards a rational classification was that taken by Bell (1892), when he divided Recent ophiurans into three orders, based on the character of the arm-vertebræ. Unfortunately his subdivision of these orders is not so satisfactory, yet no one has attempted any essential improvement on it. Whether the orders proposed by Bell represent natural groups which have a definite place in the phylogenetic history of the brittle-stars has not yet been critically determined; we can only say that they seem to be such.

Although the chief reason why our classification of the brittle-stars is so unsatisfactory is undoubtedly because no sustained attention has been given to the problems involved, there are subsidiary reasons which should not be overlooked. One of these is that the class shows a rather remarkable morphological homogeneity so that the differential characters which undoubtedly exist are very considerably overshadowed by the extraordinary development of species in the group, and as a consequence the systematic work hitherto done has been almost exclusively concerned with the description of new forms.

A second reason why so little progress has been made towards the natural classification of the group is because the development of so few species is known and in nearly all the known cases attention has been centered on the larval structures or on the metamorphosis. Until very recently the wealth of important data to be found in post-larval stages has been almost wholly overlooked, largely, no doubt, because suitable material is not easily obtained. But Ludwig (1899) and, more recently, Mortensen (1912) have made notable contributions to our knowledge of these most interesting stages.

A third reason why our progress has been so slow is the comparatively small amount of paleontological evidence available, together with the tendency of zoologists to ignore such evidence as there is. Recent work by the Sollases (1912) is an encouraging step along the right lines.

Finally, no attention whatever has been paid to localized stages, the importance of which, in both plants and animals, was pointed out by Jackson (1899) some years ago. They are remarkably well shown in the ophiuran arm, and the attempt is made in the present paper to point out some of them; the chief difficulty is our lack of knowledge, save in a very few species, of the ontogenetic stages with which to compare them.

Brittle-stars are conspicuously common on the reefs and shores of Jamaica, and when I was invited to make use of the marine laboratory of the Carnegie Institution of Washington, located, during February and March 1912, at Montego Bay, Jamaica, I very gladly availed myself of the opportunity, determined to secure, if possible, material which would throw light on the post-larval development of some brittle-star.

I wish to express here my thanks to the authorities of the Museum of Comparative Zoölogy for the necessary leave of absence from my duties there.

Material was easily secured at Montego Bay and young stages were obtained of three different brittle-stars. The purpose of the present paper is to report the results of my studies on these three species, to sum up our present knowledge of the post-larval development of brittle-stars, and to suggest a few conclusions that may be drawn from this knowledge which will be of service in future work.

MATERIAL.

Although species of *Ophioderma* and of *Ophiocoma* are the most common brittle-stars at Montego Bay, no really youthful stages of species of these genera were found. As *Ophiocoma* is known to breed in the early summer, and *Ophioderma* is also a summer breeder, at least farther north, it is quite probable that the season of the year was the reason why the young of these genera were not found. This was to be regretted, since these genera represent widely different families and in neither is there any species whose development is known beyond the metamorphosis. Grave (1900) has worked out the early development of *Ophioderma brevispina* from material collected near Woods Hole, Massachusetts, and has published a preliminary account (1898) of the early stages in *Ophiocoma echinata*. In neither case, however, were post-larval stages available, and I had therefore hoped it might be possible to supplement Grave's work from material obtained at Montego Bay. Although disappointed in this respect, I had the good fortune to find that in the seaweed and fixed animal life (sponges, hydroids, ascidians, etc.) which form great masses on the mangrove roots, at the Bogue Islands, west of Montego Bay, brittle-stars literally swarmed. Of these the commonest was *Ophiactis savignyi* (Müller and Troschel), which was exceedingly abundant in the cavities of a red sponge, individuals of all sizes, from young with disk barely a millimeter across up to adults whose disk exceeded 5 mm., occurring by the hundred. In the same sponge there also lived, although not in anything like the same abundance, the widely distributed and well-known *Amphipholis squamata* (Delle Chiaje), whose early development and metamorphosis have been studied by both Fewkes (1887) and Ludwig (1881). I secured a good series of this species and, owing to its viviparous habit, was able to get some very young material.

The third species of brittle-star of which I secured young also inhabited this red sponge and the adults and half-grown specimens were very abundant. It is *Ophiothrix angulata* (Say), a well-known West Indian species of a cosmopolitan genus, particularly interesting because it is the type genus of one of the very few well-characterized families of brittle-stars. Apparently *Ophiothrix* was not breeding, as *Ophiactis* and *Amphipholis* appeared to be, and the young were very scarce. But enough were obtained to throw considerable light on the post-larval development of the species.

METHODS.

When the abundance of *Ophiactis* in the red sponge was discovered, it was hoped that they could be kept in aquaria and studied as living material, but this proved to be impracticable. If they were removed from the sponge and put in clean water by themselves, they soon became sluggish and died in a comparatively short time; few lived more than 24 hours. On the other hand, if pieces of the sponge were placed in aquaria, the water became foul with astonishing rapidity and the death of all animals speedily ensued. The observations made on the brittle-stars in life were therefore of little importance. Material was preserved for further study by the very simple method of killing with alcohol, or with formalin in which corrosive-sublimate was dissolved, after the animals had been narcotized with magnesium sulphate (Mayer's method). The best material proved to be that which had been killed and preserved in alcohol. As the calcareous plates were the parts particularly desired for study, of course any acid reagent was out of the question. Work on the preserved material has been greatly facilitated by the use of sodium hypochlorite. This alkaline reagent is so powerful a solvent of organic matter that when used in full strength it will reduce a small brittle-star to a heap of calcareous particles in a few minutes. But as it may be diluted with water and mixes readily with glycerine without affecting the "clearing" properties of the latter, it can be perfectly controlled, and the solution of the organic matter and the separation of the calcareous plates can thus be accomplished as rapidly or as slowly as one wishes. Usually glycerine served as a clearing agent, but occasionally better results were obtained from the use of xylol. The latter, however, will not mix with the hypochlorite.

Attention has been centered on the skeleton, since it is well-known that in all echinoderms, except holothurians, modifications of the skeleton almost always accompany changes in any of the soft parts. This is particularly true apparently of ophiurans, the only soft parts which show any evident modification without corresponding skeletal changes being the podia (tube-feet), and even they show relatively little diversity.

The investigations have been strictly confined to growth-changes, as indicative of relationships within the class. I have intentionally avoided, on the one hand, any discussion of *histological* changes, partly because this was aside from the ends in view and partly because such changes have been so ably and fully described for *Ophiactis* by Simroth (1876). On the other hand, I have not entered into any discussion of the homologies of the skeleton in ophiurans as compared with starfishes, nor of the homologies of the jaws, as compared with the arms, since Ludwig's (1878, 1879, 1880, 1881) work has rendered any such contribution on my part quite superfluous. Suffice it to say that in all of my work I have had the homologies suggested by our Nestor of echinoderm morphology constantly in mind, and I have seen nothing whatever to cast any doubt upon his interpretations of ophiuran structure, with the possible exception of the homology of the peristomal plates. On this question I do not care at present to express an opinion.

RESULTS.

The facts which I have been able to ascertain will undoubtedly be more plainly set forth if each of the three species is treated by itself. *Ophiactis* and *Amphipholis* are unfortunately rather closely related to each other, the morphological differences between them being of little importance. *Ophiothrix*, on the contrary, is quite different and shows some interesting peculiarities. As *Ophiactis* seems to be undoubtedly less specialized than *Amphipholis*, it may well be the first genus discussed.

OPHIACTIS SAVIGNYI (Müller and Troschel).

The large number of localities from which this species has been recorded, led me to give special attention to the identification of the specimens from Montego Bay. I have compared them with specimens, most of them identified by Lyman, from Zanzibar, Mauritius, Singapore, the Philippine Islands, the Pelew Islands, Fiji, Hawaii, Lower California, Panama, Florida, the Bahamas, the Bermudas, and Brazil. Absolutely indistinguishable in every essential particular, these numerous specimens prove that this species is truly tropicopolitan. It is one of the small species of the genus, the disk-diameter of adults being usually about 5 mm. and very rarely exceeding 7 mm. There are usually 6 arms, but about one specimen in ten is perfectly pentamerous. In some lots the proportion of pentamerous specimens runs considerably higher than this, while in others the hexamerous symmetry is almost unvaried. I have failed to find any correlation between the pentamerous symmetry and any other character of the individual, nor is it any more frequent in adult specimens than in the young. In addition to its hexamerous symmetry and small size, *savignyi* is characterized by its color (above green, more or less variegated with whitish or yellowish; below whitish or yellowish), its rather short arms (5 to 6 times the disk-diameter), long and large radial shields, spinelets on disk especially around the margin, 5 or 6 arm-spines, and 2 (sometimes 1 or 3) oral papillæ. The genital slits are well-developed and bursæ seem to be present, so that in these particulars as well as in the presence of conspicuous radial shields, *savignyi* is easily distinguished from the European *Ophiactis virens*. Like *virens*, however, *savignyi* is characterized by the remarkable extent to which schizogony is carried as a means of reproduction. The process is apparently identical in the two species and has been very fully described by Simroth (1876), whose observations were based on the European form. The process seems to begin, in *savignyi* at least, almost as soon as the adult form is assumed, for the youngest specimen found has already divided at least once (pl. 1, fig. 2).

No evidence was secured on the important points of egg-laying and larval form in *Ophiactis*. None of the adults contained either embryos or eggs large enough to be visible under a lens. The impression gained from the examination of the living material was that the eggs are laid and fertilization and development take place outside the body of the mother. There was no indication whatever that the species is viviparous. It was not possible to decide whether egg-laying was completed for the season by March first, but the appearance of the adults and the great scarcity of very young specimens led me to the opinion that breeding was over.

My observations confirm Simroth in his statements that there is no special plane of division in schizogony, and that the process shows more or less individual diversity. Thus in fifteen young specimens selected at random, showing evidence that division had recently occurred, fourteen had 3 arms, the other only 2; the latter had 3 jaws and 3 oral shields, however. Of the fourteen 3-armed specimens three have 4 jaws and four have only 2. The plane of division, which passes through two opposite interradii, does not then divide a jaw, but passes sometimes on one side and sometimes on the other. Only about half the time does it divide the animal into perfectly complemental halves. The process of healing and the simultaneous rapid growth of the water-vascular system have been well described by Simroth. Almost, if not actually, before the circular canal is completely healed buds which will give rise to new radial canals have pushed out, one at each side of the healing margin of the now semi-circular disk, and before there is any external evidence of the new half-disk the buds of two new arms, one at each side, become visible. Before their growth has proceeded very far, however, a third arm appears between them, associated with the third outgrowth of the now completely healed circular canal. The failure of this third radial canal to start development probably accounts for some of the 5-armed individuals met with, but as the plane of division occasionally leaves 4 arms on one disk-half and only 2 on the other, it is evident that these 2-armed halves will form 5-armed adults even with a normal development of 3 new radial canals. As no 4-armed or 7-armed specimens were seen (excepting of course the 4-armed complements of 2-armed individuals), it would seem to be true that the presence of 4 arms on a regenerating half always prevents the *growth* of the third new radial canal, while the presence of only 2 arms always prevents the *suppression* of the third new arm. In very young regenerating individuals, the difference in size between the third new arm and its two fellows is usually quite marked (pl. 1, fig. 1).

As Simroth, Fewkes, and Ludwig have all pointed out, the development of the skeletal pieces of the new arms takes place rapidly at the tip of the growing radial canal, forming a covering about it and, as it gives rise to pairs of podia, forming the vertebræ and arm-plates of successive joints. In *Ophiactis* the podia are not peculiar in any way, but are simple, slightly tapering, blunt tubes with thin, smooth walls. We may therefore turn our attention to the skeletal plates.

DISK-COVERING.

In the youngest specimen found the disk measured a millimeter across, but it was only semi-circular, since division had already occurred at least once (pl. 1, fig. 2). That not more than one division had occurred is indicated by the arrangement of the plates on the disk. The older half of the animal is easily distinguished from the new one developing, the size of the plates in the two areas contrasting sharply. The older half is covered by 3 pairs of radial shields, a central plate, 3 radial plates, and 6 interradials. On the developing half-disk it is less easy to identify the plates, but there seem to be 3 pairs of radial shields, separated from each other by interradial plates. The arrangement of the plates on the older half corresponds well with that which Ludwig (1899) figures for specimens of *Ophiactis asperula* with the disk only 0.68 to 0.87 mm. across. The only difference is in the relative sizes of the different plates; in *asperula* the central and radial plates are conspicuously bigger than the radial shields, but in *savignyi* this is not so.

There seems no reason for doubting that in its earliest stages the disk-covering of *savignyi* is identical with that of *asperula*, and Ludwig (1899) has shown that the same is true of *Ophiactis kröyeri*. In *savignyi*, however, the occurrence of schizogonous reproduction in very early life interferes with the orderly and uniform development of the disk-covering, shown by *asperula* and *kröyeri*, so that after division has occurred twice it is difficult, if not impossible, to distinguish the primary plates. This is well shown by figure 1 of plate 1, which represents a specimen with a disk rather more than 1 mm. in diameter. Division has apparently occurred twice and it will be seen how irregular is the resulting disk-covering. The irregularity seems to be due to the fact that whereas, in *asperula* and *kröyeri*, the new plates are formed near the distal margins of the radial and interradial plates, in the regenerating *savignyi* they seem to be formed at the proximal edge of marginal plates. In other words, the typical disk-covering develops centrifugally, while the covering of the regenerated disk arises centripetally. As division appears to take place repeatedly, by the time *savignyi* is full grown there is not the least trace of the original primary plates nor of any very definite arrangement in the numerous small plates covering the center of the disk. The radial shields are always conspicuous and cover a large proportion of the disk. Soon after the disk is a millimeter across, spinelets arise in connection with the marginal disk-plates. These spinelets are not outgrowths of the plates, but arise from separate centers of calcification in the tissue covering their outer surface. Not often is more than one associated with a single plate, and many plates, especially near the center of the disk, have no spinelets. When fully formed the spinelets are attached to the underlying plates, but no actual union takes place and the spinelets are always movable to some extent. The number of these spinelets varies in different individuals, but they seem to be relatively most numerous in young specimens. Adult, dry specimens commonly show them plainly, but they are often difficult to detect in fresh or alcoholic adults.

MOUTH-PARTS.

As has been stated above, the plane of division in schizogony does not cut through the jaw, but passes to one side, so that the resulting animals may have either 2, 3, or 4 jaws. The formation of new jaws takes place rapidly, but follows of course the formation of the new rays. Consequently the same factors which control the new-ray formation govern the development of new jaws. In case there are, after fission, only 2 jaws on one resulting half (pl. 1, fig. 3), the outer side of each of the lateral rays must assist in the formation of new jaws, while in case there are 4 jaws each of the new-formed lateral rays will give rise to jaw-elements only on that side which is next the youngest ray. The formation of the jaws takes place as already described by Ludwig (1881) for *Amphipholis* and I have nothing of importance to add to his account. Ludwig has not discussed, however, the formation of teeth and oral papillæ, nor did Fewkes (1887) pay any special attention to these points. I found it possible to trace the development of teeth and oral papillæ in both *Ophiactis* and *Amphipholis*, but as my material was more satisfactory in the latter genus, the account may for the present be deferred. I need only say here that there is no difference between the two genera save in the number and form of the teeth and papillæ. As is well known, the torus (the plate which bears the teeth) forms at the tip of the jaw where the two jaw-plates (adambulacrals) meet. It is at first about as wide as high, but grows rapidly vertically and soon is twice as high as wide or even more. As will be shown under *Amphipholis*, the oldest tooth is at the top of the torus, the new ones forming below it. As soon as a tooth is well formed, the part of the torus against which it rests is resorbed and thus a socket is formed for it. The process of resorption goes so far that the torus becomes perforated (pl. 1, fig. 5). On an adult jaw of *Ophiactis savignyi* there are 5 or 6 teeth of approximately uniform size (pl. 1

fig. 4), but on a growing jaw the youngest tooth, the lowest, is distinctly the smallest.

ARM-BONES OR VERTEBRÆ.

Although Simroth (1876) has figured the vertebræ of *Ophiactis virens*, it has seemed desirable to give a series of illustrations of the vertebræ in *savignyi*, not merely because they are obviously different from those of *virens*, as shown by Simroth, but because the series in each arm, taken as a whole, reveals stages in development which are of particular interest. As the origin and growth of the vertebræ are in all essentials exactly as Ludwig and Fewkes have described in *Amphipholis*, there is no occasion to go into great detail here. The growing tip of the radial water-tube is protected by a cylindrical plate or, better, a calcareous cylinder, back (proximal) of which arise all the calcareous structures of the arm. The first plates to appear are the side arm-plates, but no sooner are they well under way than the rudiment of the under arm-plate appears followed by the pair of calcareous rods which are to form the vertebra, lying side by side, above (dorsal) the water-tube. They develop very rapidly and soon the proximal ends are in contact with each other (pl. 1, fig. 6). New joints are arising distal to them, and by the time half a dozen joints have appeared the two halves of the vertebra are in very close contact; when 10 joints have formed it will be found that the first-formed vertebra is now a single, well-formed, bilateral structure, which can hardly be separated into its component halves. At this time the vertebra is much longer than wide, a little wider than high, and narrower distally than proximally. It soon begins to broaden at the distal end, a sort of knob or projection forming on each side (pl. 1, fig. 8).

Further development is chiefly along three lines: rapidly increased proportional breadth, greatly increased height, and growth of spurs, knobs, ridges, and hollows. The increased breadth is easily seen by comparing the vertebra of the thirtieth segment of an adult arm (pl. 1, fig. 11) with that of the fifty-fifth (pl. 1, fig. 8); while the length has only increased 25 per cent, the breadth has increased 180 per cent; or compare a fully developed vertebra, as in the tenth segment (pl. 1, fig. 14), with the young one of the fifty-fifth segment, and it will be seen that while it is only twice as long, it is more than six times as wide. The increased height is easily shown in the same way; thus although in segment 10 the vertebra is about 8 per cent higher than long (pl. 1, fig. 18), in segment 55 it is more than three times as long as high. The development of spurs, knobs, ridges, and hollows is equally remarkable and is easily understood by an examination of the figures given. Unfortunately no detailed description of an ophiuran vertebra, with technical names for the different parts, has ever been published, Ludwig, Lyman, and others making use of descriptive phrases for the various parts. Since the structure of the vertebræ will undoubtedly play a more important part in the classification of ophiurans in the future than it has in the past, it is desirable to have a uniform nomenclature for the various parts.

Taking the fully formed vertebra of *Ophiactis* as a type (pl. 1, figs. 14 to 18), we may distinguish the following parts, when the vertebra is seen from above (fig. 14): the *alæ* form the bulk of the adoral end, their upper margins forming the *upper alar ridges;* these alar ridges are widely expanded at their inner end, but do not meet in the mid-line; the space between is of little importance in *Ophiactis*, but is very conspicuous in some genera; it may be called the *zygantrum;* the expanded inner end of each alar ridge is more or less clearly divided into three parts which may be called the *epapophyses;* on each side there is an *aboral*, *median*, and *adoral epapophysis* and in *Ophiactis* they are all distinguishable, although the aboral is the most conspicuous. Directly in front of the aboral epapophysis is a broad, nearly flat platform, the *protapophysis*, the aboral corners of which are higher than the median portion. Projecting from beneath this median portion may be seen the *zygosphene*, a shining, glassy knob which still shows evidence of its paired origin. At either side, but still lower, are the *aboral hypapophyses;* back of these and about half-way between them and the alæ are the *parapophyses*, not very conspicuous or important ridges closely associated with the median hypapophyses; back of and below the zygantrum is a conspicuous median, unpaired process, the *epanapophysis*, which is particularly noticeable in the vertebræ within the disk (pl. 1, fig. 19); on either side of the epanapophysis, but in a much lower plane, lies a *zygapophysis*.

These are all the parts which are visible from above, but if we look at the adoral surface of the vertebra, (pl. 1, fig. 17) we shall see below the zygapophyses, the adoral pair of hypapophyses, while between the zygapophyses is the important space, the *zygotreme*. Looking at the lower surface of the vertebra (pl. 1, fig. 16) a deep furrow, the *taphrus*, is seen running from between the zygapophyses to the zygosphene; it is bounded on either side by the three hypapophyses and the thin, vertical wall which connects their bases; the taphrus contains the radial water-vessel and nerve; the *lower alar ridges* form the ventral margin of the alæ.

Making use of these terms, then, we may describe the vertebra of *Ophiactis* as short and high, with a small zygantrum, a broad, low protapophysis, a well-marked zygosphene, a large epanopophysis, well-developed zygapophyses, and small, adoral hypapophyses. The basal segments of the arm are so crowded and compressed that they do not fairly show the appearance of a typical vertebra, but from the tenth to the fifteenth segment the vertebræ show clearly their characteristic features. Beyond the twentieth segment youthful characters become evident and these become more and more marked as one approaches the tip of the arm. This is well brought out by comparing a basal joint of a young arm with a corresponding joint of an adult arm. For example, the resemblance is very noticeable between the tenth vertebra (counting from the base of the arm outward) of an arm having 18 joints (pl. 1, fig. 12) and the thirtieth vertebra of an arm with more than 60 joints (pl. 1, fig. 11), but the difference between this young tenth vertebra and the tenth vertebra of the adult arm (pl. 1, fig. 14) is most striking. No doubt the existence of localized stages in the series of vertebræ of the ophiuran arm will be easily demonstrated when the details of arm-structure are worked out for a large number of species and genera.

The development of the young vertebra into the adult deserves a further word. It has already been pointed out that during this development growth longitudinally is very slow as compared with the lateral and vertical growth. Attention may now be given to the important question as to what processes of the adult vertebra are the first to develop and which are the last. In a very young vertebra the alæ are the only evident projections, but in one a little older (pl. 1, fig. 8), the aboral hypapophyses are well marked, the zygosphene is defined, and the aboral end of the protapophysis can be distinguished; there is also an indication of the epanapophysis. In the vertebra of the segment, 5 joints nearer the disk (*i. e.*, the fiftieth), the upper alar ridge is distinct and the protapophysis is fully defined. In the vertebra of the fortieth segment the parapophyses show and the aboral hypapophyses are very prominent. In the vertebra of the thirtieth segment the first indications of the epapophyses are seen in the line of distinction between the protapophysis and the alar ridges. In the vertebra of the twentieth segment this distinction is so far completed that the aboral epapophyses and the zygantrum are well defined.

Before leaving the subject of the vertebræ, a word may be said as to their articulation with each other. The alæ of course furnish the chief surface for muscular attachment, but the parapophyses and hypapophyses are important points of attachment. The zygosphene fits into the zygotreme of the next distal vertebra and is supported on each side by a zygapophysis. The aboral margin of the protapophysis fits into the space below the epanapophysis and above the zygapophyses, and the aboral hypapophyses fit into the space below and outside the adoral pair. So while the zygosphene and zygotreme furnish what might be called the axial joint, which is thus of the ball-and-socket type, too great vertical freedom is prevented by the protapophysis and epanapophysis, while excessive lateral movement is impeded by the aboral and adoral hypapophyses.

ARM-PLATES.

The sequence of formation of the arm-plates has been correctly stated by Ludwig and by Fewkes, their observations on *Amphipholis* being fully confirmed by mine on that genus and on *Ophiactis*. The 2 side arm-plates appear simultaneously, one on each side, directly back of the terminal plate, and are the first indication of the formation of an arm-segment. They very quickly meet in the mid-ventral line and a little later in the mid-dorsal line. They are followed at once by the rudiment of the under arm-plate, which arises directly in front of, or distal to, their ventral line of division. The under arm-plate is soon followed by the upper one, which is formed in a corresponding position on the dorsal side of the arm. In a normally developing young arm, the fourth segment is generally the first one that can be considered complete (pl. 1, fig. 6); the third has only a rudiment of the upper arm-plate; the second lacks the upper arm-plate altogether; the first lacks both upper and under arm-plates. It is true that the rapidity with which new segments are formed shows more or less diversity in different individuals. Apparently, in the regenerating tip of an adult arm the segments are formed more rapidly and develop much more slowly than in a young arm. As a consequence, the sixth, tenth, and fifteenth segments of such an arm are all in about the same stage of development. Simroth (1876) has correctly described how the new "arm-buds" arise on the regenerating half of the disk. As soon as they are visible, the terminal plate appears at the tip just above the water-tube. It grows down and around the tube very rapidly and soon the two sides meet and fuse in the mid-ventral line. By the time this process is complete the first pair of side arm-plates is fully formed (pl. 1, fig. 7). The first side arm-plates meet broadly both above and below, the under and upper plates being relatively very small on the young joints; but both grow more rapidly than the side arm-plates and slowly but surely force the latter apart. By the time 20 segments are formed, the side arm-plates are nearly separated dorsally and the separation is completed before 25 segments have developed. Ventrally the process is a trifle slower, but it is completed before 30 segments are formed. On the basal part of the arm, therefore, the side arm-plates are completely separated above and below, while the under arm-plates are in contact with their fellows and the upper plates with theirs.

As regards their relation to the vertebra which they inclose, in the adult arm-segment it can be easily seen that the side arm-plates are in very close conjunction with the alæ, fitting more or less neatly into the area between the alar ridge and the parapophysis. The under arm-plate is in contact with and apparently somewhat attached to the aboral and median hypapophyses. The upper arm-plate rests on and is perhaps attached to the epapophyses and even to the protapophysis.

ARM-SPINES AND TENTACLE-SCALES.

The first-formed arm-spine is the *lowest* and no additional spine ever appears normally between it and the tentacle-scale. It ordinarily appears as soon as the side arm-plate is well formed, but is usually lacking from the first segment (*i. e.*, the segment directly adoral to the terminal plate). On the second segment the lowest arm-spines are well marked; they each originate from a separate center of calcification close to the aboral margin of the side arm-plate near its lower end. The second arm-spine is the next dorsal to the lowest; it may appear almost simultaneously with the lowest or it may be wholly lacking on the second segment. Although appearing later, the second arm-spines grow more rapidly than those first developed and are soon distinctly larger. The third arm-spine of each vertical series generally appears on the sixth or seventh segment from the tip; it lies just dorsal to the second, of course. The fourth spine, just dorsal to the third, arises very much later; in some individuals it may be found on the fifteenth segment back of the terminal plate, but in other specimens as many as 25 segments may have only 3 spines on each side. In large specimens, a fifth, sixth, seventh, and very rarely an eighth spine appear in each series dorsal to the fourth, but the position of the segments on which these spines first appear differs much in different specimens. In the largest specimen seen, the basal arm-segment has 2 spines, the next 4, the next 5, the next 6, the next 7, and the next 8; then follow 13 joints, each with 7 arm-spines on each side, 23 joints with 6, 24 with 5, and 18 with 4; the rest of the arm is unfortunately missing. The species character (5 or 6 arm-spines) is thus shown from the tenth to the fifty-seventh segment. This is a much more extended series than is shown by the vertebræ, which are typical from about the eighth to the twentieth segment only. The next to the lowest arm-spine is the largest (longest and stoutest), as long as there are only 4, but as the number increases the lower spines grow very little, while the upper ones grow rapidly, so that near the base of the arm the next to the uppermost, or the uppermost, becomes the largest. At the tip of the arm, the spines are smooth, but they soon develop thorn-like projections on the lower, adoral margin, and generally on all sides, especially near the tip. Excepting on the lowest spine, these projections are neither large enough nor sufficiently definitely arranged to have any particular significance, but on the lowest spine they are more characteristic. The lowest spines of the third segment (pl. 3, fig. 12) have an enlarged base and a smooth, nearly cylindrical tip, but those of the sixth (pl. 3, fig. 13) have the thorn-like projections or "teeth" of the lower, adoral margin very conspicuous, especially the terminal one. There are half a dozen or more of these teeth at this stage, but as the spine grows older they increase in number and occupy the other angles of the spine, so that at the middle of the arm the lowest spine (pl. 3, fig. 14), although much more thorny than any of the others, does not differ from them as evidently as it does near the tip of the arm. It can not be said, then, that the lowest arm-spine of *Ophiactis* is, in any sense, characteristic.

The tentacle-scales in *Ophiactis savignyi* are large and conspicuous, although there is but one on each pore. It arises almost as soon as the lowest arm-spine, but it is associated with the ventral surface of the side arm-plate. It arises from a separate center of calcification and its rudiment appears simultaneously with that of the under arm-plate. There is nothing in the development of the tentacle-scales to determine whether they are homologous with the arm-spines or not.

SUMMARY OF GROWTH CHANGES.

1. Fission occurs as soon as adult form is assumed; it usually results in complemental halves, but may leave *four* rays on one half and only *two* on the other.
2. The 5-rayed individuals arise in either one of two ways: by the formation of a normal 3-rayed half on a regenerating 2-rayed individual,

or by the failure of the median ray to develop on the regenerating side of a normal 3-rayed individual. But only about one specimen in ten has 5 rays.

3. In fission the dividing plane does not cut through a jaw, but passes on one side or the other; accordingly a half-disk may have 2, 3, or 4 jaws; normally there are 3.
4. The disk-covering, when the adult form is first assumed, consists of the typical primary-plates, shown by Ludwig to be characteristic of *Ophiactis*, but owing to repeated fission, the covering of the disk is ultimately made up (aside from the large radial shields) of small plates with no regular arrangement.
5. The torus bears at first none, then 1, 2, 3, 4, 5, and sometimes 6 teeth, of which the oldest (first-formed) is uppermost and the youngest is lowest (most ventral).
6. Young vertebræ are very much longer than high or wide; the alæ are the first outgrowths to appear, soon followed by the aboral hypapophyses; the zygosphene, protapophysis, and epanapophysis appear almost immediately thereafter.
7. Typical vertebræ occur in the adult arm from about the eighth to the twentieth segment.
8. Of the plates covering the vertebræ, the side arm-plates appear first, followed by the under arm-plates and lastly by the upper. The side arm-plates, of any one segment, are broadly in contact with each other both above and below on the young joints, but are ultimately separated dorsally by the growth of the upper arm-plates and ventrally by the lower.
9. The lowest arm-spine is the first formed; all succeeding spines arise serially dorsal to it.
10. The typical number of arm-spines is to be found on about the tenth segment of an adult arm and thence distally for a varying number of segments, rarely as many as 40.
11. The lowest arm-spine has no characteristic form.
12. The tentacle-scales appear with the first under arm-plate; they may not be homologous with the arm-spines.

AMPHIPHOLIS SQUAMATA (Delle Chiaje).

The peculiar habitat of the specimens of *Amphipholis* collected at Montego Bay led me to question whether the species was really identical with that found on shelly bottoms in New England waters. But critical comparison of these Jamaican specimens with others from Woods Hole (Massachusetts), Casco Bay (Maine), Grand Manan (New Brunswick), Norway, and Naples has forced me to the conclusion that they can not be distinguished and are undoubtedly entitled to the name *squamata*. At Montego Bay, the species was found only in the red sponge in which *Ophiactis* occurred so abundantly, but in that situation it was fairly common. The smallest free-living specimen seen had the disk a millimeter across and of an orange-red color, a peculiarity of the young noted by Fewkes. Most of the specimens with disks more than 2 mm. across contained young in a more or less advanced stage of development. The youngest embryo examined had the disk 0.35 mm. across, and the arms, each with 3 segments, projected only 0.20 mm. beyond the disk margin. The largest adult did not exceed 3 mm. in diameter.

In two particulars the *Amphipholis* from Montego Bay showed rather striking differences from those studied at Newport by Fewkes (1887), who says that 4- and 6-armed young "were repeatedly found" and that "adults with 6 arms were common." I have not found a specimen in my Jamaican material, either adult or young, which varies in any way from the typical pentamerous condition. Again, Fewkes says that "ordinarily a gravid adult would have from 10 to 15 (generally 10) free young." In the Jamaican form the number of young ranged from 1 to 3, but in no case were more than 3 seen. There were no 2 of the 3 at the same stage of development; for example, in one typical case one young was 0.50 mm. across with 5-jointed arms, a second was 0.63 mm. across with 8-jointed arms, and a third was 0.80 mm. across with 11-jointed arms. The young are not born until the disk is nearly a millimeter across; one mother only 2.2 mm. across the disk contained a young one 0.90 mm. across. Fewkes does not mention the size of his adults, and it is quite possible that they were much larger than the Montego Bay specimens. If so, that fact might account for the physiological differences just noted, in the frequency of variation, and the number of young. Or it is possible that the small number of young may have been due to the breeding-season being nearly over at Montego Bay. No special attempt was made to settle the matter, as it was not until after my return to Cambridge that I had any doubts as to the breeding-season being at its height.

Unlike *Ophiactis*, *Amphipholis* shows no evidence of schizogonous reproduction, but ordinary reproduction by ova begins very early in life. The development has been so carefully worked out by Fewkes (1887) and Ludwig (1881), as well as by several other students, that there is little that is new for me to set forth, except in certain details omitted by these earlier writers. As in the case of *Ophiactis*, attention has been centered on the skeletal parts, as neither the podia nor any other soft parts reveal any features of interest, from the present point of view.

DISK-COVERING.

In the youngest specimens seen the disk was covered by 16 plates (a central, 5 large radials, and 10 interradials) as figured by Ludwig, but the 5 pairs of radial shields were already beginning to appear. By the time the disk is 0.80 mm. across, there are 5 more radials and 5 more interradials, while the radial shields are now easily recognized as such. The new radial and interradial plates arise between the central and the primary plates of radii and interradii. With increasing size of disk the conspicuousness of the primary plates disappears, and while they can sometimes be made out in the adult, they are not as a rule easily seen. The adult disk is covered by 150 to 300 plates. No spinelets develop in connection with any disk-scales.

MOUTH-PARTS.

My observations on the mouth-parts confirm fully the work of Fewkes and Ludwig. I am, however, able to add certain details in regard to the teeth and oral papillæ which were either overlooked by those writers or considered of too little importance to note. As mentioned under *Ophiactis*, the torus forms at the tip of the jaw as a small plate about as wide as high, but rapidly becomes vertically elongated. Before it is twice as high as long, the first tooth is formed from a triradiate spicule lying close to the torus on its inner side, near its upper end. This spicule rapidly forms a triangular pyramid, the base of which rests very closely against the torus (pl. 2, fig. 5). Fewkes says that "the teeth are not separate centres of calcification," but appear "to grow out directly from the adoral region of the torus." My first impressions were that this statement was correct, so closely are the teeth associated with the torus, but careful maceration with sodium hypochlorite made it possible to determine the truth. So closely does the young tooth press against the torus, that resorption (as stated under *Ophiactis*) takes place in the latter and a socket is formed in which the tooth sets very snugly, but probably not immovably. The first-formed tooth attains some size (pl. 2, fig. 6) before the second is formed. As the torus elongates vertically the second tooth arises below the first and subsequently a third forms beneath that, and finally a fourth below that; the maximum number in *Amphipholis* from Montego Bay seems to be 4; probably larger specimens will be found to have 5. The growth of the torus seems to be chiefly at the lower end, and that of the teeth is mainly distal. In the adult torus the sockets, in which the teeth are set, completely perforate its skeletal tissue, with the occasional or perhaps usual exception of the lowest. The torus is widest and thickest at the top.

Fewkes has laid considerable stress on the formation of a spinous projection at the distal end of the second adambulacral plate, during the formation of the jaw, which he considers homologous with an arm-spine. There is no doubt of the existence of this process. Ludwig and others refer to it and I have had no difficulty in finding it (pl. 2, fig. 1). But in following its development we find it never becomes a spine or any other special organ; it simply forms the distal, concealed end of the adoral plate, to which the second adambulacral plate gives rise. We have already seen under *Ophiactis* that the arm-spines arise from separate centers of calcification, but neither Fewkes nor Ludwig noted this fact. Had it been observed by Fewkes, he could hardly have homologized the distal process of the adoral plate with an arm-spine; he seems to have been misled by a superficial resemblance and to have overlooked the important fact that spines do not arise by budding or breaking off from previously formed plates.

The origin and development of the oral papillæ in *Amphipholis* is of especial importance, since their appearance in the adult is the character upon which the genus is based. They arise very early in the development of the jaw, for while the adambulacral plates which form the latter are still quite distinct, their rudimentary beginnings may be seen (pl. 2, fig. 2). At this stage there are two papillæ on each side of each jaw; one is at the outer (adradial) proximal corner of the first adambulacral, while the other is on the inner (proximal) side of the second adambulacral, just distal to the oral tentacle. Later a third papilla arises on the adradial side of the first adambulacral, close behind the first papilla. The time of appearance of this third papilla shows considerable diversity; usually it forms very soon after the other two, but occasionally it is delayed, and even a specimen a millimeter across may lack it (pl. 2, fig. 3). The typical generic character (pl. 2, fig. 4) is commonly recognizable by the time the disk is 1.30 mm. across. The existence of the stage with only the proximal and distal papillæ (pl. 2, figs. 2 and 3) is of extraordinary interest, for that is the condition characteristic of the genus *Amphiura* and we are therefore justified in saying that *Amphipholis* passes through an *Amphiura* stage. Evidently light is thus thrown on the phylogeny of *Amphipholis*. The appearance of the rudimentary oral papillæ and their relation to the first and second adambulacral plates, with their accompanying podia, suggest the possibility that the oral papillæ are homologous with tentacle-scales. Investigations on other genera will be necessary in order to determine the point.

ARM-BONES OR VERTEBRÆ.

Ludwig (1881) has worked out so completely the development of the vertebræ that there is really very little to be added. My observations do not disagree with his in a single essential feature, although in details of secondary hollows and ridges my impressions of an adult vertebra do not agree with his figures. The largest vertebra I have examined is relatively longer than his largest, but, as I have already stated, the Montego Bay specimens of *Amphipholis* were all small, and their arm-segments are undoubtedly relatively longer than those of larger specimens. The adult vertebra may be described as somewhat elongated, with a small zygantrum, a low, long protapophysis, a well-developed zygosphene, a large epanapophysis, well-developed zygapophyses, and very small adoral hypapophyses. In all essentials it is like that of *Ophiactis*, but relatively much longer and somewhat lower; the protapophysis is narrower, the parapophyses more conspicuous, and the epapophyses less well marked. In all these particulars the vertebra of *Amphipholis* is more youthful than that of *Ophiactis*.

ARM-PLATES.

In no particulars does the development of the arm-plates differ from what has been shown for *Ophiactis*. The side arm-plates appear first and are followed by the under arm-plate, while the upper arm-plate appears last of all. In one point, however, development does not go so far in *Amphipholis* as in *Ophiactis*. The side arm-plates are never fully separated, either above or below; at least, in the largest specimen I have examined, one which has 40 arm-segments, the side arm-plates are still distinctly in contact even in the first basal segment. In this particular character, then, *Amphipholis* is more primitive or youthful than *Ophiactis.*

ARM-SPINES AND TENTACLE-SCALES.

One of the most peculiar features of the development of *Amphipholis* is the fact that it is not the lowest arm-spine which appears first, but the next to the lowest. So unwilling was I to believe this that it was only after repeated observations, on many specimens, that I satisfied myself there is no doubt about the fact. Development at the tip of the arm is so rapid that each side arm-plate of the newest segment usually bears two spines before a new segment begins to form; this first segment may also have the rudiment of an under arm-plate. If one examines this distalmost segment when the side arm-plates have just met in the midventral line, the rudiment of an arm-spine will be found on the aboral margin of each side arm-plate. Almost immediately a second rudiment appears *below* (ventral to) the first, so that there are two rudimentary spines on each side. They remain of about equal length for some time, but the upper is the stouter and more thorny (pl. 3, fig. 11). On the third segment they are of about equal length, but on the fourth the lower is longer. By the time 8 segments are formed a third spine appears on each side arm-plate above the other two. This rapidly becomes the longest of the three, while the middle one is the stoutest and roughest. By the time 25 segments are complete a fourth spine dorsal to the third may arise, but it does not become noticeably longer than the third and is generally shorter. The development of the "second" spine before the lowest is so contrary to *a priori* expectations that some explanation is necessary. It is true that in its early appearance (pl. 3, fig. 11), it resembles the lowest arm-spine of *Ophiactis* (pl. 3, fig. 13) and it is possible to consider the two homologous, since each is the first spine formed on the segment. But in that case the *lowest* arm-spine of *Amphipholis* requires explanation, for there is nothing homologous to it in *Ophiactis.* A preferable explanation seems to me to be the suggestion that we have here an extraordinary case of acceleration in development. We have already seen in *Ophiactis* that after the "second" spine is formed it grows more rapidly than the lowest and soon exceeds it in size. Now, the whole appearance of young *Amphipholis* shows that its development within the mother's body has led to an acceleration which is most noticeable at the tips of the arms, although marked on the disk. Is it not possible that acceleration in the development of the arm-spines has led the more-rapidly growing "second" spine to appear before the lowest? Such a suggestion seems to me well within the bounds of possibility. In any case, however, neither the lowest nor the second arm-spine develops any unusual hooks or teeth or assumes any particularly characteristic form.

Although the basal joints of the arm show two tentacle-scales on each side, one associated with the under arm-plate and one with the side arm-plate, it is a remarkable fact that at the tip of the arm there are no tentacle-scales at all. It is not until a dozen or more segments are formed that the first tentacle-scale appears and it is associated with the side arm-plate, arising near its outer margin, at the base, from a separate center of calcification. The origin and appearance suggest homology with the arm-spines. Almost immediately after the formation of the first tentacle-scale, a second one associated with the under arm-plate begins to form and is usually visible after one or two segments have given rise to the first one. The exact place of appearance of the tentacle-scales is subject to a good deal of individual variation; thus in a specimen with 21 or 22 segments in each arm, the terminal 15 or 16 have no tentacle-scales, but the sixteenth or seventeenth has one associated with the base of the side arm-plate, while the second scale may be seen on the eighteenth or nineteenth segment in 4 arms, but not until the twentieth in the fifth; on the other hand, in older specimens, with 30 or 40 arm-joints, the first tentacle-scale may appear only 12 segments from the tip of the arm and the second on the fourteenth. The first tentacle-scale has every appearance of being the homologue of an arm-spine, but the second is apparently quite a different organ. It must be considered as a possibility that this *second* tentacle-scale in *Amphipholis* is homologous with the single tentacle-scale of *Ophiactis*, but the question involves the examination and study of many related genera before it can be answered.

SUMMARY OF GROWTH CHANGES IN AMPHIPHOLIS SQUAMATA.

1. The disk-covering when the adult form is first assumed consists of the typical primary plates, figured by Fewkes and by Ludwig. Rapid growth, however, soon decreases the conspicuousness of these plates and in the adult they are seldom recognizable.
2. The torus of the adult bears 4 teeth, which do not arise as outgrowths from it, but originate from separate centers of calcification. The uppermost tooth is oldest, the lowest youngest.
3. The second adambulacral plate, which becomes the adoral plate in the adult, does not bear a spine at its distal end at any stage of its development, nor does a spine arise at any time by a separation of a projection of the original plate.
4. The oral papillæ arise from separate centers of calcification associated with the first two adambulacral plates. They may be homologous with tentacle-scales.
5. At an early stage of development, *Amphipholis* has only 2 oral papillæ on each side of the jaw, as in *Amphiura*. It may therefore be said to pass through an *Amphiura* stage.
6. The vertebræ of *Amphipholis* are essentially like those of *Ophiactis*, but have retained certain youthful features, greater relative length, less relative height, narrower protapophysis, more conspicuous parapophyses, and less well-marked epapophyses.
7. Arm-plates arise in the same sequence as in *Ophiactis*, but the side arm-plates of any one segment are never separated from each other, either above or below. The arm is thus more youthful than that of *Ophiactis*.

8. The next to the lowest arm-spine and not the lowest is the first one formed, but the first segment usually has both, on each side, before the second segment arises.
9. The lowest arm-spine never develops any special or characteristic form.
10. The distal arm-segments have no tentacle-scales, but at the base of the arm each pore has two; one, associated with the side arm-plate, arises after 12 to 18 segments have been formed; the other, associated with the under arm-plate, arises one or two segments later. The former may be homologous with an arm-spine; the latter may be homologous with the tentacle-scale of *Ophiactis*.

OPHIOTHRIX ANGULATA (Say).

Two species of *Ophiothrix*, *angulata* and *œrstedii*, are very common in shallow water throughout the West Indian region. Both are exceedingly variable in coloration and the specific differences between them are often hard to make out. The commoner and more variable species is *angulata*, and at Montego Bay a dozen specimens could be gathered to every one of *œrstedii*. The latter has very characteristic lines of white or cream-color cross-banding the upper surface of the arms, and these are rarely, if ever, lacking, though they are occasionally faint. In *angulata* such cross-lines are rarely indicated, but there is present a longitudinal stripe of white, or some light shade, running the length of the arm. Although such a distinction seems trivial, especially when the rest of the coloration is very variable, it is really remarkably constant and specimens can generally be assigned to one species or the other at a glance.

As is generally the case when a species is very common, *angulata* occurs in very diverse habitats. It is quite common at Montego Bay among coral fragments on the reefs, it is very common among the eel-grass on the flats, and it is exceedingly common among the bryozoa, sponges, mollusks, hydroids, and ascidians growing in masses on the mangrove roots among the Bogue Islands. Most of the young specimens obtained were found in the last-named habitat, especially in the cavities of the same red sponge in which *Ophiactis* and *Amphipholis* occur. No very young specimens were found, the smallest having the disk 2 mm. across. While this is greatly to be regretted, much interesting information has been secured from the young ones that were obtained. No indication of schizogony nor of variation from the typical pentamerous form was seen.

COLORATION.

Neither *Ophiactis* nor *Amphipholis* has a color pattern sufficiently distinctive to make its development a matter of any significance, but as already stated, *Ophiothrix angulata* is most easily distinguished from its nearest ally by a characteristic color pattern. The development of this pattern, therefore, is of no little interest. The youngest joints at the tip of the arm are colorless and contain no pigment. In the third, fourth, or fifth segment, however, a little pigment begins to appear and gives a tinge of color, deepening with the increasing age of each successive segment. This pigment is bright purple of a deep shade. It first appears in the side arm-plates near their upper ends and gradually spreads distally and to some extent ventrally. It soon invades the margins of the upper arm-plates and follows them to their distal end. In a typical case it is very sharply confined to the sides of the upper arm-plates and fails to cross from one side arm-plate to its fellow of the same segment. Consequently there is an unbroken, unpigmented (*i. e.*, apparently white) stripe along the dorsal surface of the arm. In some specimens pigment fails to invade the distal corners of the upper arm-plates and thus there appears to be a row of white spots along each side of the stripe; or the pigment may fail in the spine-bearing ridge of the side arm-plates and then the dorsal white area of the arms is markedly increased. On the lower side of the arms the pigment also spreads longitudinally in the side arm-plates and in the margins of the lower arm-plates, but it rarely if ever crosses the latter. In other specimens the pigment spreading in the margin of the upper arm-plates follows back along the converging sides to the proximal end and there is confluent with its fellow of the other side and with the pigment of the side arm-plates. In such cases the longitudinal white line is broken into a series of spots, formed by the mid-anterior and central parts of the upper arm-plates. When pigment is formed very abundantly the white stripe, both dorsally and ventrally, is very narrow and the general coloration is uniform deep purple. Many specimens, however, are not at all deep purple, but are very light colored, or are brownish, reddish, or greenish. This diversity of color is very easily explained. Light-colored specimens are simply those which have developed little pigment. Green specimens are those in which the purple pigment is masked by a green coloring-matter acquired after the formation of the purple; whether this green matter is another pigment or consists of symbiotic algæ I am not prepared to state, as no study of the point was made on living animals. Brown and red shades are produced by the masking of purple by other substances. In all cases, however, purple pigment is the primitive coloring-matter.

The coloration of *Ophiothrix œrstedii* begins, like that of *angulata*, by the development of pigment in the upper part of the side arm-plates. But the pigment spreads laterally and not longitudinally and the whole development of the color-pattern is thus entirely different from that of *angulata* and there is never, and naturally there can not be, an uninterrupted white stripe either above or below. The first bit of pigment to appear may generally be seen in the third or fourth arm-segment in the upper part of the adoral (proximal) portion of the side arm-plate. This rapidly spreads across to meet its fellow from the opposite side and also descends along the side arm-plate ventrally, where it also ultimately meets its fellow from the opposite side and thus completes a narrow purple ring around the arm. Meanwhile another patch of pigment arises just above the upper arm-spine on the side arm-plate and spreads on to the upper arm-plate and down along both sides of the spine-bearing ridge of the side arm-plate. The later behavior of this pigmented area varies more or less in different specimens. In what may perhaps be considered typical *œrstedii*, the two margins (adoral and aboral) of the area accumulate all the pigment and the nearly or quite unpigmented area between them separates them sharply from each other. In such specimens the upper arm-plate is crossed by two heavily pigmented lines, one of which passes down the side arm-plate adoral and the other aboral to the spine-bearing ridge. These lines extend across the under arm-plates and thus form rings encircling the arms. Each arm-segment, in an individual colored like this, has therefore three pigmented rings, one near its aboral margin, distal to the spines, one near its middle just proximal to the spines, and the third at its adoral margin. In many specimens, however, the ring either just distal or just proximal to the arm-spines is indistinct or lacking and the one which is present is very broad on both the upper and under arm-plates. The same obscuring of purple pigment by green and other coloring matters, referred to under *angulata*, occurs in this species also.

It is obvious from the above account that the color pattern of neither of these species of *Ophiothrix* can be derived from that of the other very easily, since one is due to a longitudinal and the other to a transverse distribution of the pigment. While it is true that some specimens of *angulata* have the dorsal white stripe so much broken up, and so much white present elsewhere on each segment, that they are easily confused with *œrstedii*, such specimens do not show definite transverse pigmented rings. Possibly further rearrangement of their pigment might give rise to rings and we could thus say the transverse pattern was evolved from the longitudinal. Evidence, however, that such a development actually occurred is wanting, for *œrstedii* certainly goes through no stage of development wherein it shows any longitudinal distribution of the pigment.

PODIA.

As is well known, the podia of adult *Ophiothrix* are remarkable for their highly papillose surface. It is a matter of some interest, therefore, to note that the podia of the 3 or 4 terminal segments of each arm are perfectly smooth, those of the next 5 or 6 older ones are rough with small papillæ, while it is not until some 9 or 10 segments are developed that the characteristic papillose podia are present.

DISK-COVERING.

One of the most interesting facts in the development of *Ophiothrix* was discovered in the study of the disk-covering. Although no specimens seen were small enough to show simply the primary plates, the specimen only 2 mm. across the disk shows certain primary plates, among which the central one is conspicuous (pl. 3, fig. 18). In a specimen 3.5 mm. across the disk (pl. 3, fig. 19), it will be noticed that the central plate is not only relatively but *actually* smaller than when younger. Evidently a remarkable process of resorption is going on. The extent of this resorption is well shown by the following table:

Diameter of disk in millimeters.	Diameter of central plate.	Length of radial shields.	Ratio of radial shields to central plate.
2	0.60	0.55	0.91
3	.50	1.00	2.00
3.5	.36	1.20	3.33
5	.22	1.85	8.40

Besides the change in size, another change is going on in this plate, during the growth of the disk that is no less remarkable. In the youngest specimen examined the plate is a smooth, thin sheet of lime, entirely unperforated except for a number of minute holes around the margin. As resorption goes on these holes encroach more and more on the plate, not by increase of size so much as by increase of number. When the plate is only 0.25 mm. across, the unperforated area has practically disappeared, and after that stage is reached it is no longer practicable to distinguish the plate from the numerous other small plates at the center of the disk. It can not be said whether the plate is resorbed entirely or whether a minute portion persists. It will be noticed that this plate is utterly unlike anything hitherto reported among echinoderms. Instead of beginning as a triradiate spicule, and steadily increasing in size by dichotomous branching and fusing of the branches, as an echinoderm plate typically does, this plate starts as a large, homogeneous disk which by a process of resorption gradually becomes like its associated plates in both size and structure. In the present state of our knowledge it is futile to speculate on the significance or homologies of this peculiar plate.

Very early in the formation of the disk-covering, but not while the primary plates (excepting indeed the central) are still conspicuous, there begin to arise (in association with the plates) vertical rods trifurcate at their free end. These trifurcate spinelets are usually found one to a plate, but on the radial shields there may be a number, arranged in series of 3 or 4, parallel to the radial margin of each plate. At first there are no spinelets associated with the central plate, but when the disk is about 4 mm. across there may be as many as 5 spinelets upon it. During youth the spinelets are all of approximately uniform height and terminate in 3 sharp teeth of moderate length; but as maturity is reached some of these spinelets grow out into spines, not unlike the arm-spines in length and appearance. They are two or three times as long as the spinelets. The number and distribution of these disk-spines is very diversified and the appearance of the disk is greatly modified by their appearance. As a rule, it may be assumed that the presence of these spines in abundance is indicative of age and their absence is indicative of youth, but the rule is by no means unvarying. The number of spines and spinelets on the radial shields is another variable factor in the appearance of the species. When the radial shields are small (*i. e.*, in the young individuals) a few spinelets (3 to 6) will give them the appearance of being well covered, but as they increase in size, if the number of spinelets does not increase they soon have the appearance of being quite bare. In adults the shields may have very few spinelets, possibly none, and no spines, but it is just as common to find each shield with 10 or 12 spinelets and 3 or 4 spines. The bareness of the radial shields is therefore not a reliable specific character in *angulata*.

MOUTH-PARTS.

The mouth-parts of *Ophiothrix* are essentially different from those of *Ophiactis* and *Amphipholis*, since there are no oral papillæ, but a group of dental papillæ are borne on the lower (ventral) end of the torus, below the teeth. None of my specimens are young enough to show a stage of development in which teeth are present but no dental papillæ, though there can be no possible doubt of the existence of such a stage. In the youngest specimen I have examined, the torus is already expanded at its lower end (pl. 3, fig. 15) and bears a group of 6 or 7 dental papillæ, above which are 4 teeth (pl. 3, fig. 17). Resorption back of the teeth goes on as in the genera already described, but in *Ophiothrix* the foramina thus formed are often bisected by a more or less complete bar at right angles to the long axis of the foramen (pl. 3, fig. 16). This indicates that the fully developed teeth have two slightly separated roots and shows greater specialization than in *Ophiactis* and *Amphipholis*. The number of teeth in *angulata* is 4 or 5, while the number of dental papillæ increases throughout growth, and a large specimen may have as many as 17 (in the big East Indian *Ophiothrix longipeda* there may be more than 30). The first dental papillæ arise in a pair, side by side, below the lowest tooth; beneath them the growing torus expands a little and a new papilla forms near the margin on each side; these two are thus a little separated from each other. A third pair arises below them at the sides of the still expanding torus and the space thus left near the center of the expanded portion of the torus is filled by the formation of a seventh papilla. Subsequently, although the torus may increase much in length, it does not expand greatly and the dental papillæ are thus arranged in two slightly curved marginal rows (one on each side) and an irregular median series. In the adult, resorption has formed foramina back of the upper dental papillæ just as it has back of the teeth (pl. 3, fig. 16). It is perfectly clear, therefore, from all these facts, that the dental papillæ are strictly homologous with the teeth and are not in any way to be homologized with the oral papillæ of other genera. As already stated, there are no oral papillæ in *Ophiothrix*, the oral tentacles being unprotected and conspicuously exposed on the hollowed sides of the jaw.

ARM-BONES OR VERTEBRÆ.

The vertebræ of *Ophiothrix* are as different from those of *Ophiactis* and *Amphipholis* as are the jaws, yet their development is so similar as to call for no especial comment. In the young vertebra of *angulata* (pl. 2, fig. 7), besides the excessive length, we note the very low proximal (adoral) and the very high distal (aboral) ends, the slight development of the alæ, the well-developed aboral and median hypapophyses, the conspicuous protapophysis, and a pair of hollowed projections above the zygosphene, which we may call the *zygocœles*. In the later development of the vertebra the length only increases about one-half, while the height anteriorly increases 3.5 times, and posteriorly more than 6 times. The adult vertebra is about as high as it is long, while the width of the alæ exceeds the total length. Seen from above (pl. 2, fig. 9), the most striking feature is the very narrow protapophysis, the immense zygantrum, the very small and insignificant epanapophysis, the reduced epapophyses (particularly the median one), the broad parapophyses and hypapophyses. Seen from the side (pl. 2, fig. 8) the great height of the protapophysis, the bulging zygocœles, the long zygosphene, and the prominent hypapophyses, all attract attention. Looking at the vertebra from below (pl. 2, fig. 11), the breadth of the taphrus and zygosphene are the most notable features. Looking at the aboral end (pl. 2, fig. 10) we are again struck by the high, narrow protapophysis, the conspicuous zygosphene and the zygocœles, while the broad alæ furnish a fitting background. At the adoral end (pl. 2, fig. 12) the reduced area of the alæ caused by the huge zygantrum, the small zygotreme, within which is a small knob that may be called the *zygophore*, and the large adoral zygapophyses are the principal features. We may then say that the adult vertebra is short and high, as in *Ophiactis*, but, in contrast to that genus, the zygantrum is large, the protapophysis is narrow, high, and projecting, the epanapophysis is insignificant, and the adoral hypapophysis is large.

The joint formed by two vertebræ is more complicated than that in *Ophiactis*. The protapophysis of each vertebra fits into the zygantrum of the next distal segment and a compact mass of muscles, attached at their outer ends to the sides of the cavity, hold the protapophysis in position; the inner ends of these muscles are attached on either side of the protapophysis. The zygocœles serve as sockets for the zygapophyses, while the epanapophysis of the distal vertebra rests lightly on them, the zygosphene meanwhile fitting into the zygotreme and resting against the zygophore. The aboral hypapophyses fit outside and beneath the adoral pair of the distal segment. This articulation is, therefore, considerably more complex than the one described on p. 102 and yet it may permit just as much freedom of movement. The lateral flexures of the arm could certainly be made more vigorously and a curved position held more rigidly than in forms with less-developed zygantra and protapophyses. Possibly the reduced epanapophysis permits a greater freedom in vertical movements, but it may be that the larger adoral hypapophyses counteract this tendency.

Although the development of the vertebra is along the same lines as in *Ophiactis*, there is a constantly increasing difference between that genus and *Ophiothrix*. After the two halves of the vertebra have come to lie close beside each other, the progress of development in the two genera is quite unlike. There is at no time an "*Ophiactis* stage" in the development of the *Ophiothrix* vertebra. No other fact noted has so strongly impressed me with the radical difference between *Ophiothrix* and the other two genera studied.

ARM-PLATES.

In the development of the arm-plates, *Ophiothrix* shows a striking difference from *Ophiactis* and *Amphipholis*. As in those genera, the side arm-plates are the first to appear and are almost immediately followed by the under arm-plate, but in *Ophiothrix* the growth of the under arm-plate is so rapid and vigorous that the side arm-plates never meet ventrally, but are from the first kept apart by the under arm-plates. The latter are in contact with each other throughout the entire length of the arm. The upper arm-plates, on the contrary, are very small near the tip of the arm and it is not until 15 or 20 segments have been formed that they are sufficiently large to separate wholly the side arm-plates. Even at the base of the arm, the basal (adoral) end of the upper arm-plates is so narrow that the side arm-plates of any one segment are not widely separated from each other as they are ventrally. The spine-bearing ridge of the side arm-plates is very well developed, so that the arms appear to be constricted between them, and this appearance is accentuated by the fact that the broader, distal end of each upper arm-plate is somewhat swollen. The side arm-plates, like the vertebræ, are relatively very much longer distally than near the base of the arm.

ARM-SPINES AND TENTACLE-SCALES.

In *Ophiothrix*, as in *Ophiactis*, the lowest arm-spine is the first to appear. It is, on the first segment, a simple, smooth, straight rod with an enlarged base (pl. 3, fig. 1), but by the time a second segment has formed it begins to curve at the tip and becomes broader and somewhat flattened (pl. 3, fig. 2). On the third segment it is distinctly curved at the tip and a tooth is evident on the concave side (pl. 3, fig. 3). On the fourth segment this tooth has become conspicuous and another one has arisen below it (*i. e.*, nearer the base of the spine), while the spine-base is notably large and projecting (pl. 3, fig. 4). On the sixth segment these various features are all accentuated (pl. 3, fig. 5) and on succeeding segments the spine may be said to show its characteristic form (pl. 3, fig. 6). As the animal matures, these lowest arm-spines begin to undergo a sort of retrograde change which well illustrates Hyatt's principle of senescence. Thus if the lowest arm-spine on the twentieth or thirtieth segment from the mouth be examined, on an adult arm, it will be found essentially like that on the twentieth segment from the tip. But if one from somewhere about the twelfth basal segment be looked at (pl. 3, fig. 7), it will be found to be obviously different from any of the lowest arm-spines of the middle portion of the arm; except that it is immensely stouter, it is more like that of the fourth segment from the arm-tip. It has one notable peculiarity in that foramina are beginning to open through it. Examination of the lowest spine of segment nine, counting from the mouth, shows (pl. 3, fig. 8) a still further reduction of teeth, particularly the terminal one, while there is a corresponding development of the foramina. The lowest spines of the segments still nearer the mouth (pl. 3, figs. 9 and 10), show these tendencies carried still further. Indeed, except for their smaller size, these basal lowest spines are not essentially different from the ordinary spines of the arm.

The development of the other arm-spines offers no such interesting features as those shown by the lowest. The next to the lowest is the second one to appear and is generally present on the second segment. The others appear in regularly vertical sequence dorsally. The third spine is to be found on the fourth segment from the tip and the fourth on the ninth. It is not until about 40 segments are developed that a fifth spine appears, while the arm has no less than 60 joints when the sixth spine is to be seen. A seventh spine will arise if about 75 joints are formed, and an eighth if the number is about 90. I have not found more than 8 spines in any specimen, and think that 6 or 7 is the characteristic number for the species.

The tentacle-scales are reduced to very narrow, sharp spinelets, which are quite lacking at the tip of the arm. The first indication of them is on the sixth or seventh segment, where a minute one is to be found on each side, connected with the lowest part of the side arm-plate. They never reach a large size, but even on the basal segments give the impression of being functionless remnants. There is no indication whatever of homology with an arm-spine.

SUMMARY OF GROWTH CHANGES IN OPHIOTHRIX ANGULATA.

1. Although the coloration is distinctive, it is acquired very early without passing through any recognizable stages. It is due to the deposit of purple pigment in the arm-segments *longitudinally* and the usually complete failure of any pigment to cross the median line either dorsally or ventrally. When the color is other than some shade of purple, it is due to the masking of the purple pigment by a secondarily added color.
2. The first-formed podia are smooth, as is usual in ophiurans, and the papillose condition characteristic of the genus *Ophiothrix* is only acquired after about 10 segments are complete.
3. The central plate of the youngest specimens examined is a disproportionately large, homogeneous, thin disk with a few minute perforations around the margin. During the growth of the disk this plate is gradually resorbed, becoming not only much smaller (actually as well as relatively) but more and more reticulate from the increasingly numerous foramina.
4. The disk-plates carry trifid spinelets, which not only become more numerous with growth of the disk, but have a tendency to elongate into slender spines. The number of these disk-spines is very much subject to individual diversity.
5. There are no oral papillæ in *Ophiothrix*, but after 4 or 5 teeth are formed, dental papillæ (homologous with the teeth, but much

smaller) arise in double and then in triple series ventral to the teeth. The torus expands correspondingly, and in maturity the lower dental papillæ may be in irregular quadruple or quintuple series, though the *lowest* series are triple or only double, like the highest. Resorption of the torus occurs back of the largest dental papillæ just as it does back of the teeth.

6. The vertebræ are remarkable for the high, narrow protapophysis anteriorly and the large zygantrum and very small epanapophysis posteriorly. The chief articulation between two vertebræ is formed by the protapophysis of one and the zygantrum of its distal fellow. Other peculiarities of the mature vertebræ are a pair of zygocœles above the zygosphene and a small, round knob, the zygophore, in the zygotreme. The zygapophyses and adoral hypapophyses are well developed.
7. The side arm-plates are separated throughout the whole length of the arm, even in the first segment, by the under arm-plates, so that ventrally the two side arm-plates of any given segment are never in contact. Dorsally those of the first 15 or 20 segments do meet each other in the mid-dorsal line, but thereafter the upper arm-plates keep them apart. The spine-bearing ridges of the side arm-plates are quite prominent, especially on the older segments.
8. The lowest arm-spine, the first to arise, begins as a straight, slender rod, but rapidly develops into a characteristic 3-toothed hook. At the base of the arm, by a process of senescence, it is gradually transformed into a nearly straight, rough, fenestrated spine like those dorsal to it.
9. There are only 4 (distally fewer) arm-spines on the first 40 segments and the full number for the species (6 or 7) does not appear until 60 or 75 segments are complete.
10. The tentacle-scales are reduced to mere spinules associated with the basal part of the side arm-plate. They do not appear until after 6 or 7 segments are formed and they never seem to be of any functional importance.

SUMMARY AND CONCLUSIONS.

Although references to changes in appearance, or in details of structure, during the transition from young to adult brittle-star are to be found in many of the writings of Lyman, Lütken, Verrill, Grieg, Koehler, de Loriol, and other less well-known workers, no attention to the sequence or significance of these changes has been paid, up to the present time, save by Ludwig and Mortensen. And although it has been a generally accepted and well-known fact that the terminal segments of the adult ophiuran arm are the youngest, no use has been made of the important corollary that these segments reveal the developmental stages through which the arm has passed. The present report has endeavored to make full use of this corollary in studying the development of *Ophiactis*, *Amphipholis*, and *Ophiothrix*. Its great value lies, of course, in the fact that even where only a single specimen of a species is available, and that specimen adult, if a single arm is complete to its terminal plate the development of that species throughout its post-larval growth, so far as the arms are concerned, can be read almost as plainly and satisfactorily as if a large series of young specimens were available. Obviously this is not true of the disk. I would emphasize, therefore, as the first conclusion of these studies, this truth of the very great importance of localized stages in the distal part of the ophiuran arm. The other conclusions which follow are taken directly from Ludwig's very valuable paper "Jugendformen von Ophiuren" (1899), supplemented by Mortensen's observations on *Asteronyx* (1912) and by my own work. The following list shows the species of brittle-stars, the growth-changes of which have been more or less fully studied:

Ophiactis asperula (Philippi).
    kröyeri Lütken.
    savignyi (Müller & Troschel).
Amphipholis patagonica Ljungman.
    squamata (Delle Chiaje).
Amphiura magellanica Ljungman.
Ophiacantha vivipara Ljungman.
Ophiothrix angulata (Say).
Ophiomyxa vivipara Studer.
Asteronyx loveni Müller & Troschel.

This list strikingly demonstrates the paucity of facts on which to base a classification of brittle-stars. We have a fair knowledge concerning the growth-changes of 10 of the species (out of approximately 1,100!), but these represent only 7 genera and perhaps 5 families. It may be added that a considerable number of facts are recorded concerning changes during development from young to adult of several euryalids (*Euryale*, *Gorgonocephalus*), but in no one species has any series of changes been followed.

The following conclusions, a summary of our knowledge to date, will serve as a basis for further work and may prove useful in future attempts to properly locate doubtful genera and difficult species. Continued study of growth-changes will ultimately lead to a natural classification of ophiurans.

1. The terminal segments of the arm are the youngest; passing from the terminal plate towards the disk, each succeeding segment is older. The segments in their individual development pass through the same stages that the arm has passed through in its development and therefore the terminal portion of the arm is made up of *localized stages*, to use Jackson's (1899) expressive term, which reveal the developmental or ontogenetic stages of the arm as a whole. The study of the terminal portion of the arm in great detail is necessary therefore to the proper understanding of the relationships of any brittle-star.
2. The original disk-covering in ophiurans consists of a central and 5 radial plates; interradial plates are a somewhat later addition; the radial shields still later; further development of both radial and interradial plates between the primary plates is a more advanced stage; the development of spinules and spines in connection with the disk-plates is further evidence of specialization; and the resorption of the disk-plates or their concealment by thick skin or by a coat of granules must be regarded as still more advanced stages in the development of disk-coverings.
3. The *radial shields* are originally small and comparable to any of the other secondary disk-plates. Their development to a large size is evidence of specialization. The larger the radial shields in proportion to the other disk-plates, the more specialized is the disk-covering, other factors (such as granule formation) being equal.

4. The *oral shields* lie originally on the dorsal surface and only by subsequent developmental changes come to lie on the ventral side. The apparent exception shown by *Asteronyx* seems to me an undoubtedly secondary condition; this is indicated by their late and unequal appearance.
5. The *adoral plates* develop from the second pair of adambulacral (= side arm) plates. A large size *relatively*, as compared with the oral shields, is a primitive condition, but a large size *actually*, so that they are equal to or exceed the basal side arm-plates, is a secondary and specialized condition. On the other hand, their great reduction or entire absence is also a very specialized condition.[1]
6. The jaws (*oral plates*) arise, in large part at least, from the first pair of adambulacral plates. Obviously the more clearly they show their origin the more primitive is their character, while the more completely they are fused and overshadowed by either the torus or the adoral plates, the more specialized is their condition.
7. The *torus* arises, at the tip of the jaw, as a small plate not much higher than wide. A low, wide torus, therefore, indicates a primitive condition, while a high, narrow one or a high one expanded at the lower end indicates specialization.
8. The *teeth* arise in association with the torus, but not as a part of it. The uppermost tooth of the adult was the first one developed, the later teeth appearing below it successively. Obviously, a small number of teeth is a primitive condition, and the same is true where the lower teeth are evidently smaller than the uppermost. Young teeth are sharply pointed; therefore pointed teeth are evidently more primitive than those which are rounded or truncate. A large number of truncate teeth of equal size shows a decidedly specialized condition.
9. The *dental papillæ*, where they occur, are homologous with the teeth, but are a modified form of the latter. Their occurrence is therefore undoubtedly a mark of specialization, the degree of which may be indicated by their number and arrangement.
10. The *oral papillæ* arise in connection with the first and second adambulacral plates (*i. e.*, the orals and the adorals) and appear to be homologous with tentacle-scales. There is as yet no evidence to determine whether their entire absence is a primitive or highly specialized condition. Possibly it may be either. There is evidence to show that at least a relatively primitive condition is indicated when there is one papilla in connection with each oral and each adoral plate. There can be scarcely any doubt that the presence of more than one papilla in association with each of these plates indicates specialization, the degree of which is suggested by the number of such papillæ. The primitive form of oral-papillæ appears to be scale-like, flat with rounded tip; pointed and spine-like papillæ are specialized forms.
11. The *genital-slits* or bursal openings appear very early, one on each side of the base of the arm. The evidence is still lacking as to whether

---

[1] In Mortensen's (1912) very valuable and interesting account of growth-changes in *Asteronyx*, he speaks of the "seitenmundschilder" being resorbed and later as being greatly reduced. But examination of his admirable figures shows there has been no resorption; the fact is that having reached a relatively large size quickly, their later growth has been slower than that of the rest of the disk; thus in his specimen 1.9 mm. across the disk, the adoral plates are each 0.55 mm. long, in the specimen 3.5 mm. across the disk, they are 0.60 mm. long, and in the specimen 25 mm. across they are 3 mm. long. Surely there is no resorption here.

their absence is a primitive or specialized condition. Perhaps it may be either. In any case, the fusion of the margins of the slit so as to form *two* openings on each side of the arm-base is undoubtedly a highly specialized condition.

12. The arm-bones or *vertebræ* arise by the fusion of two skeletal pieces lying side by side above the radial water-tube. They are at first relatively elongated and low, with the two component halves distinguishable and the articulation resembling a simple ball-and-socket joint. Specialization is indicated by loss of indication of the bilateral origin, by greatly increased height, and hence a relatively short longitudinal axis, a greatly increased number of elevations, projections, and ridges for the attachment of muscles, and an articulation complicated by development of zygapophyses, protapophysis, and epanapophysis. Owing to changes from compression and other causes the vertebræ of the basal arm-segments do not reveal the typical form for the species. At about 8 or 10 segments from the mouth the vertebræ of an adult ophiuran with 40 or more arm-joints are fairly typical, but after a dozen, or even fewer (in less mature individuals) segments further out, youthful characters begin to show and the vertebræ become less and less typical as we approach the terminal segments of the arm.
13. The *terminal* plate of the arm is the first formed. It is originally a flat or concave plate on the upper side of the tip of the water-tube. It grows down and around the tube and by ventral union becomes a cylinder. The distal margin of this cylinder may bear one to several teeth or spinelets. It may become enlarged proximally and even conspicuously cup-shaped, but such changes indicate specialization of some kind. The most primitive condition is undoubtedly a simple plate or a half-formed cylinder; a completed cylinder shows at least some specialization.
14. The *side arm-plates* are the first plates of an arm-segment to appear. They grow rapidly and soon meet each other in the mid-dorsal and mid-ventral lines, where they are in close contact, although they do not fuse. They inclose the rudiments of the vertebræ, which do not arise until they are well begun. In later development they may be more or less separated from each other ventrally by the development of the under arm-plates and dorsally by the upper arm-plates. At first they are low and longitudinally elongated, the whole segment being long and flat. In their usual development the height increases much more rapidly than length and they consequently tend to become short and high. The distal margin is somewhat thickened and bears one or more arm-spines. It may become notably enlarged and a conspicuous spine-bearing ridge may be developed, which in the course of growth comes to lie in the median vertical region of the plate. The distal margin of the lower end of each side arm-plate may be more or less deeply grooved for the passage of the podium (tube-foot) and usually a tentacle-scale arises at the same point. Evidently then, long, low side arm-plates, meeting above and below and with no spine-bearing ridge or tentacle-groove, show a primitive condition of the arm-segment, while short, high side arm-plates separated above and below, with a conspicuous spine-bearing ridge and a noticeable tentacle-groove, indicate considerable specialization. All conditions between these two extremes may be found.

15. The *under arm-plate* arises very soon after the formation of the side arm-plates and may even precede the formation of the vertebral rudiments. It is at first small and lies on the oral side of the arm, in the median line just distal to the side arm-plates. It may grow backward (adorally) sufficiently to completely separate the side arm-plates and it then comes in contact with its fellow on the succeeding segment. In such cases the under arm-plates are more or less clearly in contact throughout the entire length of the arm. There is no doubt that small, widely separated under arm-plates are the simple, primitive arrangement and large under arm-plates in contact with each other indicate specialization. The absence of under arm-plates or their occurrence in irregular series and of diverse sizes are certainly indicative of specialized conditions.

16. The *upper arm-plates* are the last of the arm-plates to arise, but they appear usually not long after the under arm-plates and follow a similar line of development. Small, widely separated upper arm-plates are undoubtedly a primitive condition, while large upper arm-plates, in contact with each other and separating the side arm-plates, are certainly specialized. On the other hand, absence of upper arm-plates, if associated with large side arm-plates broadly in contact in the mid-dorsal line, shows a primitive type of structure, while absence of upper arm-plates if associated with widely separated side arm-plates is probably a highly specialized condition.

17. The *lowest arm-spine* is the first to appear, as a rule, though the one just above it may accompany or, in very rare cases, slightly precede it. Succeeding spines arise dorsal to the earlier-formed and the number increases slowly with the age of the segment until the number characteristic of the species is attained. This number is commonly to be found on about the tenth segment from the mouth and thence distally for a variable number of segments. On the basal arm-segments the number is always fewer than normal, but whether the influence of the disk has promoted resorption or prevented formation of the full number has not been ascertained.

18. The *hook-shaped form* of the young lowest arm-spine is not characteristic of any particular family of brittle-stars, but its persistence and perfecting on the mature segments of the middle arm may be a family or at least a generic character. Young spines arise as straight rods, but soon become hooked or give rise to tooth-like projections. They usually acquire a secondary straightness. Young spines are solid, but may become hollow with increasing size. Hollow spines undoubtedly indicate a specialized condition.

19. The *tentacle-scales* may arise as early as the under arm-plate and before the lowest arm-spine, or their appearance may be delayed until after several spines have been developed. Each tentacle-scale is at first flat and rounded and is associated with the ventral, distal margin of the side arm-plate. It may be homologous with an arm-spine, but its position ventral to the lowest arm-spine counts against that view. The evidence is as yet inconclusive whether the absence of tentacle-scales is a primitive condition or not. When two tentacle-scales are present, the second one arises in connection with the under arm-plate a little later than the first one. Its occurrence is almost certainly a specialized condition and it can not be homologized with an arm-spine. A spine-like tentacle-scale is certainly a modified form.

20. The *podia* arise as smooth, paired outgrowths of the radial water-vessel just proximal to the terminal plate. Each one is associated with a side arm-plate. They ordinarily remain smooth throughout life, but in some brittle-stars they are rough, minutely or conspicuously papillose. Such changes are obviously specializations and such podia are often less retractile than usual.
21. The number of arm-segments included in the disk increases with age and such segments are commonly more or less modified by their position.
22. The *number of arms* is determined when the metamorphosis occurs or when the typical ophiuran form is assumed. New arms never arise subsequently, except in schizogonous species, when they develop in connection with the new disk formation. A 5-rayed individual never becomes 6-rayed after its 5 arms are fully formed nor does a 6-rayed individual ever become 5-rayed by autotomy and resorption, as has sometimes been supposed. A 5-rayed or 6-rayed young brittle-star will remain such throughout life unless schizogony occurs.

MUSEUM OF COMPARATIVE ZOÖLOGY,
Cambridge, Mass., March, 1913.

LITERATURE CITED.

BELL, F. J. 1892. A contribution to the classification of Ophiuroids, etc. Proc. Zool. Soc., London, pp. 175–183.
FEWKES, J. W. 1887. On the development of the calcareous plates of *Amphiura*. Bull. M. C. Z., vol. 13, pp. 107–150.
GRAVE, C. 1898. Embryology of *Ophiocoma echinata* Agassiz. Prelim. Note. Johns Hopkins Univ. Circ., vol. 18, pp. 6, 7.
——— 1900. *Ophiura brevispina*. Mem. Biol. Lab., Johns Hopkins Univ., vol. 4, No. 5, and also in Mem. Nat. Acad., Washington, vol. 8, pp. 83–100.
JACKSON, R. T. 1899. Localized stages in development in plants and animals. Mem. Boston Soc. Nat. Hist., vol. 5, pp. 89–153.
LUDWIG, H. 1878. Beiträge zur Anatomie der Ophiuren. Zeits. f. w. Zool., vol. 31, pp. 346–394.
——— 1879. Das Mundskelet der Asterien und Ophiuren, etc. Zeits. f. w. Zool., vol. 32, pp. 672–688.
——— 1880. Neue Beiträge zur Anatomie der Ophiuren. Zeits. f. w. Zool., vol. 34, pp. 333–365.
——— 1881. Zur Entwicklungsgeschichte des Ophiurenskelettes. Zeits. f. w. Zool., vol. 36, pp. 181–200.
——— 1899. Jugendformen von Ophiuren. Sitz. d. K. Preuss. Akad. der Wiss. Berlin, vol. 14, pp. 210–235.
LYMAN, T. 1882. *Challenger* Ophiuroidea. Reports on the Zoology of H. M. S. *Challenger*, vol. 5, pt. 14, pp. 1–386.
MORTENSEN, T. 1912. Über Asteronyx loveni M. Tr. Zeits. f. w. Zool., vol. 101, pp. 264–289.
SIMROTH, H. 1876–77. Anatomie und Schizogonie der *Ophiactis virens* Sars. Zeits. f. w. Zool., vol. 27, pp. 417–485; vol. 28, pp. 419–526.
SOLLAS, I. B. J., and W. J. 1912. *Lapworthura:* A typical brittle-star of the Silurian Age, etc. Phil. Trans. (B), vol. 202, pp. 213–232.

LIST OF PLATES.

EXPLANATION OF LETTERING.

A = Ala.
AH = Anterior hypapophysis.
E = Epanapophysis.
Ep = Epapophyses.
LAR = Lower alar ridge.
MH = Median hypapophysis.
P = Protapophysis.
Pa = Parapophysis.
PH = Posterior hypapophysis.
T = Taphrus.
UpAR = Upper alar ridge.
Z = Zygosphene.
Zc = Zygocœle.
Zg = Zygapophysis.
Zp = Zygophore.
Zt = Zygotreme.
Zy = Zygantrum.

PLATE 1.

Ophiactis savignyi (M. & T.).

FIG. 1. A young individual, showing bases of 3 arms, and 3 very youthful arms, of which the median is evidently the youngest. ×40.
2. Disk of smallest individual seen, showing primary plates on older portion. ×40.
3. Mouth of a young specimen, showing 2 old jaws and 3 pairs of old oral tentacles, and 4 young jaws. ×90.
4. Side view of a young jaw with 4 teeth and an old jaw with 5; 2 oral tentacles are also shown. ×90.
5. Torus of a young individual. ×90.
6. Fourth segment from tip of arm, showing skeletal parts, as seen from below. ×90.
7. A very young arm, with only one segment; seen from below. ×90.
8. Vertebra of fifty-fifth segment from mouth in an arm with 70 joints; seen from above. ×40.
9. Vertebra of fiftieth segment of same arm; from above. ×40.
10. Vertebra of fortieth segment of same arm; from above. ×40.
11. Vertebra of thirtieth segment of same arm; from above. ×40.
12. Vertebra of tenth segment of arm with only 18 joints; from above. ×90.
13. Vertebra of twentieth segment of arm with 70 joints; from above. ×40.
14. Vertebra of tenth segment of same arm; from above. ×40.
15. Same vertebra as fig. 14; seen from aboral end. ×40.
16. Same vertebra; seen from below. ×40.
17. Same vertebra; seen from adoral end. ×40.
18. Same vertebra; seen from side. ×40.
19. Vertebra of second segment of arm with 70 joints; seen from above. ×40.

PLATE 2.

FIGS. 1 to 6.—*Amphipholis squamata* (Delle Chiaje).

FIG. 1. One of the second pair of adambulacral plates, with its adjoining oral tentacle, from a specimen 0.65 mm. across the disk; to show posterior (aboral) spinous projection. ×375.
2. One of the oral plates ("jaw") and its adjoining adoral plate, from a specimen 0.80 mm. across disk; to show origin of first 2 oral papillæ, in connection with them, but from separate centers of calcification. ×375.
3. A jaw, and adjoining parts, from a specimen 1 mm. across disk; to show *Amphiura*-stage of development. ×90.
4. A jaw, and adjoining parts, from a specimen 1.35 mm. across disk; to show the *Amphipholis* character attained.
5. Side view of torus and first tooth, from a specimen 0.65 mm. across disk. ×375.
6. Side view of torus and first tooth, also from a specimen 0.65 mm. across disk but somewhat older. ×375.

FIGS. 7 to 12.—*Ophiothrix angulata* (Say).

FIG. 7. Vertebra of sixth segment from tip of arm; from the side. ×90.
8. Typical vertebra; from the side. ×40.
9. Same vertebra; from above. ×40.
10. Same vertebra; showing aboral surface. ×40.
11. Same vertebra; from below. ×40.
12. Same vertebra; showing adoral surface. ×40.

PLATE 3.

FIGS. 1 to 10.—*Lowest arm spine of Ophiothrix angulata (Say).* ×100.

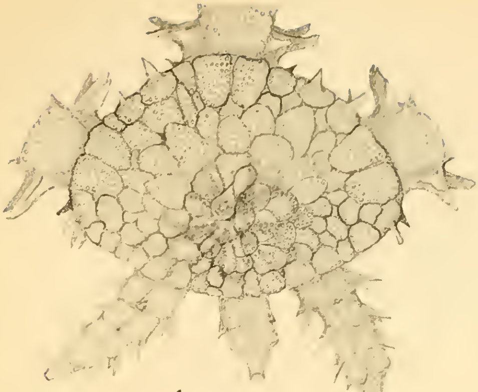
FIG. 1. From first (next to terminal plate) segment.
2. From second segment.
3. From third segment.
4. From fourth segment.
5. From sixth segment.
6. From middle portion of the arm (any segment).
7. From twelfth segment, counting from mouth.
8. From ninth segment from mouth.
9. From sixth segment from mouth.
10. From third segment from mouth.
These spines are all shown in the same position. Figure 6 shows the appearance of the typical spine characteristic of the genus; figures 1–5 show its development, and figures 7–10 its senescence. Spines, like figures 9 and 10, are very little different from the ordinary arm-spines.
11. Next to the lowest arm-spine of *Amphipholis squamata* (Delle Chiaje) from third segment, counting from tip of arm. ×375.

FIGS. 12 to 14.—Lowest arm spine of *Ophiactis savignyi* (M. & T.). ×375.

FIG. 12. From third segment from tip of arm.
13. From sixth segment.
14. From middle of arm (any segment).

FIGS. 15 to 19.—*Ophiothrix angulata (Say).*

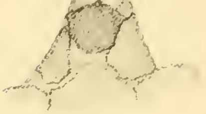
FIG. 15. Torus of specimen 2 mm. across disk. ×90.
16. Torus of adult, 5 mm. across disk. ×40.
17. Torus, teeth, and dental-papillæ of young, 2 mm. across disk, seen from the side. ×90.
18. Central plate, radial shields, and part of disk of a specimen 2 mm. across disk. ×40.
19. The same of a specimen 3 mm. across disk. ×40.

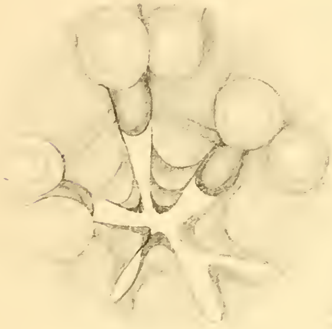

1


5

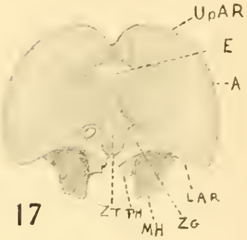

2


6


7


3


4



17


8

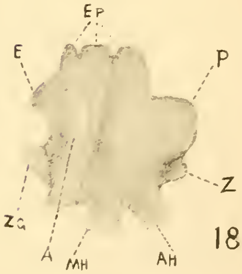

10


9


11

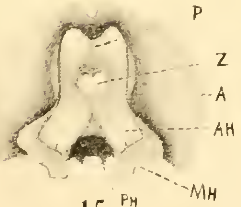

13

14

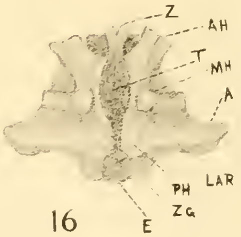


18

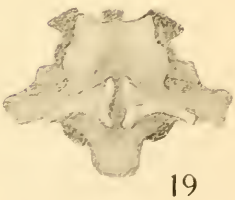

12



15



16


19

1

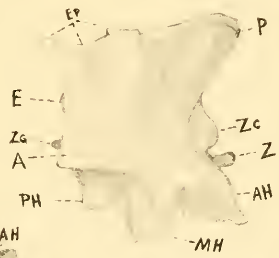
2

4

5

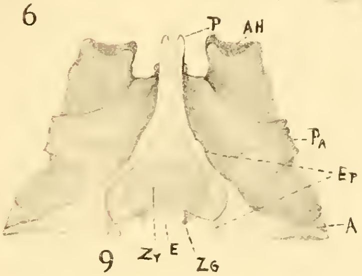
3

6



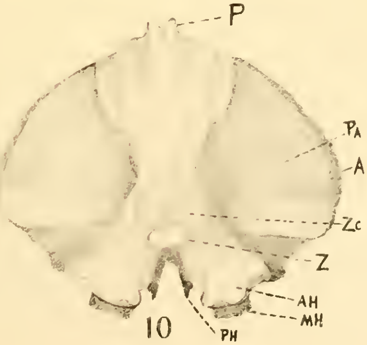
8

7

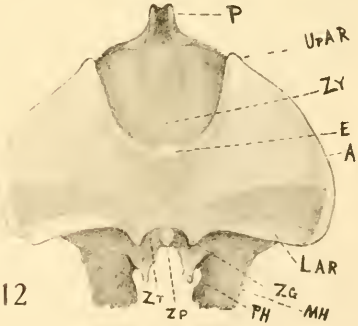


9

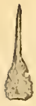
11



10



12



1

2

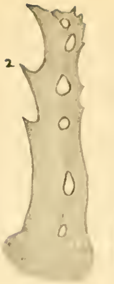
3

4

5

6

7



8

9

10

11

12

13

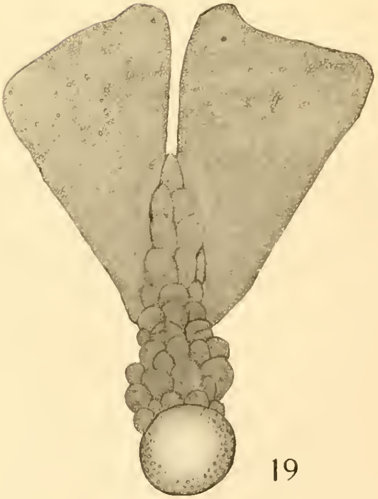
14

15

16

17

18



19

VIII.

THE EARLY INFLUENCE OF THE SPERMATOZOAN UPON THE CHARACTERS OF ECHINOID LARVÆ.

By DAVID H. TENNENT,
Bryn Mawr College.

Eleven text-figures.

THE EARLY INFLUENCE OF THE SPERMATOZOAN UPON THE CHARACTERS OF ECHINOID LARVÆ.

By David H. Tennent.

The question of the influence of the spermatozoan upon the character of the larva has been the basis of a vast amount of discussion among students of embryology. From the time of the early disagreement between the animalculists and the ovists it has proved a fruitful subject for speculation.

In more recent times, since the evolution of the school of developmental mechanics, various attempts have been made at an exact determination of the rôle played by the spermatozoan or by some of its parts. It is conceded that the characters resident in the male parent are transmitted to the offspring by the spermatozoan, either by the chromatin or by the cytoplasm, or possibly by both. But there is no general agreement as to the time in the individual history when "paternal" characters may become evident. There is a fairly general opinion that the egg conditions development, that it is responsible for at least the early developmental processes, and that the sperm, although instigating development, places no paternal stamp on the offspring until relatively late.

Boveri's (1895) classical experiment, criticized adversely by various investigators, but confirmed by Herbst (1907), in which enucleated egg fragments of one species of sea-urchin, fertilized by sperm of another species, gave rise to larvæ which were paternal with respect to the skeleton, showed that in the absence of female nuclear material the sperm nuclear material might assume the direction of some phases of development by the time of the pluteus stage, but there has been little evidence, one way or the other, regarding younger stages. Here the evidence has been negative in so many instances that a positive generalization is often heard to the effect that in development the influence of the spermatozoan is not shown in the character of early embryos.

The discussion between Boveri and Driesch on this subject, in 1903–04, resolved itself finally into a simple difference of opinion in regard to the earlier or later time at which certain characters made their appearance in Echinoid hybrids. Boveri (1895, 1903, 1904) presented evidence on the form of the larvæ, the skeleton, the number of chromatophores, the pigment content of the chromatophores, the arrangement of the chromatophores, the number of primary mesenchyme cells, and, under certain circumstances, the size of the larvæ. Driesch (1903) considered the same points, but by the evidence neither was able to change essentially the belief of the other.

About five years ago the controversy was given a somewhat different form as a result of the researches of Loeb (1908) on heterogeneous hybridization. In this work an echinoid egg, *Strongylocentrotus*, was fertilized by molluscan sperm, *Chlorostoma*, and the resulting plutei were taken as evidence that the inheritance was purely maternal, *i. e.*, from the egg alone. The reason for this was shown by Kupelwieser (1909), who worked out the cytology of the cross *Echinus microtuberculatus* female by *Mytilus galloprovincialis* male and was able to show that true fertilization did not take place, the male nucleus never fusing with the female nucleus, but instead lying at one side of the mitotic figure during division, the larvæ resulting from the cross being, in effect, parthenogenetic.

Herbst (1906) obtained a closely similar result by a combination of artificial parthenogenesis and fertilization, in which the larvæ were held to the maternal type. During segmentation the paternal nuclear material lags and may fail to take part in the segmentation. Development in such cases may be in reality maternal, but it is parthenogenetic.

Results again resembling these were obtained by Günther Hertwig (1912), when he inseminated sea-urchin eggs with spermatozoa which had been subjected to radium rays and found that here again the male nucleus failed to take a normal part in the processes of fertilization and cleavage.

We must distinguish between the cases afforded by this work of Loeb, Kupelwieser, and Hertwig, which deals in fact with a type of parthenogenetic development, no fertilization taking place, and cases in which true fertilization occurs, *i. e.*, the union of an egg and sperm nucleus, although here again we must distinguish between cases in which the union is only temporary and those in which it is permanent. From work done by Baltzer (1909, 1910), Herbst (1909, 1912), and Tennent (1912), evidence has been gained which has proved that even though the two nuclei unite, some of the chromosomes may be eliminated later.

In Godlewski's (1906) fertilization of the echinoid egg with crinoid sperm the union of the nuclei seems to have been permanent. In his fertilization of enucleated fragments of sea-urchin eggs with crinoid sperm, the young stages (gastrulæ, four cases) were larvæ which followed the sea-urchin type.

Finally "partial fertilization," discussed by Boveri and Herbst, also represents a true fertilization, although the union between the nuclei may be delayed until after segmentation has begun, and the resulting pluteus may be in part maternal, in part hybrid in nature.

The consideration of these points makes it clear that we have no established evidence of the influence of the sperm on the characters of stages younger than the pluteus and that new observations based on favorable material is desirable. I count myself fortunate in obtaining material of this nature while on the expedition made by the Department of Marine Biology to Montego Bay, Jamaica.

MATERIAL AND METHODS.

One of the abundant reef sea-urchins at Montego Bay is the primitive form *Cidaris tribuloides*. The living egg of *Cidaris* is exceedingly transparent and the union of the male and female nuclei may be followed in it without difficulty; it may be fertilized readily in the laboratory with its own sperm or with the sperm of other sea-urchins abundant in the vicinity, among these being *Toxopneustes* (*Lytechinus*) *variegatus* and *Hipponoë* (*Tripneustes*) *esculenta*. These crosses are easily made. The eggs may be fertilized at once after their removal from the gonad, without artificial aid, although as a check against the possibility of chance fertilization with *Cidaris* sperm they were kept for 2 hours before making the fertilizations. A portion of the eggs was always kept as an unfertilized control.

Many investigators will recognize the convenience and advantage of supplying developing larvæ with an almost complete change of water from time to time. I found it possible to do this by centrifuging the contents of the finger bowls, which I used as aquaria, withdrawing the water from above the larvæ and replacing with fresh water. This method was used only after the third day. This material was centrifuged only long enough to throw the larvæ down to the end of the tubes. The plutei treated in this manner kept in better condition than those not centrifuged and thus not given as complete a change of water. Owing to my limited time no attempt was made to rear the larvæ to metamorphosis. Every possible precaution was taken to avoid chance fertilization or contamination of any nature of the cultures.

Since the completion of the investigation is being delayed by the pressure of teaching it seems best to present at this time the results that were obtained with the living material, leaving the cytological analysis of fixed material for a later time. The outline figures used in illustrating the paper are from camera-lucida sketches made from living larvæ.

INVESTIGATION.

In its normal development *Cidaris* proved of interest, (1) because of its slowness of development when compared with *Hipponoë* or *Toxopneustes;* (2) in the difference in the site of its mesenchyme formation; (3) in the place of the appearance of the larval skeleton.

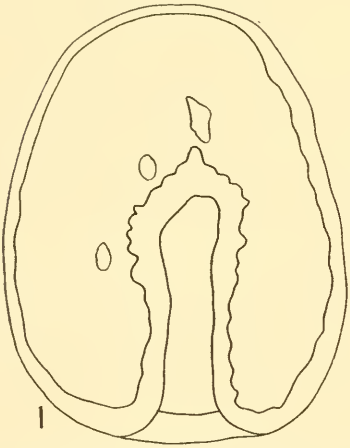
The anaphase of the first cleavage begins about 50 minutes after insemination. The cleavage is like that of other echinoids. The blastula stage is reached in 16 to 18 hours, depending on the lot of eggs; gastrulation begins in 20 to 23 hours; mesenchyme formation begins in 23 to 26 hours, the mesenchyme cells arising from the inner end of the archenteron; chromatophores appear in about 44 hours; the enterocœle arises as a single pouch in 44 to 50 hours; in 55 hours two enterocœles may be seen, formed by the division of the single vesicle; in 72 to 73 hours the beginning of the formation of the skeleton may be noted. Even at this time, the beginning of the fourth day, the body has not begun to assume the form of an echinopluteus, and it is not until the fifth day that the arms begin to push out. These facts are of interest when compared directly with those regarding the development of *Toxopneustes.*

The processes are here shown in parallel. The hours mentioned indicate hours after fertilization.

Cidaris.	Hours.	*Toxopneustes.*	Hours.
Blastulæ (swimming)	16 to 18	Blastulæ (swimming)	5.5
		Mesenchyme	8
Gastrulæ (beginning)	20 to 23	Gastrulæ (beginning)	9
Mesenchyme	23 to 26		
Chromatophores	44	Chromatophores	15 to 16
Skeleton (beginning)	72 to 73	Skeleton (beginning)	15 to 16
Pluteus	120	Pluteus	24

The earliest striking difference between the two forms is in the time and place of mesenchyme formation, *Cidaris* in this respect resembling the crinoids more closely than the echinoids.

No mesenchyme is formed until the archenteron has pushed well into the blastocœle (fig. 1). The cells then push out from the end and from just behind the end of the archenteron. During the next few hours the migration of cells from the archenteron continues, while the cells within the blastocœle increase in number by division. A network formed by fine protoplasmic processes, as in other echinoids, is formed (fig. 2).



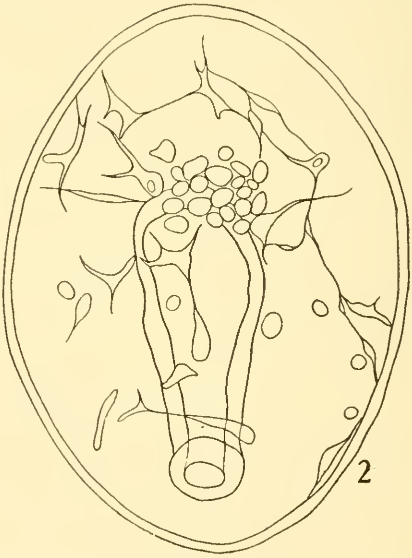
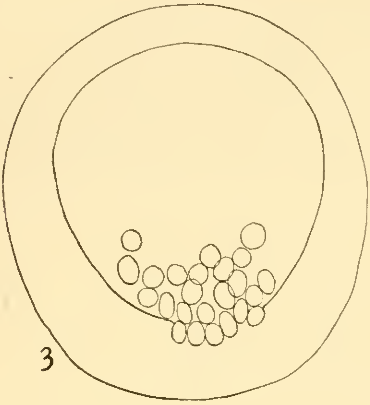
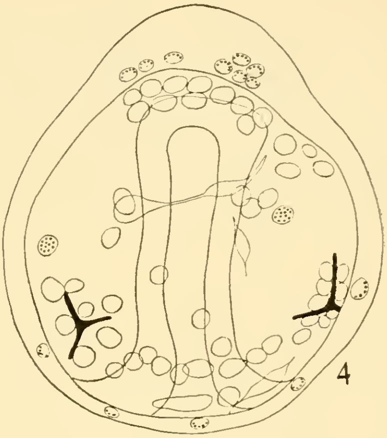
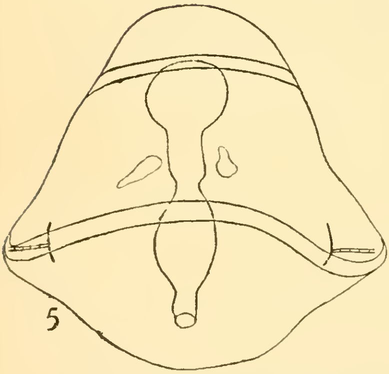


Fig. 1.—Optical section, *Cidaris* gastrula, showing beginning of mesenchyme formation. 23 hours.
Fig. 2.—Optical section, later *Cidaris* gastrula. 41 hours.

In *Toxopneustes*, it will be recalled, the micromere end of the blastula becomes flattened and the primary mesenchyme cells push into the blastocœle before gastrulation begins (fig. 3). This mesenchyme is first scattered throughout the blastocœle, the greater number of the cells remaining, however, at the posterior pole. When the archenteron pushes in they lie as a ring about it, later becoming aggregated in two groups, one at each side of the base of the archenteron; in each group the characteristic skeletal spicules arise. The secondary mesenchyme is given off from the end of the archenteron after this has grown well toward the anterior end of the blastula (fig. 4).







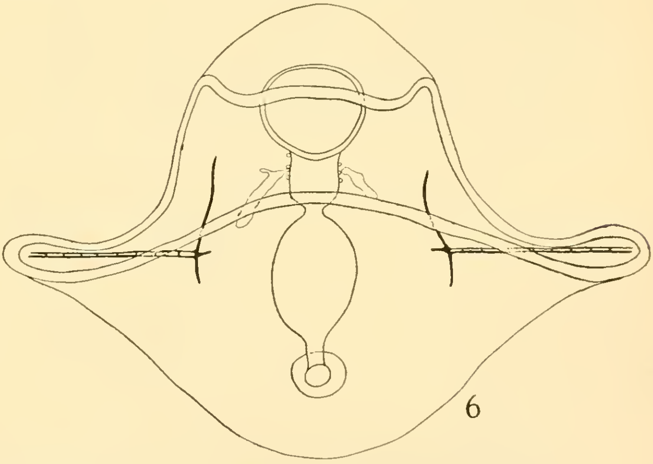


FIG. 3.—Optical section, *Toxopneustes* blastula, showing beginning of primary mesenchyme formation. 8 hours. Drawn from preserved material.
FIG. 4.—Optical section of *Toxopneustes* gastrula, showing formation of secondary mesenchyme and of skeleton. Chromatophores in blastocœle and wall. 41 hours.
FIG. 5.—Young *Cidaris* pluteus, showing character and position of early skeleton. 73 hours.
FIG. 6.—*Cidaris* pluteus. 6 days.

In the case of *Cidaris*, after the formation of the primary enterocœle and the dorsal water-tube (50 hours), the gastrula begins to elongate and to become broader at the posterior end. When the primary enterocœle separates into right and left enterocœles (the left remaining in connection with the water-tube (55 hours),two ciliated bands make their appearance, the posterior band about one-third the length of the body from the posterior end of the body, the preoral band somewhat less than one-third the length of the body from the anterior end. Between these bands the body now begins to be somewhat concave. In general appearance at this time the larva resembles that of *Asterias* more than it does that of an echinoid. At 66 hours the bands are well developed and the region between the bands has become still more concave.

Between this time and 72 hours a further increase in size and change in form of the body is apparent, the posterior half becoming much broader and the posterior end more rounded, while by reason of this change of form the anal region has been shifted forward. During the period from 60 to 65 hours the œsophagus, stomach, and intestine differentiate from the archenteron. About 72 hours after fertilization the first indication of a larval skeletal system may be noted in the triradiate spicules arising in groups of mesenchyme cells in the broadest part of the body, about the level of the anterior half of the stomach, and just beneath the postoral band of cilia. The laterally directed axis is seen to be double and gives rise to a rod of the latticed type (fig. 5). During the next day the body continues to increase in size, the anterior and posterior ciliated bands become connected about the edges of the ventral depression, and the postero-lateral (?) arms begin to push out laterally from the body. A short medio-dorsal rod may be seen developing in the skeletal system (fig. 6).

7

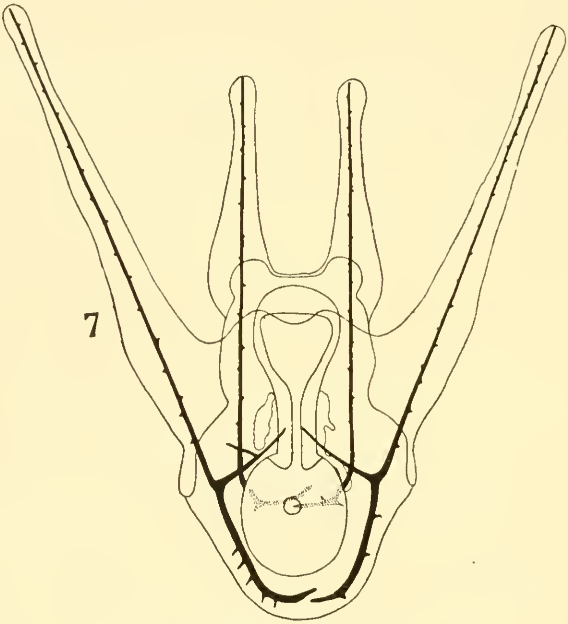


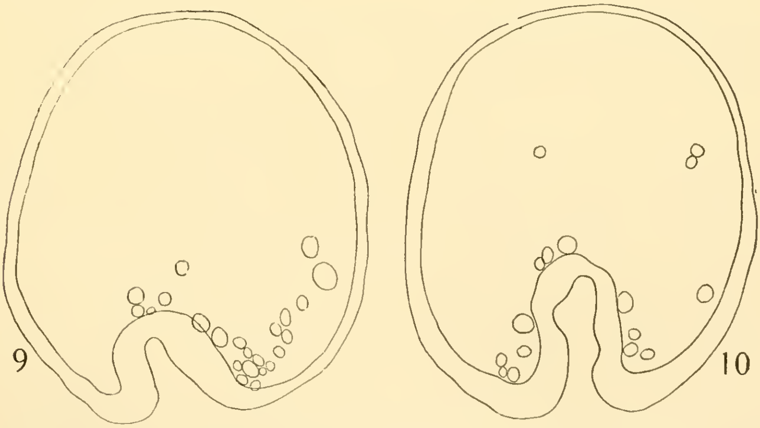
FIG. 7.—*Toxopneustes* pluteus. 6 days.

A brief inspection of a figure of a *Toxopneustes* pluteus of the same age, 6 days (fig. 7), is sufficient to convince one of the striking difference in form. It is evident from a comparison of the development of these two forms that if a cross between the two were possible valuable data might be afforded.

THE CIDARIS FEMALE BY TOXOPNEUSTES MALE CROSS.

The cross is easily made, the *Cidaris* eggs requiring no treatment in order that fertilization may be accomplished. The eggs may be fertilized with *Toxopneustes* sperm immediately after their removal from the ovary, but as a check against the possibility of chance fertilization with *Cidaris* sperm they were kept for 2 hours before inseminating with the foreign sperm. More than 90 per cent of the eggs fertilized; the typical fertilization membrane appeared shortly after the addition of the sperm. In this cross no difference from the characteristic normal *Cidaris* development was noted before the beginning gastrula stage. The fertilization-cleavage interval was not lessened, as in the case of certain other echinoid crosses that I have described. In point of time the appearance of the mesenchyme seemed slightly hastened, although the gain in time is not great enough to warrant a general conclusion, since it is quite within the range of variation between different lots of straight-fertilized eggs. My statement regarding a possible slight hastening refers to comparative straight and cross fertilization in the same lot of eggs. Even here I prefer to draw no conclusions, since I have made the comparison with only eight lots of eggs. As to the *place* of mesenchyme formation there is no chance for either personal equation in the observer or individual variation in the larvæ to play a part.

Fig. 8.—Optical section of portion of *Toxopneustes* ♂ × *Cidaris* ♀ gastrula, showing primary mesenchyme cells at base of archenteron. 24 hours.



Figs. 9 and 10.—Optical section of *Toxopneustes* ♂ × *Cidaris* ♀ gastrula, showing primary mesenchyme cells. 24 hours.

In the hybrids the mesenchyme arises from the sides and around the base of the archenteron, close to its point of union with the blastopore (figs. 8, 9, 10). This was true in every instance. The difference between the normal and the hybrid was so striking that it needed no confirmation by other observers, but purely as a matter of personal interest I asked four other investigators at the laboratory to look at the two sets of living larvæ and describe their observations to me. The independent observation of each of these investigators was a confirmation of my own.

The succeeding stages show considerable variation. In some the growth of the archenteron ceases and the blastocœle becomes filled with a mass of opaque cells (fig. 11). In others gastrulation continues. In a few cases a small skeletal spicule was formed in the mass of mesenchyme cells at the base of the archenteron. I was unable to keep the hybrid material alive beyond the gastrula stage.

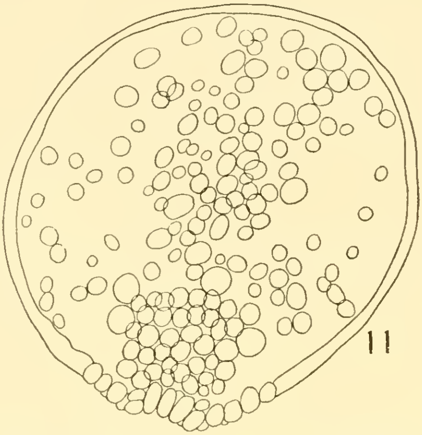


FIG. 11.—Optical section of *Toxopneustes* ♂ × *Cidaris* ♀ abnormal gastrula; blastocœle nearly filled with opaque cells. 40 hours.

GENERAL DISCUSSION.

We have already noted Boveri's conclusions regarding the early influence of the sperm on development. My results confirm his general thesis as to an earlier influence than that commonly accepted, although my conclusion is based on evidence not afforded by his crosses.

In the nature of the case the results given by inseminations in which the sperm nucleus does not unite with the egg nucleus are without direct value in this connection. They may have an indirect value in showing that the sperm cytoplasm, if it has become a part of the egg cytoplasm, has not influenced the early development. As has already been indicated, the larvæ obtained from such inseminations are essentially parthenogenetic.

The only investigation of which I know, which is closely comparable to mine, is that of Godlewski (1907), and even here we are comparing the reciprocal cross between forms whose early development is similar. In Godlewski's cross the fertilization of echinoid eggs (primary mesenchyme formed in the blastula stage) with crinoid sperm (crinoid mesenchyme formed in the gastrula) resulted in larvæ which followed the maternal course of development; this was true even for the fertilized enucleated egg fragment.

In my own work a cross made on material with similar differences of development, namely, the *Cidaris* egg (mesenchyme formed in the gastrula), with *Toxopneustes* or *Hipponoë* sperm (echinoids in which the primary mesenchyme is formed before gastrulation), gave larvæ in which the mesenchyme was formed at the beginning of gastrulation, the mesenchyme arising at the sides and base of the archenteron.

We may ask this question: Is the foreign sperm better able to hasten than to retard certain characteristic processes? It is not now possible to answer this question, but it is one which should incite investigation.

The objection may be raised that as I was unable to keep the hybrid larvæ alive beyond the gastrula stage, the cells which I observed passing into the blastocœle were abnormal and indicated an abnormal condition of the larvæ. Certainly they were not normal *Cidaris* larvæ; they were hybrids, and as hybrids they were normal. The larvæ were not the formless aggregations of cells obtained in some crosses, but proceeded on a perfectly regular course of development. Even granting that when compared with larvæ derived from straight fertilized *Cidaris* eggs, they were not normal, it must be admitted that the abnormality was in the direction of normal *Toxopneustes* mesenchyme formation and also that the condition was brought about by the use of the foreign sperm and that the result indicates that the sperm is able to exert an influence on the character of development at a stage earlier than that heretofore demonstrated.

Shearer, De Morgan, and Fuchs (1911), as well as some other recent workers on the hybridization of echinoids, have come to the conclusion that the early larvæ are of too variable a nature to afford any definite evidence of parental influence. In order that I may not be misunderstood, let me quote directly from the paper mentioned:

> As the result of extensive investigation of the early larval history of our various crosses, we have come to the conclusion that these are too variable to afford any definite evidence of parental influence and especially is this true with regard to the skeleton, heretofore considered the chief index of inheritance.

This conclusion was reached after the investigation of three species of *Echinus*. The authors make the statement with regard to the forms upon which they have worked and do not apply it to all cases. The investigation of a sufficient number of properly chosen forms will convince any investigator that parental influence may be indicated even in early larval stages, and especially is this true with regard to the skeleton.

LITERATURE.

Baltzer, F. 1909. Die Chromosomen von *Strongylocentrotus lividus* und *Echinus microtuberculatus.* Arch. f. Zellforsch., Bd. 2.

——— 1910. Über die Beziehung zwischen dem Chromatin und der Entwicklung. Arch. f. Zellforsch., Bd. 5.

Boveri, Th. 1895. Über die Befruchtungs- und Entwickelungsfähigkeit kernloser Seeigeleier und die Möglichkeit ihrer Bastardirung. Arch. f. Entwickelungsmech., Bd. 2.

——— 1903. Über den Einfluss der Samenzelle auf die Larvencharaktere der Echiniden. Arch. f. Entwickelungsmech., Bd. 16.

——— 1904. Noch ein Wort über Seeigelbastarde. Arch. f. Entwickelungsmech., Bd. 17.

Driesch, H. 1903. Über Seeigelbastarde. Arch. f. Entwickelungsmech., Bd. 16.

Godlewski, E. 1906. Untersuchungen über die Bastardierung der Echiniden- und Crinoidenfamilie. Arch. f. Entwickelungsmech., Bd. 20.

Herbst, C. 1906. Das Beherrschen des Hervortretens der mütterlichen Charaktere. Arch. f. Entwickelungsmech., Bd. 22.

——— 1907. Auf der Suche nach der Ursache der grösseren oder geringeren Ähnlichkeit der Nachkommen mit einem der beiden Eltern. Arch. f. Entwickelungsmech., Bd. 24.

——— 1909. Die cytologischen Grundlagen der Verschiebung der Vererbungsrichtung nach der mütterlichen Seite. 1. Mitteilung. Arch. f. Entwickelungsmech., Bd. 27.

——— 1912. Ibid. 2. Mitteilung. Arch. f. Entwickelungsmech., Bd. 34.

Loeb, J. 1908. Über die Natur der Bastardlarve zwischen dem Echinodermenei und Molluskensamen. Arch. f. Entwickelungsmech., Bd. 26.

Kupelwieser, H. 1909. Entwicklungserregung bei Seeigeleirn durch Molluskensperma. Arch. f. Entwickelungsmech., Bd. 27.

Hertwig, G. 1912. Das Schicksal des mit Radium bestrahlten Spermachromatins im Seeigelei. Arch. Mic. Anat., Bd. 79.

Shearer, DeMorgan, and Fuchs. 1911. Preliminary notice on the experimental hybridization of echinoids. Jour. of the Marine Biol. Association, vol. 9.

Tennent, D. H. 1912a. The behavior of the chromosomes in cross-fertilized echinoid eggs. Jour. Morph., vol. 23.

——— 1912b. Studies in cytology. II. Jour. Exp. Zool., vol. 12.

IX.

STUDIES OF JAMAICA ECHINI.

BY ROBERT TRACY JACKSON.

Twenty-one figures, including one plate.

STUDIES OF JAMAICA ECHINI.

By Robert Tracy Jackson.

It was my privilege to join the Carnegie Institution of Washington expedition to Jamaica in the spring of 1912. While there, studies were made of the later stages of development and the variation of a number of species of regular Echini. All the material studied was collected at Montego Bay, close along shore in shallow water of less than a fathom in depth. This locality is very favorable for studying these animals, as abundant material can be obtained, on the reefs or grass-covered bottom, by wading in water usually less than 3 feet in depth. The observations are in extension of those recently published in the "Phylogeny of the Echini" (Memoirs Boston Society of Natural History, vol. 7, 1912). As only a few species are involved, they are taken up systematically, giving under each the results of the observations.

Eucidaris tribuloides (Lamarck).

This species is fairly common at Montego Bay, so that sufficient material was available for laboratory work, but it was not so abundant as the other species of regular Echini studied. It occurs in shallow water and is surprisingly dull and sluggish, presenting none of the activity of motion seen in *Centrechinus* or the more passive *Tripneustes*. In collecting *Eucidaris*, one simply picks them up, and in no case observed did the animal cling to the ground by its tube-feet. The adults at Montego Bay are rather small for the species, not attaining the size of specimens seen from the Bahamas. An average adult from Montego Bay measures about 30 to 35 mm. in diameter. Material from Port Antonio, Jamaica, also is small, but is very abundant, as I had over 500 specimens collected at that locality. Of a limited number of specimens of this species from the Bahamas, the largest noted is 52 mm. in diameter. Only a few young specimens of *Eucidaris* were found at Montego Bay. In individuals measuring up to 10 mm. in diameter the ocular plates are all exsert and the genital pores are wanting. There was not sufficient young material to study the periods at which the ocular plates travel in and reach the periproct. In the adult of this species, typically (58 per cent), oculars V, I, IV are insert, as previously ascertained from an examination of 849 specimens from several localities. A specimen measuring 11 mm. in diameter has all five genital pores in place, as have also all larger specimens. Whether the genital pores would come in at this exact period of growth could only be known from observations on a larger series of specimens than was available. In living specimens, opened when perfectly fresh, it was found that the teeth extend only very slightly above the base of the foramen magnum. As this structure is very shallow in *Eucidaris*, the dorsal border of the tooth very nearly coincides with the upper limits of the lantern, but the tooth does not extend horizontally over the top of the lantern as in *Strongylocentrotus* (Phylogeny of the Echini, p. 179, plate 5, figs. 1, 6). The dental capsules, which are the fleshy bags inclosing the base of the teeth, are small in *Eucidaris*, not large and inflated as they are in *Strongylocentrotus* and in the Echinidæ.

The Cidaridæ, the sole family representing the order Cidaroida, is the only group of modern Echini that extends back into the Palæozoic. The Palæozoic species, which belong to the genus *Miocidaris*, present only slight differences from recent typical members of the order. As an ancient group that has suffered comparatively little change in its whole geological history the structure and development of the Cidaridæ is of especial interest. Something is known of the post-embryonic development of cidarids, due principally to Loven's critical study of young *Goniocidaris* (Echinologica, Stockholm, 1892), but further knowledge of the developing stages of this primitive archaic type is much to be desired.

CENTRECHINUS SETOSUS (LESKE).

The most abundant sea-urchin at Montego Bay is *Centrechinus*[1] *setosus* (Leske), which abounds in countless profusion in shallow water on the reefs. In strong distinction from the quiescent habits of *Eucidaris*, *Centrechinus* is a most active animal, moving about freely and actively and waving its long spines in a threatening fashion. The spines are so sharp and cause such poisonous wounds that they are a constant menace to bathers, and specimens have to be collected with caution or serious results will follow. The tube-feet have only the slightest hold on the sea-floor, so that specimens can be picked up with long-handled forceps without any perceptible resistance. In this *Centrechinus* differs markedly from *Tripneustes*, *Strongylocentrotus*, or *Echinometra*, which on a rocky surface cling tenaciously by the tube-feet. Young specimens of *Centrechinus* have spines which are strongly banded; white and very dark, nearly black, alternating. The light and dark bands are of about equal width. The spines are long in young as well as in adults, and a specimen 12 mm. in diameter has spines 36 mm. in length. A specimen 60 mm. in diameter has spines up to 150 mm. in length. From this it occurs that a small specimen looks rather big with spines extending radially, and a large specimen is menacing indeed when the needle-like sharpness of these weapons is considered. Banded spines as a

---

[1] *Centrechinus* is a name which I gave (Phylogeny of the Echini, p. 27) to replace the name *Diadema*, which in post-Linnæan usage is preoccupied for a crustacean. To replace an old, established name is unfortunate, and some objection has been raised to my action. As *Diadema* has been in current use as a generic name for sea-urchins, Gastropoda, and Lepidoptera, it seems that the rule of priority must be maintained and a new generic name substituted for *Diadema* in these three groups.

character are retained until individuals are about 20 to 25 mm. in diameter, after which they are typically a deep uniform black. As an exception, a specimen 40 mm. in diameter was seen, in which all the spines were banded as in youth. Frequently in immature specimens the older ventral spines are banded when the dorsal spines, situated on the later-added and therefore younger plates are quite black. In adults, no case of banded spines was seen, but occasionally pure white spines are interspersed with the black, and in a few cases observed all the primary spines were white in the adult. Whatever the color of the spines, the test is of a dark, uniform black in life.

In the family of the Centrechinidæ, *Centrostephanus longispinus* (Phillipi), from the Mediterranean, in adults has spines which are banded white and light brown, the pattern recalling those of young *Centrechinus*. In *Echinothrix calamaris* (Leske), from the Pacific, the spines are very variable in adults, being all dark, purple or green, all white, or banded; great diversity may occur in the spines of one individual. In other families of Echini, banded spines occur occasionally as species characters; they are a feature of *Cœlopleurus maculatus* A. Agassiz and Clark, and are common in species of the Temnopleuridæ.

In my previous studies of ocular plates and their variation in this species, there was a limited number (110) of developing specimens, and of these very few were really small. Of adults, 1,168 were examined from various localities. With a good series of developing specimens from a single locality, certain differences are brought out from the earlier limited observations. There are also differences in the percentages of adult characters from what obtained in the species as a whole from different localities. In table 2 (page 156) are given the characters of developing series, and the variations of adults of this and other species are considered. The aberrant variations are given in detail only under the consideration of the species in the text.

As to the developing series of *Centrechinus setosus*, in 50 specimens from 4 to 15 mm. in diameter, all the oculars are exsert (fig. 1). In 103 specimens 15 to 20 mm. in diameter, 78 per cent have all oculars exsert, 4 per cent have ocular I insert, and 5 per cent have ocular V insert. In 2 per cent oculars I, V are insert, and in 7 per cent oculars I, V, IV have reached the periproct. Of aberrant variants of this size there are 5 per cent, one specimen having ocular IV only insert; one having I, IV insert; two having V, IV insert; and one has oculars I, V, IV, III insert. It is interesting to see that at this youthful period, while a high percentage have oculars all exsert, many stages of development as regards the oculars are presented by some of the specimens. Of the next larger size, 20 to 25 mm., 270 specimens, 51 per cent still have all the oculars exsert; 1 per cent have ocular I insert; and 16 per cent have ocular V insert; 11 per cent have oculars I, V, and 17 per cent have oculars I, V, IV insert. In one specimen, 0.4 per cent, oculars I, V, IV, II are insert. There are eight aberrants, or 3 per cent; of these, 1 has ocular IV insert; 1 has I, IV, and 6 have oculars V, IV insert.

In the next larger series, 25 to 30 mm. diameter (240 specimens), 21 per cent have all oculars exsert; 3 per cent have ocular I, and 8 per cent have ocular V alone insert; 14 per cent have oculars I, V, and 45 per cent have oculars, I, V, IV insert. As this last is the species character, it is of note that this is the first stage at which this species feature has become a dominant character. In 1 per cent, oculars I, V, IV, II, and in 1 per cent all oculars are insert. Seventeen specimens, or 7 per cent, have an aberrant arrangement. Of these, 4 have ocular IV only insert; 11 have oculars V, IV, one has I, V, II, and one has oculars I, V, IV, III insert. The occurrence of I, V, II insert as an aberrant variant is of interest because this, as previously shown, is a common aberrant when three oculars reach the periproct in the Echinidæ and Strongylocentrotidæ, and occurs also in the Stomopneustidæ. I have not found a case of I, V, II insert in the Cidaridæ, and it is the only case seen in *Centrechinus setosus*, although in this species, 1,398 cases of I, V, IV insert have been observed.

In the next series of *Centrechinus setosus*, 30 to 35 mm. diameter, 245 specimens, 10 per cent have all oculars exsert; 2 per cent have I only; and 12 per cent have V only insert; 5 per cent have I, V, and 63 per cent have I, V, IV insert; 4 per cent have I, V, IV, II insert. Of aberrants, there are 4 per cent, these consisting of 8 specimens with oculars V, IV insert, and 2 with oculars I, V, IV, III insert.

The next series, measuring 35 to 40 mm. in diameter, 169 specimens, has 5 per cent with all oculars exsert; 2 per cent with I only; and 3 per cent with V only insert; 5 per cent have I, V, and 71 per cent have I, V, IV insert; 6 per cent have I, V, IV, II, and 2 per cent have all oculars insert. Aberrants are 5 per cent; of these, two specimens have ocular IV alone insert; 1 has I, IV; 4 have V, IV; and 2 have I, V, IV, III insert.

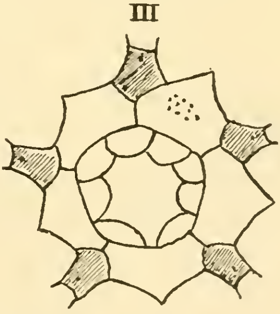
The series 40 to 50 mm. in diameter is considered the last of the developing series. Of this size, 162 specimens, 4 per cent have all oculars exsert, 1 per cent have ocular I, and 0.6 per cent have ocular V only insert; 6 per cent have oculars I, V, and 70 per cent I, V, IV insert; 9 per cent have oculars I, V, IV, II, and 6 per cent have all oculars insert. Of aberrants there are 3 per cent, one specimen having V, IV and 4 having I, V, IV, III insert. The series 35 to 40 mm. and 40 to 50 mm. in diameter make a close approach to the mature series as regards the species character of I, V, IV insert, but these two younger series have more of the developing and fewer of the progressive characters than are seen in the older series.

While *Centrechinus setosus* is profusely abundant at Montego Bay, specimens do not attain as large a size as in Florida, from which locality many individuals exceed 100 mm. in size. Of the adult series from Montego Bay, 50 to 80 mm. in diameter, 162 specimens, one specimen, or 0.6 per cent, had ocular V only, and one had oculars I, V insert, both of these specimens are between 50 and 60 mm. in diameter; 73 per cent have I, V, IV insert, the species character; 13 per cent are progressive variants with I, V, IV, II insert and 10 per cent are extreme progressive variants with all oculars insert; 3 per cent are aberrant variants, all five specimens having oculars I, V, IV, III insert.

Considering the ocular-plate arrangement in *Centrechinus* from Montego Bay as a whole, it is seen, as shown clearly in table 2 (page 156), that from all exsert, the character of the young, there is a steady progressive series with growth in the development or traveling in of ocular plates. *Centrechinus* is a member of the most primitive suborder, the Aulodonta, of the Centrechinoida, and as such is worthy of special attention, for, as shown by Professor Hyatt, primitive types in a group have a slow development as compared with specialized types, and in character approach nearest to the next lower series of their own phylum. The development of *Centrechinus* amply bears out this important truth.

Of the total 1,401 specimens of *Centrechinus setosus* listed from Montego Bay, the aberrants are 59 in number, of which 8 have ocular IV only insert; 3 have oculars I, IV insert; 32 have oculars V, IV insert; 1 has oculars I, V, II insert, and 15 have oculars I, V, IV, III insert. It is noteworthy that in the mature series (50 to 80 mm. diameter) the only aberrants that occurred were cases of oculars I, V, IV, III insert, thus indicating that the other aberrants seen in immature individuals may be considered as irregularities in the order of sequence of the coming in of ocular plates, rather than as aberrants that would have retained the given character if they had lived to grow up.

In specimens of *Centrechinus* up to 14 mm. in diameter (48 individuals), all the genital plates are imperforate (fig. 1), whereas in those 14.5 mm. and all larger with very few exceptions, all genital plates have the genital pores.[1] In comparison with this, the specialized *Strongylocentrotus dröbachiensis* attains its genital pores when between 5 and 10 mm. in diameter (Phylogeny of the Echini, pp. 131, 170). *Centrechinus* has all oculars exsert up to 15 mm. diameter, and with intermediate stages still has 4 per cent all exsert when 40 to 50 mm. diameter. *Strongylocentrotus dröbachiensis*, on the contrary, has typically oculars all exsert only in very young specimens and has only 29 per cent with all exsert in specimens (51) between 2.5 and 4 mm. in diameter; further, it has only 4 per cent with oculars all exsert in specimens (82) between 4 and 5 mm. diameter. *Centrechinus* first attains the species character of oculars I, V, IV insert as a dominant feature (45 per cent) when it is 25 to 30 mm. in diameter. *Strongylocentrotus dröbachiensis* attains I, V insert, the species character, as a dominant feature (52 per cent) when 5 to 10 mm. in diameter. In *Centre-*



1

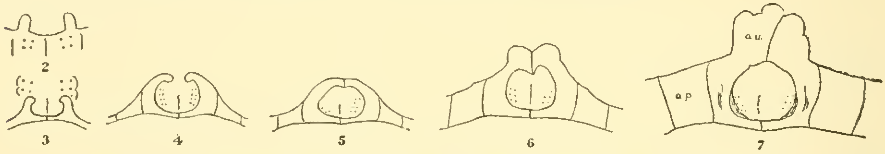
FIG. 1.—*Centrechinus setosus* (Leske). Montego Bay, Jamaica. × 12. Diameter 11 mm. Oculars all exsert. No genital pores, large marginal plates in periproct. All these are youthful characters.

---

[1] I regret to say that by error in the figure published of a young *Centrechinus* (Phylogeny of the Echini, fig. 88, p. 106), genital pores are shown. The specimen has no pores and they were inadvertently drawn.

chinus when oculars begin to enter the periproct, the first to enter is V or I, but in the Montego Bay series V is by far the more common,[1] they being in the ratio of 102 of ocular V to 23 of ocular I. In this feature *Centrechinus* makes an approach to the Cidaridæ, in which group, when one ocular is insert, it is almost always ocular V. As previously shown, when in the Centrechinoida four oculars reach the periproct, it is typically I, V, IV, II, and when any other combination exists it is nearly always I, V, IV, III. This combination, while rare in the Centrechinoida as a whole, is relatively more frequent in *Centrechinus* and is a typical feature or a frequent variant in some species of the Cidaridæ. In this feature also, therefore, *Centrechinus* makes a certain approach to the Cidaroida.

In *Centrechinus*, when opened fresh and alive, it is found that the teeth extend above the base of the foramen magnum about to the upper line of the lantern, but the proximal base of the teeth does not extend horizontally over the lantern as in the Echinidæ, Strongylocentrotidæ, and Echinometridæ. Further, the dental capsule, inclosing the base of the tooth, is small. In the limits of the teeth dorsally and the small dental capsule, as well as in the grooved teeth, *Centrechinus* makes a close approach to the characters of the Cidaridæ as represented by *Eucidaris tribuloides*.



Figs. 2–6.—Perignathic girdle in *Aspidodiadema* and its development in *Centrechinus*.

2.—Adult *Aspidodiadema meijerei* (Döderlein), Pailolo channel, Hawaiian Islands. The auricles are separate spur-like styles.

3.—*Centrechinus setosus* (Leske), Montego Bay, Jamaica. Specimen 5 mm. diameter. Auricles are separate styles, apophyses faint.

4.—The same. Specimen 10 mm. diameter. Auricles are more developed and arch over the ambulacra.

5.—The same. Specimen 25 mm. diameter. Auricles meet over the ambulacra in a slender arch.

6.—The same. Specimen 70 mm. diameter. Auricles developing a high plate-like character, apophyses also are high.

7.—*Centrechinus setosus*, Bermuda. Specimen 110 mm. diameter. Auricles have developed a high plate-like character; apophyses are high ridges.

Very little attention has been paid to the development of the perignathic girdle excepting by Lovén, who described it in *Cidaris* and *Strongylocentrotus* (Echinologica). I also have published a few observations on the development and variation of the perignathic girdle. *Centrechinus*, while being a primitive type in many respects, has in the adult a specialized perignathic girdle having high auricles which meet in a broad plate-like arch over the ambulacra and also high apophyses on the interambulacral areas (fig. 7). Such being the character of the adult, it is of much interest to follow the development of this, which is one of the most specialized perignathic girdles known in Echini. When a specimen is 5 mm. in diameter, the apophyses show only slight indications of development and the auricles stand up as separate, blunt, spur-like processes on either side of the ambulacrum (fig. 3).

---

[1] In previous observations from various localities with limited material, ocular I predominated over V numerically.

The upper ends of the auricles at this early stage are slightly flattened, but do not arch over the ambulacrum at all. In a specimen 10 mm. in diameter, the apophyses have developed somewhat, and the auricles are inclined over the ambulacral area, but do not meet (fig. 4). In specimens 25 mm. in diameter the apophyses have developed into distinct elevated ridges, and the auricles have met over the ambulacral areas as slender arches (fig. 5). From this point on to the adult the development of the perignathic girdle is marked by the increase in height of the apophyses and concurrently the increase in height and the lamellar expansion of the auricles (figs. 6, 7).

In seeking comparisons to these stages of *Centrechinus* in the adults of related forms, it is found in *Aspidodiadema meijerei* (Döderlein), *A. nicobaricum* Döderlein, and *Dermatodiadema horridum* A. Agassiz, representing the family Aspidodiadematidæ, that the auricles exist as small conical spurs situated on either side of the ambulacral areas, and apophyses are not developed (fig. 2). This condition corresponds with the first stage noted in the development of *Centrechinus* (fig. 3). This relation of the perignathic girdle is of much interest because in the Aspidodiadematidæ the simple ambulacral plates, the large primordial ambulacral plates on the peristome, the large apical disk and simple spur-like auricles are all primitive characters, indicating that the family is more primitive structurally than is the still primitive family of the Centrechinidæ. While primitive in many characters, the Aspidodiadematidæ is specialized in that all the oculars reach the periproct, and *Centrechinus*, while belonging to the primitive suborder Aulodonta, is specialized in its great development of the perignathic girdle. This shows how primitive and specialized features may be combined in one and the same type.

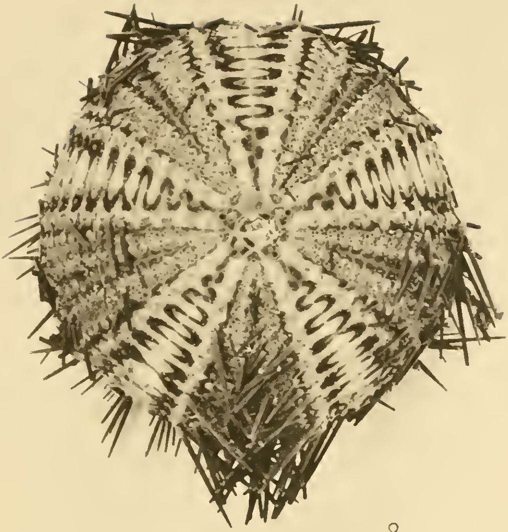
Mr. Agassiz (Panamic Echini, 1904, p. 59) says of the Aspidodiadematidæ: "The auricles are most irregularly developed. They are either wanting or mere projections, slightly raised." I have examined three representative species and a number of specimens of this family, and find no evidence that the auricles are irregularly developed. In adults they are not wanting except where broken off. They are perfectly definite spur-like projections, and of much interest as being structurally the most primitive auricles known in any of the adult Centrechinoida. As the Cidaroida have apophyses but no auricles, and as these structures make their first known appearance in the Centrechinoida, the simplicity of their structure in adults of the Aspidodiadematidæ and in the young of *Centrechinus* is of particular interest.

TOXOPNEUSTES VARIEGATUS (Lamarck).

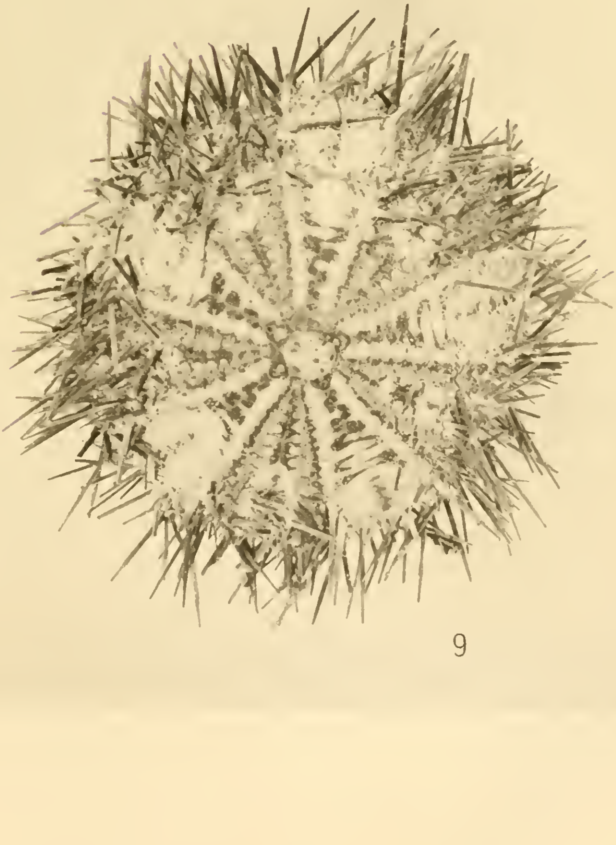
A common species at Montego Bay is *Toxopneustes variegatus* (Lamarck), which is found abundantly on the grass-covered bottom in shallow water. Specimens attain a large size, some measuring 70 mm. in diameter. Few young specimens were found, though this is perhaps due to the fact that special search was not attempted, from limitations of time. The test is mottled green and white, with green spines as the prevailing color. Some young specimens show on the green and white groundwork purple primary tubercles and purplish spines. A peculiar color-pattern was observed as a relatively rare variation in the fact that in the interambulacral areas of some specimens the green followed a zigzag pattern on a white ground and extended thus from the apical disk adorally, but in no case observed extended further than the ambitus. The zigzag green color-pattern on a cream-white ground of a specimen measuring 45 mm. in diameter is shown in fig. 8. The lower figure on the same plate is of a somewhat larger specimen, measuring 48 mm. in diameter, in which the zigzag pattern occurs only near the apical portion of the test. Both of these specimens with others figured in this paper are now in the collections of the Museum of Comparative Zoölogy, at Cambridge, Mass. This type of color-pattern was quite new to Dr. Clark and Professor Tennent, both of whom had worked on the species, and I had never seen it before, although I have studied many specimens from different localities.

Being busy with other species, no attempt was made to collect a large series of *Toxopneustes variegatus* for a study of ocular plates, but 400 specimens are tabulated. These are of various sizes, but none were young and they were not graded into sizes for comparison. Of this series, 2 specimens, 0.5 per cent, have ocular I only insert as arrested variants, and one specimen, 0.3 per cent, has ocular V only insert; 84 per cent have oculars I, V insert (figs. 8, 9), which is the species character in all localities; 15 per cent are progressive variants with oculars I, V, IV insert. Four specimens, 1 per cent, are aberrant variants and all of these have oculars I, V, II insert. The ocular character is practically the same as I showed previously in this species from several localities, but the Montego Bay material has a somewhat lower percentage of I, V and corresponding higher percentage of I, V, IV insert. My previous observations on 1,043 specimens gave 90 per cent I, V insert and 8 per cent I, V, IV. Comparison of the tabulation of this species may be made with that of the closely allied *Toxopneustes atlanticus* (A. Agassiz) from Bermuda, in which I showed (Phylogeny of the Echini, p. 161) that the mature series (45–77 mm. diameter) has a much higher percentage (28 to 29 per cent) of oculars I, V, IV insert than has *Toxopneustes variegatus*. The Montego Bay experience in the cases of several species brought out the fact clearly that for a close study of variation it is very desirable to tabulate ocular plate characters in specimens from a single definite locality because considerable difference in a given species may occur in different localities.

In *Toxopneustes variegatus*, when opened fresh, it is found that the proximal part of the teeth extend horizontally over the top of the lantern and the teeth are bent back on themselves in the same plane, also the dental capsules which inclose the base of the teeth are large and bladder-like, in these characters differing from *Eucidaris* and *Centrechinus*, but agreeing with *Strongylocentrotus* as I previously described it. In a young specimen 12 mm. in diameter, the auricles are still separate, but in larger specimens they are



8



9

joined in an arch over the ambulacral areas. In large adults the apophyses are developed as a moderate ridge and auricles are joined in a delicate arch which never becomes heavy, as in large specimens of *Tripneustes*.

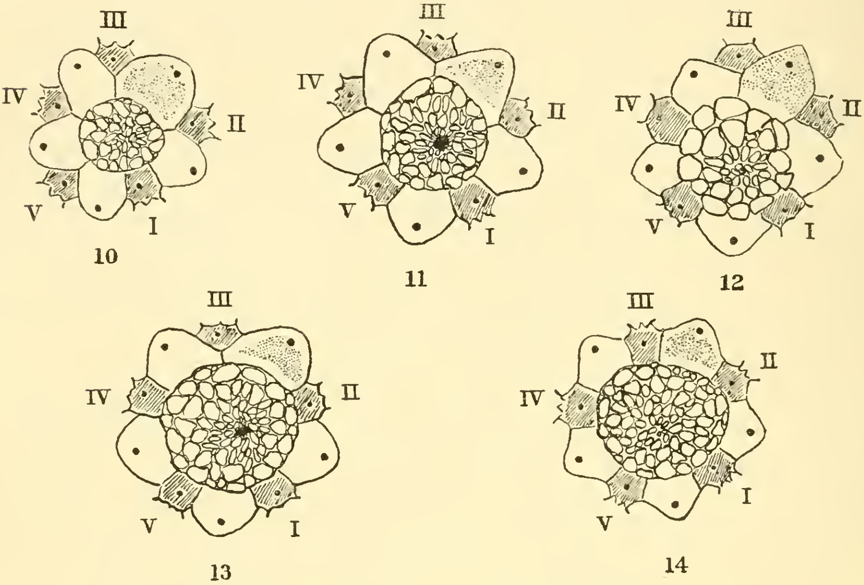
TRIPNEUSTES ESCULENTUS (Leske).

One of the abundant species at Montego Bay is *Tripneustes esculentus* (Leske). It occurs on grass bottom and also on the reefs in shoal water, and is a strikingly handsome sea-urchin when alive, with its white spines against the dark purplish groundwork of the fleshy covering of the test. The larger individuals live out in the open in full view, but young specimens are found only in crevices or on the under side of rocks. The young are not common, and although sought for diligently, no very young specimens were found and only a limited number of the youngest seen were obtained. Perhaps some other time of year, as summer or autumn, would be more favorable for young material of this species. In *Tripneustes esculentus* from this locality the ocular plates continued to travel in or enter the periproct, from the youngest to the largest series of specimens observed, as shown by the tabulation. For this reason, as regards the feature of ocular plate development, what is called the developing series for this species in the table is arbitrarily drawn at a maximum of 70 mm.

Taking up the developing series: Ten specimens of 20 to 25 mm. diameter have 50 per cent with ocular I only insert, and 50 per cent with oculars I, V insert. Younger specimens would doubtless have all oculars exsert as a developing stage. The next size, 25 to 30 mm. diameter, 21 specimens, has 24 per cent with ocular I only insert and 76 per cent with I, V insert. The relations of these two younger series shows that it is a period of rapid development. The next series, 30 to 40 mm. diameter, 60 specimens, has 12 per cent with I only insert; 80 per cent with I, V insert; 2 per cent with I, V, IV and 2 per cent with I, V, IV, II insert. Three specimens, 5 per cent, are aberrant with I, V, II insert. This stage, while holding the I only insert as a developing character, has attained the I, V; the I, V, IV; and the I, V, IV, II insert; which are each respectively the feature of the species as a character in one or more of the several localities from which material was studied, but the relative proportions of the three characters differ from that of any known adult series.

The series 40 to 50 mm. diameter, 42 specimens, has lost the I insert as a youthful character; 90 per cent have oculars I, V insert; 2 per cent have I, V, IV, and 2 per cent have I, V, IV, II insert. Five per cent are aberrant, one of the two specimens having I, V, II insert and the other V, II insert. This stage has the highest percentage of I, V insert of any age of material from Montego Bay. The series 50 to 70 mm. diameter, 34 specimens, has 53 per cent with oculars I, V insert; 18 per cent with I, V, IV; and 6 per cent with I, V, IV, II insert. Aberrants are 24 per cent, eight specimens, all of which have oculars I, V, II insert. The developing series in its later phases may be compared broadly with material from Bermuda or other localities for the species in which oculars I, V insert is the adult local character, as it is the youthful character in these immature stages from Montego Bay.

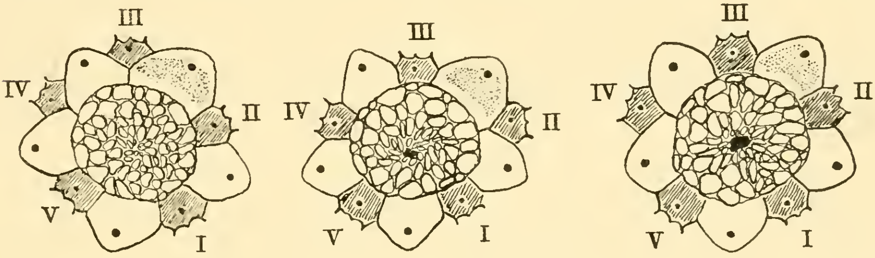
The next larger series, 70 to 90 mm. diameter, 125 specimens, has one specimen with ocular I insert as an arrested variant; 30 per cent have oculars I, V insert. The latter, which was the leading character in the later developing stages, has now passed into the phase of an arrested variant. 34 per cent have oculars I, V, IV insert, and this is the dominant character of this age. As a phase it can be compared with a series of adults from the Bahamas in which locality I, V, IV insert is the typical character. Twenty-eight per cent have oculars I, V, IV, II insert, which at this stage may be considered a progressive character as it is at all other known localities for the species. In 8 per cent the ocular arrangement is aberrant, all of the ten specimens having oculars I, V, II insert.



Figs. 10–14.—Normal ocular plate arrangement in *Tripneustes esculentus* (Leske), Montego Bay, Jamaica. All figures nearly × 2.

10.—Diameter 99 mm. Ocular I only insert, an extreme arrested variant.
11.—Diameter 114 mm. Oculars I, V insert, an arrested variant for the locality.
12.—Diameter 110 mm. Oculars I, V, IV insert, an arrested variant for the locality.
13.—Diameter 115 mm. Oculars I, V, IV, II insert, the typical character for the locality.
14.—Diameter 106 mm. All oculars insert, a progressive variant.

The next series, 90 to 110 mm. diameter, 200 specimens, has one specimen with ocular I only insert as an arrested variant (fig. 10), and one specimen with ocular V alone insert. For ocular V only to be insert is a rare variation in *Tripneustes* and is unusual in the family Echinidæ. In 22 per cent oculars I, V are insert. This, which was the character of the later developing series and is the character of adults at Bermuda and Florida, has dropped considerably in its percentage as an arrested variant. In 24 per cent oculars I, V, IV are insert. This character for Montego Bay has at this stage dropped into the phase of an arrested variant, though it was the dominant character in the series 70 to 90 mm. in diameter and is the adult character in a series from the Bahamas. Forty per cent have oculars I, V, IV, II insert. This is the first series in which this character is a dominant feature at Montego Bay, and for all earlier stages in this locality and for all other localities known it is a progressive character. Two per cent have all oculars insert as a progressive variant (fig. 14). It is somewhat striking that with four oculars insert as a dominant character, there should not be more specimens with all oculars insert. In this series, 25 specimens, 13 per cent, have an aberrant arrangement of ocular plates. Of these aberrants, 22 have oculars I, V, II insert; two have I, V, IV, III insert (fig. 16), a very rare variant in the Echinidæ when four plates reach the periproct, but although rare here, it is a common character in the Cidaridæ and a not rare variant in *Centrechinus setosus*. One aberrant specimen of *Tripneustes* has oculars I, V, II, III insert (fig. 17). This, which is a right-handed equivalent of I, V, IV, III (just as I, V, II is a right-handed equivalent of I, V, IV) is a unique variant for Echini as far as my experience goes. In the Centrechinoida, as tabulated in my preceding memoir and in the present paper, 619 specimens are recorded, in which four plates reach the periproct. Of these, in 554 specimens (89.5 per cent) it is oculars I, V, IV, II the bivium and posterior pair of the trivium, in 64 specimens (10.3 per cent) it is the aberrant arrangement I, V, IV, III, and in the one specimen cited (0.16 per cent) it is I, V, II, III. (Compare figs. 13, 16, 17.)



15 16 17

FIGS. 15–17.—Aberrant ocular plate arrangement in *Tripneustes esculentus* (Leske), Montego Bay, Jamaica. All figures nearly × 2.

FIG. 15.—Diameter 115 mm. Oculars I, IV, II insert, a common aberrant variant, a right-handed equivalent of the normal character I, V, IV insert.
FIG. 16.—Diameter 106 mm. Oculars I, V, IV, III insert, a rare aberrant variant, but the usual one when four oculars but not I, V, IV, II are insert.
FIG. 17.—Diameter 102 mm. Oculars I, V, II, III insert, a unique aberrant variant, a right-handed equivalent of I, V, IV, III insert.

The series containing the largest specimens, 110 to 132 mm. diameter, 82 specimens, has 13 per cent with oculars I, V insert as arrested variants (fig. 11); 24 per cent with I, V, IV insert as arrested variants (fig. 12); and 43 per cent with I, V, IV, II insert as the local character of the species (fig. 13). Five per cent have all oculars insert as a progressive variation, and 15 per cent, 12 specimens, are aberrant in ocular arrangement. Of these aberrants, 11 specimens have oculars I, V, II insert (fig. 15), and one has V, IV, II insert. In this specimen genitals 5 and 1 are fused, mechanically shutting out ocular I from access to the periproct.

The series of *Tripneustes esculentus* from Montego Bay is very interesting from the point of view of ocular development on several accounts. The specimens show a direct progressive increase in the number of oculars insert and the relative percentages of the same from the youngest to the largest series observed. In specimens fully matured, as regards this character, and including from 90 to 132 mm. in diameter, they have as the dominant character (40 to 43 per cent) the oculars I, V, IV, II insert. This is the only locality known for this species, and it is the only recent species known[1] in which four oculars reach the periproct as a typical character. In previous studies of *Tripneustes esculentus*, many specimens were tabulated from several localities, but without detailed measurements of the size of the specimens. As the material was from various sources, it is impossible to go over it again to ascertain the sizes but it is fair to say that the material was practically all adults. With this qualification it is interesting to compare the tabulations of *Tripneustes esculentus* from the several localities from which there was sufficient material to give any reasonable basis for consideration.

TABLE 1.

No. of specimens.	Locality.	Ocular I insert; V, IV, II, III exsert.		Ocular V insert; I, IV, II, III exsert.		Oculars I, V insert; IV, II, III exsert.		Oculars I, V, IV insert; II, III exsert.		Oculars I, V, IV, II insert; III exsert.		All oculars insert.		Arrangement of oculars aberrant.	
		p. ct.	No.	p. ct.	No.	p. ct.	No.	p. ct.	No.	p. ct.	No.	p. ct.	No.	p. ct.	No.
193	Bermuda..	2	3	.....	.....	61	117	35	67	2	3	0.5	1	1	2
112	Florida...	.....	.....	1	1	46	52	29	33	12	13	.....	.....	12	13
160	Bahamas..	.....	.....	0.6	1	22	35	46	73	27	43	2	3	3	5
282	Jamaica[1]..	0.4	1	0.4	1	19	54	24	67	40	114	3	8	13	37

[1] 90 to 123 mm. diameter.

As shown in table 1, *Tripneustes* from Bermuda is characterized strongly, 61 per cent, by having oculars I, V insert, with 35 per cent I, V, IV insert as progressive variants, also in 2 per cent I, V, IV, II, and 0.5 per cent all oculars one insert as progressive variants. The aberrants are few, 1 per cent, one specimen having I, V, II and one having V, IV, II insert. This Bermuda lot is the most primitive of the species that I know of as regards ocular arrangement in adults.

Tripneustes from Florida has 46 per cent with oculars I, V insert, which is still the dominant character, but with a lower percentage than at Bermuda. As progressive variants, 29 per cent have I, V, IV insert, and 12 per cent have I, V, IV, II. The aberrants are 12 per cent, all being cases of I, V, II insert. Florida specimens, while having oculars I, V insert as the character, have a lower percentage of this character and a higher percentage of progres-

---

[1] In *Acrosalenia pseudodecorata* Cotteau, from the Bathonien of France, oculars I, V, IV, II are said to be insert as a species character (Phylogeny of the Echini, p. 112).

sive variants than Bermuda material, hence it is structurally an advance on that and a step towards the next higher advance as represented in the series from the Bahamas.

Material from the Bahamas collected by C. J. Maynard has only 22 per cent of I, V insert. This is not the character of the locality and has therefore passed into the phase of an arrested variant. There are 46 per cent with oculars I, V, IV insert. This is the dominant character of the Bahama material, while it would be a progressive variant for Bermuda and Florida, and further, would be an arrested variant for the Montego Bay series. In the Bahamas, 27 per cent have I, V, IV, II insert, a common progressive variant, and 2 per cent have all oculars insert. The aberrants are relatively few, 3 per cent, four of the aberrants having I, V, II insert and one having I, V, IV, III insert. Structurally, in its percentages of ocular arrangement, the Bahama material is intermediate between the Florida and Montego Bay series.

The Montego Bay material, considering only the two largest-sized series tabulated on page 156 and treating them as a single series of 90 to 132 mm. diameter, has 19 per cent with oculars I, V insert as a moderately common arrested variant, but with the lowest percentage of any of the localities given. In 24 per cent oculars I, V, IV are insert, which, for this locality, is an arrested variant, though it is a progressive variant for Bermuda and Florida, and a dominant character for the Bahamas. In 40 per cent, oculars I, V, IV, II are insert, the dominant character for this locality, though it is a progressive variant for all the other localities; 3 per cent have all the oculars insert, which as a progressive variant, is only a slight advance on that existing in the other regions cited. The aberrants, 13 per cent, have already been considered above, and do not need further mention excepting that it is interesting that most of them are cases of I, V, II insert, as in other localities.

In all the localities given *Tripneustes esculentus* is an abundant form, and in all attains a large size. The specimens from Bermuda were collected for me and averaged very large, the largest measuring 145 mm. in diameter, yet this locality has the lowest ocular index. The cause of the progressive evolutionary series as marked by the higher and higher percentages of ocular plates reaching the periproct is unknown, but it is a fact that it exists and points to the desirability of studying large series of specimens from different localities.

In *Tripneustes esculentus*, when opened alive, it is seen that the teeth extend above the top of the lantern and horizontally over the top of the same. The proximal end of the tooth is curved back on itself and is grooved, the keeled character developing as one passes orally along the tooth. The dental capsules are relatively large, all this structure coinciding with that previously described in *Strongylocentrotus dröbachiensis*. In a young specimen of *Tripneustes*, 24 mm. in diameter, the auricles are slender, but already meet in an arch over the ambulacra. In large adults the auricles are quite massive and are fused over the ambulacra in a long median symphysis. They may attain a height of 14 mm. or more. The apophyses are also relatively high and massive in large specimens.

ECHINOMETRA LUCUNTER (Linné).

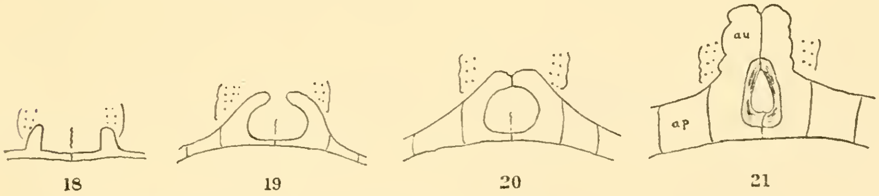
Close in to shore on the coral rock at Montego Bay and in very shallow water *Echinometra lucunter* (Linné) occurs in abundance. Not only adults but individuals of all sizes, down to very young, live in the same exposed situation, where they get the full beat of the waves on shore. This species clings tenaciously to the rock and has to be pulled off from the rock with some effort. The ocular development of this species is very interesting, but unfortunately this was not appreciated until it was too late to gather more material and only a limited series was collected. These were supplemented by a few specimens collected at the same time by Mr. G. M. Gray. A large series could easily be obtained in this locality. As *Echinometra lucunter* is more or less elliptical in horizontal outline, being elongated in the plane of the axis of interambulacrum 3 and ambulacrum I, the measurements of sizes are given in length instead of in diameter, as in the other species considered.

Considering the developing series of *Echinometra*, a set of 34 specimens measuring 4.5 to 15 mm. in length have all the oculars exsert. Of this series, those from 4.5 to 10 mm. in length (26 specimens) were all wanting in genital pores, but these pores exist in all the larger sizes examined. The series 15 to 20 mm. in length, 23 specimens, has 91 per cent with all oculars exsert and 9 per cent with ocular V insert. While ocular I is the first to enter the periproct in the Echinidæ and Strongylocentrotidæ, it is ocular V that typically enters the periproct first in the Arbaciidæ and the Echinometridæ, thus indicating family distinctions in ocular development.

In the series 20 to 25 mm. in length, 58 specimens, in 71 per cent oculars are all exsert and 29 per cent have ocular V insert. In the 25 to 30 mm. series, 110 specimens, 34 per cent have oculars all exsert; 2 per cent have ocular I insert. These are the only cases with ocular I only insert found in Montego Bay material and it is a rare variation in the genus and family, as previously shown. In 54 per cent ocular V is insert. This series is the first stage in growth in which the typical species character of V insert is a dominant feature. In 10 per cent, oculars V, I are insert and in the limited number of specimens this is the first stage at which this character appeared. With more material some specimens would probably be found having I, V insert at an earlier stage of growth. This series is considered the last of the developing stages, but the line as regards ocular development is arbitrary because, as seen in the later series, oculars continue to come in with increasing size of the individuals.

Of the series 30 to 40 mm. in length, 175 specimens, 17 per cent have oculars all exsert as arrested variants, 58 per cent have ocular V alone insert as the typical species character, and 25 per cent are progressive variants with oculars V, I insert. The percentage of V insert at this age is quite near that of the next larger series, but there are more arrested and fewer progressive variants than in the older series. The series 40 to 52 mm. in length, 103 specimens, includes the largest specimens collected at Montego Bay. From other localities specimens may attain a length of 90 or more millimeters. Of this series, 7 per cent have all oculars exsert as arrested variants; 66 per cent have ocular V insert as the maximum development of the species character in the locality; 26 per cent have oculars V, I insert as progressive variants. One specimen, 1 per cent, has oculars V, II insert as an aberrant variant, and this was the only aberrant found in the whole series of 503 specimens collected at Montego Bay.

Considering the ocular arrangement of *Echinometra lucunter* at Montego Bay as a whole: It is a desirable type to study because its species character is to have one ocular insert, and this is a very unusual feature in Echini, otherwise occurring only in the recent Saleniidæ and in *Echinus magellanicus* Philippi from South America. Other Echini, both recent and fossil, are characterized as the species feature of adults by having all oculars exsert, or two oculars insert, or three or more insert, usually three or five. Five insert is a not unusual feature in both living and fossil types as far back as the Palæozoic. In *Echinometra lucunter* it is seen that oculars are all exsert up to a comparatively large size, 15 mm., after which oculars travel in gradually with increasing size, the highest percentages of insertness being in full-grown specimens. Comparing the present tabulation of this species with that previously published (Phylogeny of the Echini, p. 163), it is seen in both that ocular V insert is the species character, though in Bermuda material oculars V, I insert is nearly as frequent. In both lots ocular I insert is a rare feature, and aberrant ocular arrangement is rare. As material previously tabulated was not graded by size, no comparison can be made in this respect.



FIGS. 18–21.—Development of the perignathic girdle in *Echinometra lucunter* (Linné).

FIG. 18.—Young specimen from Montego Bay, Jamaica. Specimen 5 mm. long. Auricles are erect separate styles.

FIG. 19.—The same. Specimen 8 mm. long. Auricles arched over the ambulacrum but separate, apophyses developing.

FIG. 20.—The same. Specimen 15 mm. long. Auricles joined in suture over the ambulacrum.

FIG. 21.—Large adult from Bermuda. Specimen 65 mm. long. Auricles produced vertically as high spoon-like plates, apophyses high ridges.

The teeth of *Echinometra lucunter* extend horizontally over the top of the lantern and the proximal end of the tooth is bent back on itself and in the same plane, as previously described in *Strongylocentrotus*. The proximal part of the tooth is grooved, the keel developing as one passes adorally;

TABLE 2.—*Typical ocular plate arrangement and variation of Echini from Montego Bay, Jamaica.*

Total No. of specimens.	Species and series.	Specimens observed.	Size of specimens.	All oculars exsert.		Ocular I insert; V, IV, II, III exsert.		Ocular V insert; I, IV, II, III exsert.		Oculars I, V insert; IV, II, III exsert.		Oculars I, V, IV insert; II, III exsert.		Oculars I, V, IV, II insert; III exsert.		All oculars insert.		Arrangement of oculars aberrant.	
				p. ct.	No.	p. ct.	No.	p. ct.	No.	p. ct.	No.	p. ct.	No.	p. ct.	No.	p. ct.	No.	p. ct.	No.
			mm.																
			Diam.																
	Centrechinus setosus:																		
1,239	Developing series........	50	4 to 15	100	50	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
		103	15 20	78	80	4	4	5	5	2	2	7	7	.....	.....	.....	.....	5	5
		270	20 25	51	138	1	4	16	43	11	30	17	46	0.4	1	.....	.....	3	8
		240	25 30	21	51	3	6	8	19	14	33	45	109	1	3	1	2	7	17
		245	30 35	10	25	2	4	12	29	5	13	63	154	4	10	.....	.....	4	10
		169	35 40	5	8	2	3	3	5	5	9	71	120	6	11	2	4	5	9
		162	40 50	4	6	1	2	0.6	1	6	10	70	113	9	15	6	10	3	5
				.....	358	.....	23	.....	102	.....	97	.....	549	.....	40	.....	16	.....	54
162	Developed series...........	162	50 80	.....	.....	.....	.....	0.6	1	0.6	1	73	118	13	21	10	16	3	5
1,401																			
400	*Toxopneustes variegatus*.......	......	....	.....	.....	0.5	2	0.3	1	84	335	15	58	.....	.....	.....	.....	1	4
	Tripneustes esculentus:																		
167	Developing series........	10	20 25	.....	.....	50	5	.....	.....	50	5	.....	.....	.....	.....	.....	.....	.....	.....
		21	25 30	.....	.....	24	5	.....	.....	76	16	.....	.....	.....	.....	.....	.....	.....	.....
		60	30 40	.....	.....	12	7	.....	.....	80	48	2	1	2	1	.....	.....	5	3
		42	40 50	.....	.....	.....	.....	.....	.....	90	38	2	1	2	1	.....	.....	5	2
		34	50 70	.....	.....	.....	.....	.....	.....	53	18	18	6	6	2	.....	.....	24	8
				.....	.....	.....	17	.....	.....	.....	125	.....	8	.....	4	.....	.....	.....	13
407	Developed series.........	125	70 90	.....	.....	0.8	1	.....	.....	30	37	34	42	28	35	.....	.....	8	10
		200	90 110	.....	.....	0.5	1	0.5	1	22	43	24	47	40	79	2	4	13	25
		82	· 110 132	.....	.....	.....	.....	.....	.....	13	11	24	20	43	35	5	4	15	12
574				.....	.....	.....	2	.....	1	.....	91	.....	109	.....	149	....	8	.....	47
	Echinometra lucunter:																		
			Length.																
225	Developing series........	34	4.5 to 15	100	34	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
		23	15 20	91	21	.....	.....	9	2	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
		58	20 25	71	41	.....	.....	29	17	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....
		110	25 30	34	37	2	2	54	60	10	11	.....	.....	.....	.....	.....	.....	.....	.....
				.....	133	.....	2	.....	79	.....	11	.....	.....	.....	.....	.....	.....	.....	.....
278	Developed series.........	175	30 40	17	30	.....	.....	58	102	25	43	.....	.....	.....	.....	.....	.....	.....	
		103	40 52	7	7	.....	.....	66	68	26	27	.....	.....	.....	.....	.....	.....	1	1
503				.....	37	.....	.....	.....	170	.....	70	.....	.....	.....	.....	.....	.....	.....	1

the dental capsules are large, embracing the base of the tooth as in the Echinidæ and Strongylocentrotidæ. The perignathic girdle of *Echinometra lucunter* in the adult is highly specialized, having relatively high ridge-like apophyses and extravagantly developed auricles which meet over the ambulacra and are produced dorsally as spoon-shaped plates with a long median symphysis (fig. 21). In young specimens, 5 mm. in length, the auricles exist as simple erect styles situated on either side of the ambulacra but not arched over the same (fig. 18). In specimens 10 mm. in length, the auricles arch over the ambulacra, but are still separate, not meeting in median suture (fig. 19). In a specimen 15 mm. in length, the auricles have met over the ambulacra and are joined by median suture, and the apophyses exist as moderately developed ridges (fig. 20). From here on to the adult condition the apophyses increase in height and the auricles gradually take on an extensive vertical enlargement of their upper border (fig. 21). In *Echinometra viridis* A. Agassiz, *E. oblonga* Blainville, and *E. vanbrunti* A. Agassiz, in adults, the auricles are relatively slender, but are united in suture over the ambulacra; there is no vertical extension in a spoon-like fashion, however, and the auricles closely resemble the condition of *E. lucunter* when about 15 mm. in length.

In *Echinometra mathei* Blainville, in a young specimen 8 mm. long from Mauritius, the auricles are still separate, but in the adult the auricles are joined in suture and with moderately developed spoon-like processes, but not as high processes as are those in adult *E. lucunter.* In *Heterocentrotus trigonarius* (Lamarck), from Mauritius, a young individual 9 mm. in length, has the auricles still separate, but in the adult of this species auricles are arched and united over the ambulacra and with moderately developed spoon-like processes.

SUMMARY AND CONCLUSIONS.

Montego Bay, Jamaica, is an excellent locality for studying Echini on account of the number of species there available and the abundance of material. It is an ideal place for a student who wishes to supplement studies on northern species by observations on tropical forms.

Some 2,878 specimens of regular Echini were collected and studied, but in no case did any specimen show a departure from the typical pentamerous system. This is mentioned as in previous studies it was found that, on the average, completely or partially trimerous, tetramerous, or hexamerous specimens occurred a little oftener than once in a thousand specimens.

In the "Phylogeny of the Echini," page 91, it is stated that "all the evidence goes to show that the full number of oculars that are to become insert are developed early in the life of the individual and apparently later no change in this respect takes place." It was assumed that in Echini specimens of about half the mature size could be accepted as showing the mature characters as regards oculars, and the tables of ocular plate variation, while based principally on adults, were made up on the basis of considering specimens more than half-grown as being fully developed in this respect. This view was based largely on studies of *Strongylocentrotus dröbachiensis*, and in this species the view was fully justified. It is doubtless true of many species, perhaps most species of Echini, that specimens half-grown have practically the full character as regards ocular development. It is not entirely true, however, of all species, for as shown in this paper, in *Centrechinus setosus*, *Tripneustes esculentus*, and *Echinometra lucunter* (table 2), ocular plates continue to come in or enter the periproct as a developing character until nearly or quite grown; therefore, as a result in these species, the largest numbers in percentage of oculars insert may be found in the series of largest specimens. This is not true of selected individuals. That is, the largest specimen does not necessarily have more oculars insert than a smaller individual, but taking a large series of individuals of these species, as shown in the table, the average of each size up to the largest has more oculars insert than any of the preceding sizes. This late coming in of oculars in some species is of interest as showing the mobility in adjustment of the test to allow these changes to take place. It is also of interest in support of the view urged so much by Professor Hyatt, that changes are taking place constantly throughout the life of the individual.

Centrechinus setosus is slow and very gradual in developing its characters. It is slow in acquiring genital pores and very slow relatively in having ocular plates enter the periproct. Up to 15 mm. in diameter no oculars have yet entered the periproct. In the series 20 to 25 mm. in diameter, a little more than half of the specimens still have all oculars exsert. When 35 to 40 mm. in diameter, which is about half-grown for the locality, the species character of I, V, IV insert is developed to a high point, 71 per cent, practically the maximum percentage; but at this age there are more specimens representing developing characters and fewer representing progressive characters than in older series. The maximum of the species character and also the maximum of the progressive characters of I, V, IV, II, and all oculars insert, is seen in the largest specimens of 50 to 80 mm. diameter. The slow rate of development of *Centrechinus* as here shown (p. 156) is graphically brought out by comparing it with that of the development of *Strongylocentrotus dröbachiensis* given in the "Phylogeny of the Echini," page 142. *Centrechinus* is a relatively primitive (and geologically old) genus in the lowest suborder (the Aulodonta) of the Centrechinoida. On the other hand, *S. dröbachiensis* is a highly accelerated species in the highest suborder (the Camarodonta) of the Centrechinoida. As Professor Hyatt showed fully in his studies of fossil Cephalopoda, primitive genera have a slow development and specialized genera have a highly accelerated development. I have shown the same thing in Pelecypoda where the primitive *Avicula* and *Pecten* have a relatively slow development, whereas the specialized *Spondylus* and *Ostrea* have an accelerated development.

Another feature of note in the ocular arrangement of *Centrechinus setosus* is the fact that while ocular I or ocular V may be the first to enter the periproct, V is by far the more common, and in so far makes an approach to the character of the Cidaridæ where ocular V alone is frequently insert, but I alone is rarely insert. In higher groups of the Centrechinoida, when one ocular is insert, the order is more definitely fixed, as in the Arbaciidæ and Echinometridæ, where V is typically and I is rarely insert; or in the Echinidæ and Strongylocentrotidæ, where I is typically and V is rarely insert. Another ocular peculiarity of *Centrechinus* is that where four plates reach the periproct, I, V, IV, III insert is a rather frequent aberrant variant. This is a very rare character in the higher Centrechinoida but is a common character in the Cidaridæ.

Of the ocular characters of *Toxopneustes variegatus*, no special comment is called for. It is simply the record from a definite locality, whereas my previous record of the species was based on specimens from several localities. The peculiar zigzag pattern of color ornamentation shown recalls the somewhat similar pattern seen in some of the Temnopleuridæ.

In *Tripneustes esculentus* the ocular arrangement (figs. 10–17) is one of the most interesting that has been found in any Echini. Two oculars insert is commonly given as the species character, and it is the dominant character in some localities (Bermuda, Florida). In Montego Bay this character is acquired up to 90 per cent in specimens 40 to 50 mm. in diameter, much less than half-grown. But in Montego Bay, as a local character, the species has gone much further and passed through a phase in which oculars I, V, IV are insert like Bahama material, and finally takes on oculars I, V, IV, II insert as the fully matured adult character. It is an exceptionally interesting case as being the acquirement in late stages of growth as a typical feature of a character which is a normal progressive variant of its own species in other localities and also a typical advanced character in all Echini which have four oculars insert. Looking at the test of a nearly grown *Tripneustes* with its solid heavy plates, it is astonishing to realize that they are still plastic and capable of allowing the readjustment of parts indicated by the separation of genitals and traveling in of oculars so as to reach the periproct. Not less surprising is the power of the law of ocular development, that not any ocular, but a certain specific ocular, is the one that is selected by the laws of growth to change its relative position. I know of no more striking case of the definiteness of action in the growth of organisms.

As stated, *Echinometra lucunter* is one of the very few species of Echini characterized by having one ocular insert; therefore a series showing its development is of interest. Four of the six species in the genus *Echinometra* are characterized by having all oculars exsert as the species feature, and in these to have one ocular insert is a progressive variant. Also as a family character, all exsert is the leading feature. Therefore for the genus and for the family, *Echinometra lucunter* can be considered an advanced type as regards ocular arrangement. In accordance with this fact it is not strange, it might even be expected, that it would take on its advanced character of oculars insert at a somewhat late stage as it does. The dominance of V insert, 54 per cent, is first attained when the specimens are 25 to 30 mm. in diameter, about half grown, and the relative increase of V insert progresses somewhat up to the largest series recorded. Having oculars V, I insert is a progressive character for this species, and this feature comes in late, progressively increasing in frequency up to the largest size recorded. To have oculars V, I insert as a typical character is the feature of *Echinometra van brunti* A. Agassiz, from Lower California and South America, and in this respect it is the most specialized species in the genus and family.

In the "Phylogeny of the Echini" much attention was given to ocular plate arrangement and development of the same. The results for the Centrechinoida are there briefly summarized in pages 92–94. As observations on the Montego Bay series have materially extended the results in some important particulars, a brief statement of the laws of ocular arrangement is given here. In the "Phylogeny" the results of tabulating ocular plates in young and adults of the order Centrechinoida are given for 48,541 specimens. Those given above include in addition 2,878 specimens, or including both, 51,419 specimens. By the law of ocular development as worked out in this order, the oculars when entering the periproct, do so in the sequence I, V or V, I, IV, II, III (figs. 10–14), and it is seen by the following how closely this rule is adhered to. Of the total 51,419 specimens of Centrechinoida observed, oculars are all exsert in 6,763 specimens, all others having one or more oculars insert. In 3,708 specimens, one ocular is insert, and of these in 3,679 cases it is either ocular I (fig. 10) or ocular V, that is, 99.22 per cent are correct by rule. There are only 29 exceptions.[1] In 35,951 specimens two oculars are insert, and of these, in 35,611 cases, it is oculars I and V, or the bivium (fig. 11), that is, 99.05 per cent are correct by rule. In all of the 340 exceptions[2] one of the two plates insert is either I or V. In 3,820 specimens, three oculars reach the periproct, and of these, in 3,426 cases, it is oculars I, V, IV, the bivium and the left posterior plate of the trivium (fig. 12), that is, 89.68 per cent are correct by rule. Of the 394 exceptions in 360 cases, the order is I, V, II insert (fig. 15), that is, the right posterior plate of the trivium is insert instead of the left posterior as usual. These may therefore be considered as right-handed specimens. Of the total 3,820 specimens with three oculars insert, 3,786, or 99.37 per cent, have either oculars I, V, IV, or oculars I, V, II insert.[3] In 619 specimens, four oculars reach the periproct, and of these in 554 cases, it is oculars I, V, IV, II the bivium and posterior pair of the trivium (fig. 13); that is, 89.50 per cent are correct by rule.[4] In 558 cases all five oculars are insert (fig. 14). In the

---

[1] Of these exceptions, 18 have ocular IV alone insert, three have ocular III alone insert, and eight have ocular II alone insert.

[2] Of these exceptions, in 101 cases, oculars I, IV are insert; in one case oculars I, III are insert; in 56 cases oculars I, II are insert, which is the species character in *Gymnechinus robillardi* (Loriol) and *G. pulchellus* Mortensen; in 113 cases oculars V, IV are insert; in 4 cases oculars V, III are insert; and in 65 cases oculars V, II are insert.

[3] Of the other 34 exceptions to the rule where 3 oculars are insert, in 4 cases oculars I, V. III are insert; in one case oculars I, IV, II are insert; in 11 cases oculars V, IV, III are insert; and in 18 cases oculars V, IV, II are insert.

[4] Of the 65 exceptions in 64 cases, the arrangement is oculars I, V, IV, III insert (fig. 16); this character which is rare in the Centrechinoida as a whole, occurred principally in *Centrechinus setosus* (47 cases), but it is a common character in the Cidaroida, the other 17 cases of I. V, IV, III insert are scattered through a number of species of the Centrechinoida. One aberrant with four oculars insert has oculars I, V, II, III reaching the periproct (fig. 17). This, which may be considered a right-handed equivalent of I, V, IV, III as far as experience goes, is a unique variant in Echini.

"Phylogeny" a detailed discussion is given of the bearing of aberrant variants which, although aberrant, follow quite definite lines of their own. Of the total 51,419 specimens considered above, 50,591, or 98.39 per cent, are correct by rule as regards ocular arrangement, and 828 specimens (of which 360 are I, V, II as above noted), or 1.61 per cent, have an aberrant arrangement.

From the above records it is seen that ocular plates in the Centrechinoida follow a very definite line as regards which ones reach the periproct, and by their arrangement emphasize a bilateral symmetry through the axis of ambulacrum and ocular III and interambulacrum and genital 5. This is the axis on which the irregular types develop an elongate form, eccentric periproct and other features of bilaterality, and it was urged by Lovén as the correct axis for orienting Echini. Mr. A. Agassiz (*Challenger* Echini, pp. 4–6) criticizes Lovén's determination of the antero-posterior axis in Echini. His argument, however, simply shows that he misunderstood Lovén's point of view.

In accordance with what I previously showed in *Strongylocentrotus* it is seen that the perforation of the genital plates by the genital pores originates at quite definite periods. In *Centrechinus setosus* the genitals are imperforate in specimens up to 14 mm. in diameter, after which with few exceptions all specimens have developed the genital pores. In *Echinometra*, genitals are imperforate up to 10 mm., after which all plates are perforate. Both of these are later in developing than *Strongylocentrotus dröbachiensis*, which is imperforate only up to 5 mm. in diameter, after which in most cases the genitals are perforate.

In *Eucidaris tribuloides* and *Centrechinus setosus* the teeth extend to the upper line of the lantern, but do not extend horizontally over the top of the same; also, in both the dental capsules embracing the base of the teeth are small. These are both doubtless primitive conditions, and are opposed to the condition found in the Echinidæ and Strongylocentrotidæ. In *Toxopneustes variegatus*, *Tripneustes esculentus*, and *Echinometra lucunter* the teeth extend horizontally over the top of the lantern, the proximal end of the tooth is grooved, not keeled, the keel appearing further down the tooth, all as in *Strongylocentrotus*. This grooved character is of interest as a localized stage in development, as it shows that the young growing point of the tooth has the character retained throughout life in the Aulodonta, Cidaroida, and Palæozoic genera, in which the teeth are always grooved. In *Toxopneustes*, *Tripneustes*, and *Echinometra* the dental capsules are large, here again being like the character of *Strongylocentrotus* and differing from the condition in *Eucidaris* and *Centrechinus*.

In *Centrechinus setosus* the perignathic girdle is specialized in the adult, with high apophyses and high laminar auricles joined over the ambulacra. In the young, the apophyses are very slight and the auricles are simple spur-like processes, as in the adult Aspidodiadematidæ, which represent the simplest auricles known. Later, in *Centrechinus*, the auricles arch over the ambulacra, but without fusion. Then they fuse in delicate arches, a condition comparable to that of the adults of *Chætodiadema pallidum* A. Agassiz and Clark and *Centrostephanus rodgersi* A. Agassiz. Later still, in *Centrechinus*, the auricles develop laminar expansions on their upper border, which in large specimens become extensive.

In *Echinometra lucunter*, the perignathic girdle is also very specialized, attaining an extravagant development of the auricles. In the young, however, the auricles exist as simple separate styles. Later they arch over the ambulacra, but without being in contact; still later they join over the ambulacra as delicate arches, a condition comparable to that seen as the adult character in simpler species of the genus. Finally, the auricles take on a great development of the dorsal border, producing the spoon-like arches characteristic of the species.

As shown and urged by Hyatt from his studies of Cephalopoda, and as I have shown in previous studies, in the present study of Echini, and in plants, development, that is the addition of differential characters, continues more or less markedly throughout the life of the individual, and a study of such development yields facts of value in the structure, the morphology, and the phylogenetic relations of the group in hand.

X.

THE SPERMATOGENESIS OF THE MONGOOSE; AND A FURTHER COMPARATIVE STUDY OF MAMMALIAN SPERMATOGENESIS, WITH SPECIAL REFERENCE TO SEX CHROMOSOMES.

BY H. E. JORDAN,
Professor of Histology and Embryology, University of Virginia.

One plate and nine text-figures.

THE SPERMATOGENESIS OF THE MONGOOSE; AND A FURTHER COMPARATIVE STUDY OF MAMMALIAN SPERMATOGENESIS, WITH SPECIAL REFERENCE TO SEX CHROMOSOMES.

By H. E. Jordan.

INTRODUCTORY.

In view of the recent discovery of heterochromosomes in a number of the higher vertebrates it seemed desirable that the spermatogenesis of still other forms should be carefully studied with particular attention to the possible presence and variable behavior of homologous "accessory" chromosomal elements. While this study was in process opportunity was afforded to collect in Jamaica, British West Indies, material of the mongoose.[1] This material is interesting in a number of respects and serves well as a starting-point for such comparative study as will appear from its description. Other material at hand includes that of cat, squirrel, pig, rabbit, white mouse, sheep, horse, mule, bull, and dog.

HETEROCHROMOSOMES LACKING IN MALE.

MONGOOSE.

Spermatogonial nuclei more generally contain three plasmosomes (fig. 1), though there may be more or fewer. Only a very few nuclei were seen in mitosis. Many stages of apparent amitosis are present (fig. 2). The rarity of mitotic figures and of binucleate cells indicates that the prevailing type of division among the spermatogonia is amitotic. The presence, however, of a few binucleate spermatocytes and spermatids shows that cell-body divisions do not always follow the nuclear divisions.

The primary spermatocytes contain a single nucleolus (plasmosome), seen only in the resting condition of the nucleus. The fact that this body never appears subsequently makes the synapsis and division stages of the mongoose especially favorable for study with reference to the presence of an "accessory chromosome." There can be no confusion here between a plasmosome and a chromosome-nucleolus, as has apparently been the case in some forms. Moreover, the early disappearance of the plasmosome in mongoose gives support to the general conclusion that synaptic and post-synaptic chromatin elements are chromosomes, more especially when invariably on the nuclear membrane instead of being disposed at random.

The synizesis phase is characterized by a very compact, deeply chromatic mass of simple threads (fig. 4). The mass is situated at the pole of

---

[1] This opportunity occurred during a month's stay at the temporary Marine Biological Laboratory of the Carnegie Institution of Washington at Montego Bay in the spring of 1912. I take this occasion to express my thanks for the privileges of the Institution's expedition to Jamaica, and for daily kindnesses on the part of the director, Dr. Alfred G. Mayer.

the nucleus, frequently, but not invariably, next the idiosome. The remainder of the nuclear space remains empty, except for a few delicate linin threads, more abundant in the vicinity of the mass. All about the idiosome are pale spherical mitochondria, now apparently present for the first time; but no clue appears as to their origin.

The fact that the synizesis nucleus is not appreciably larger than that of the resting stage shows that synizesis is not due to mechanical factors consequent upon a great increase in nuclear sap. On the contrary, this phenomenon is unquestionably the result of the specific activity of the chromatic nuclear thread. Its frequently polar position may be due to idiosome influence.

In the bouquet stage the simple threads emerge from the synizesis mass in pairs (fig. 5) and unite side by side (parasynapsis). The nucleus is still of approximately the same size; and again the chromatin threads give evidence of a specific activity. The process continues until the previously empty nucleus is filled with double threads crossing in every direction throughout the nucleus (fig. 6). Subsequently the nucleus enlarges somewhat, and the double threads shorten and thicken (fig. 7). The beginning of division of the idiosome marks this as the early prophase. The bivalent chromosomes appear more chromatic and knobbed at the ends, an early indication of tetrad formation. Figure 8 illustrates a later prophase stage, in which the chromosomes have become still shorter, uniformly chromatic, and more compact, a number appearing as complete tetrads.

The point of special interest is that nowhere throughout these early phases has the slightest evidence of an accessory chromosome appeared. No evidence would be expected to appear subsequently, and this is actually the case, as shown in figures 9 to 17. At metaphase the chromosomes are all arranged in a very compact equatorial plate (figs. 9 and 10). No chromosome seems marked by peculiar behavior or uncommon size. An accurate count seems impossible. Innumerable division figures appear, but the chromosomes are so closely compacted as to preclude definition of limits. A most careful study warrants only the statement that the number of chromosomes is somewhere around 24.

A resting stage ensues, but without chromosome-nucleolus, in contradistinction to the usual condition in forms with an accessory chromosome, or without even a plasmosome. The division figures of the second mitosis are smaller, somewhat less compact, and seem to consist of fewer chromosomes. We may be dealing here, as in the opossum, with a second pairing, or a hemioid group (Jordan, 1911). The smaller size of the chromosomes, however, makes this a little doubtful.

Figure 14 illustrates a resting spermatid, with conspicuous idiosome. At the next step in the metamorphosis (fig. 15) the cell has elongated, the nucleus has become more dense and in consequence smaller, and the idiosome has given place to the archoplasmic sphere. The latter contains centrally a chromatic granule, presumably the centrosome (fig. 15). The sphere seems to have arisen directly from the idiosome by process of vesiculation and rejection of one or several small plastin particles. The condensing nucleus moves into an elongating projection of the cell, and then to and beyond the periphery (figs. 16 and 17). Meanwhile the "sphere" has flowed backward over the elongating nucleus, its lateral limits being marked by a distinct line for some distance on either side of the growing axial filament. The filament is marked proximally by two granules (the products of the original centrosome, fig. 15), the anterior one at the point of attachment to the nucleus, the posterior one passing along the axial filament as the "ring centrosome" (figs. 17 and 18) to the posterior end of the middle piece. At the later and adult stages the middle piece is attached to the head by a delicate neck (fig. 20, drawn in the living condition), in which appears a knob, the proximal centrosome, or "end knob" (figs. 19 to 21). The posterior limit of the middle piece is defined by the termination of the spiral filament. The latter arises by a coalescence of mitochondria included within the limits of the backward-extending sphere (middle piece). The remaining mitochondria fail of inclusion and are cast off with the discarded cytoplasm. This observation, made also in a number of other forms (*e. g.*, opossum, Jordan, 1911; *Euchistus*, Montgomery, 1912), invalidates any hypothesis attributing specific hereditary significance to mitochondria.

CAT.

The later steps in the spermatogenesis of the cat, including the spermatid and subsequent stages, have recently been described by Leplat (1910). As to the prespermatid stages, it may be said in brief that they are essentially similar to those described for mongoose, and no convincing evidence appears at any stage of heterochromosomes. Respecting the postspermatid stages also, the similarity amounts practically to an identity; and my own observations on these stages agree essentially with those made and illustrated by Leplat.

More recently Gutherz (1912) has described and illustrated (in two figures) first spermatocytes of the cat stained both in the iron-hematoxylin and the Biondi mixtures. His conclusion confirms my own as to the probable absence of heterochromosomes. However, he figures a synaptic (synizesis) and a postsynaptic stage in which appear heterochromosome-like elements in iron-hematoxylin preparations. The true acidophile nature of these bodies, however, is revealed in the Biondi material. On the basis of this observation he casts doubt upon the interpretation as a heterochromosome of the element described by Winiwarter and Sainmont in their iron-hematoxylin preparations of the oöcyte of the cat. I can only add that my material (also stained with iron-hematoxylin) reveals elements somewhat similar to those described and illustrated by Gutherz for the first spermatocytes, but which, on grounds of morphology, location, relation to spireme, and general behavior, I can not interpret as typical X-elements. Moreover, in well-decolorized preparations their non-chromatic nature is likewise revealed. The illustrations of the oöcytes of the cat by Winiwarter and Sainmont (see figs. 27*a*, 33, and 44) answer to the main criterion, namely morphological, for the presence of a heterochromosome, "split monosome." A comparison of the illustrations of the spermatocytes and oöcytes of the cat as given by Gutherz and by Winiwarter and Sainmont respectively does not seem to warrant the conclusion of an homology between the hypothetical X-element in the male and that in female germ-cells of the cat. In short, the oöcytes would seem to contain, the spermatocytes to lack, typical X-elements.

SQUIRREL.

The spermatogenesis of the squirrel has been described in two papers by Van Mollé (1906, 1907). The cells are relatively very large and the idiosome is very distinct. My observations agree with the illustrations of Van Mollé with respect to the absence of heterochromosomes. Duesberg (1910) has recently questioned the accuracy of Van Mollé's observations with respect to the details of the later stages in the metamorphosis of the spermatid. Interest in these details is outside the scope of this contribution, and my observations on these points have not yet been carried to an extent where I might confidently presume to express an opinion. The absence of any accessory chromosomal element during the growth period appears unquestionable.

PIG.

It will suffice for present purposes to state simply that evidence of an accessory or heterotropic chromosome at early stages of the spermatogenesis of the pig is completely lacking in my material. The cells here are relatively small; but the fixation is good and reveals clearly all the details of structure, and every phase is abundantly represented prior to the division phases; occasionally first maturation groups are also present.[1]

RABBIT.

Exactly the same statement holds for the rabbit as for the pig; and I make it with greater confidence, since the material is more extensive including besides adult testes those of new-born and young individuals.

In all of the foregoing instances the spermatogonia contain plasmosomes. The resting primary spermatocytes also contain either plasmosomes or karyosomes (net-knots), or both, all of which disappear in early presynapsis. It seems legitimate to assume, on the basis mainly of this observation, that in mammals generally plasmosomes almost invariably disappear before

---

[1] However, no chromosome counts were attempted. In view of J. E. Wodsedalek's recent work ("Accessory Chromosomes in Pig;" Science, N. S., vol. XXXVIII, No. 966, pp. 30-31) reporting two additional chromosomes or accessories in half of the secondary spermatocytes—this number (10) corresponding with the reduced number in the eggs—the pig can no longer be listed under "exceptions." In the absence of definite evidence during the growth period, the final criterion for the presence of heterochromosomes must be an actual count.

Since the appearance of Wodsedalek's complete paper (Biol. Bull., 25: 1), I have carefully re-examined my sections of the pigs' testes. Mitoses are too infrequent to warrant any statement concerning the presence or absence of accessory chromosomes on the basis of appearances at metaphase, or of chromosome counts. My conclusions rested upon evidence drawn from a study of appearances during the growth stages Including the early prophase. As to the resting spermatogonial and primary spermatocyte nuclei I find no such constancy with reference to nucleoli as Wodsedalek records. The number, both of the large and smaller nucleoli, is very variable. Three or four large nucleoli are common. Moreover, with reference to the chromosome-nucleoli I can not find in my preparations (of young testes) any cells to parallel his illustrations 21, 23, 24, and 25. My material does not confirm his finding that "two large round nucleoli remain very conspicuous throughout the process of growth of the primary spermatocyte."

synapsis, and can thus produce no confusion at those stages where heterochromosomes when present are most conspicuous, *i. e.*, synaptic and early postsynaptic stages. The conclusion that heterochromosomes are wanting in the male of the mongoose, cat, squirrel, pig, and rabbit is, of course, based on the assumption that if present they would be conspicuous at the same stages in which they are so strikingly in evidence in the group of mammals next to be described. The final test must, however, in these cases be an actual count of chromosomes.

HETEROCHROMOSOMES PRESENT IN MALE.

WHITE MOUSE.

Spermatogonial and spermatocyte resting nuclei agree in being vesicular and having a delicate chromatic reticulum with numerous net-knots (figs. 22 and 23); they differ in that the spermatocyte nucleus has a bilobed or double chromatin (chromosome) nucleolus.

The Sertoli cell has a still more vesicular nucleus, which is very conspicuous by reason of a characteristic trilobed, deep-staining nucleolus, the central section being invariably the larger. This peculiar type of nucleolus is as characteristic of the Sertoli cell as its peculiar shape, and suggests interesting speculations concerning the relationship between nucleolar morphology and cell functions.

My earlier observations led me to the conclusion that the synapsis phenomenon (*i. e.*, synaptic knot, contraction or bouquet phase, or synizesis stage)[1] was lacking in the auxocytes of the white mouse. Further careful search has disclosed a few cells in the condition illustrated in figure 24. This is tentatively interpreted as synapsis (polarized amphitene). If the nucleus is normal, as it appears to be, the paired threads unmistakably indicate synapsis. I find that Regaud (1909, 1910) reports his failure to find a synapsis phase also in the rat. This phase is assuredly not accentuated in white mouse. Nothing more closely resembling synapsis than the nuclear arrangement illustrated in figure 24 could be found in my material. This, however, seems sufficiently suggestive of true synapsis to show that something similar to synapsis actually occurs in the mouse, perhaps too rapidly to appear except very occasionally in "fixed" preparations. If the phenomenon is really lacking the "synapsis" figure does not appear essential to the pairing of the chromosomes in the formation of the haploid group.

During synapsis (parasynapsis) and early postsynapsis (figs. 24 and 25) the chromatic accessory body (chromosome) is apparently usually single, usually oval, sometimes slightly bilobed, and occasionally wedge-shaped or even irregular. During later postsynaptic (fig. 26) and prophase (fig. 27) stages, this element again appears invariably double, frequently in the form of a longitudinally split rod. There is no unequivocal evidence that the

---

[1] Synapsis is assumed to take place during the period of contraction or "synizesis"; hence the terms are here used interchangeably.

pair may entirely and widely separate, as is the case in the mule for example. The double nature of the heterochromosome suggests a pair of idiochromosomes; but the fact that during and immediately after synapsis this element appears single invalidates somewhat such an assumption, and suggests rather a double accessory chromosome, or X-element of Wilson. In leptotene and diplotene phases it very frequently lies in a clear space free of threads, a condition similar to that described by Wilson (1912) for *Largus* and *Oncopeltus*.

Figure 27*a* would seem to permit of not the slightest doubt of the presence of a "sex chromosome" (Wilson) in the white mouse. Its later history, however, is still obscure. Division figures are very abundant in my material and the preservation is nothing short of superb, but at no later stage can I with certainty identify this body. Occasionally a spindle appears with a large chromosome in advance of the main metaphase group (fig. 27*b*), but the instances seem too rare to have much significance apart from morphological marks of identification from among the chromosomes of the metaphase plates.

SHEEP.

In sheep I am able to distinguish the "X-element" during the presynaptic (fig. 28), synaptic (fig. 29), and postsynaptic (fig. 30) stages. Both in the first and second stages it is usually attached to the chromatic spireme, or one of its segments. During the postsynaptic stages it is usually split or bilobed, and, as at earlier stages, frequently but not invariably lies close to the idiosome. Synapsis is effected by side-by-side union. In the sheep, also, this accessory chromosome eludes later certain identification.

HORSE.

As previously briefly noted (Jordan, 1911, 1912), during postsynaptic stages the horse shows frequently a tripartite X-element (fig. 33), usually next the idiosome. In the resting phase of the primary spermatocyte (fig. 31), and during synapsis, it appears double. Further clear tracing of this body seems impossible. The evidence is thus far from sufficient to warrant even an inference as to whether we are here dealing with a multiple X-element (as in *Sinea*, for example, according to Payne, 1909) or a pair of idiochromosomes. Both conditions have been described for mammals; for example, man as having a double X-element (as in *Syromastes*—Wilson, 1909) by Guyer (1910), and guinea-pig with a pair of heterochromosomes, by Miss Stevens (1912). The only point sought to establish is the presence of "sex chromosomes" of some sort.

Kirillow (1912) has recently published the first number of his projected studies on the spermatogenesis of the horse. The accompanying illustrations, including all the chief stages, give no indication of a heterotropic body so conspicuous in my preparations; nor is any mention made of such body. His observations on the germ-cells of the horse lead him to accept the opinion of Regaud (1909, 1910) that "the appearance or failure of synapsis is a variable factor in different species" (Kirillow, p. 145); that is, synapsis (contraction phase) is regarded as a normal phase in the auxocytes of some forms (species), but is thought not to appear in others.

MULE.

The presence of an accessory chromosome in the mule was also noted briefly in an earlier paper (Jordan, 1911, 1912). Here it usually appears double in pre- and post-synaptic stages (figs. 34 and 36). At synapsis it appears as a single large oval chromatic body (fig. 35). It is very clearly recognizable among the prophase chromosomes as a large paired element (fig. 37). Since at certain phases (synapsis) it may be a single compact body, it is perhaps more legitimate to regard it as a double X-element.

In the case of the mule it will be impossible further to trace this body with any degree of certainty. As first noted by myself (see quotation from my unpublished manuscript in a paper by Dr. R. H. Whitehead, "A Peculiar Case of Cryporchism, and its Bearing upon the Problem of the Function of the Interstitial Cell of the Testis," Anat. Record, Aug. 1908; vol. II, No. 5), spermatogenesis in the mule does not ordinarily proceed beyond the early prophase. This is the cause of the sterility of mules bred *inter se;* the mule does not generally produce ripe spermatozoa. My observations were subsequently confirmed by Poll (1911), who succeeded in observing a few first maturation spindles at metaphase.

BULL.

The spermatogenesis of the bull has been fully described by Schoenfeld (1901). My observations agree essentially with his illustrations. Schoenfeld figures a stage similar to my illustration of postsynapsis (fig. 38), where a single large, oval, chromatic "accessory chromosome" appears among the bivalent threads, close to the idiosome. This element, at this as well as at earlier and later stages, Schoenfeld describes as the "corpuscle intranucleare." In the light of what we now know of "sex-chromosomes" generally, and in mammals more particularly, this body may, I believe, be regarded confidently as an accessory chromosome.

DOG.

Figure 39 illustrates a resting primary spermatocyte with pale plasmosome and chromatic, bilobed chromosome nucleolus. No very satisfactory synapsis stages could be observed in my material.[1] Figures 40 and 41 illustrate two successive postsynaptic phases in which the X-element is conspicuously present as a chromatic, sharply contoured, irregularly oval body close to the idiosome. We are probably here again dealing with an accessory chromosome. The attempt further to trace this body, however, was very disconcerting by reason of the absence of definite marks of identity, lack of clear delimitation of the relatively large number of small chromosomes, and confusing contradictions of trying observations. In short, any further analysis was unsuccessful.

---

[1] That is, from the standpoint of a conspicuous "X-element."

DISCUSSION.

Heterochromosomes are apparently lacking in mongoose, cat, squirrel, pig, and rabbit, and appear to be present in white mouse, sheep, horse, mule, bull, and dog. On the basis of what was already known regarding man (Guyer, 1910; Gutherz, 1912),[1] rat (Guyer, 1910), armadillo (Newman and Patterson, 1910), guinea-pig (Stevens, 1912), and opossum and bat (Jordan, 1911, 1912), heterochromosomes were suspected in mammals generally. With respect to heterochromosomes, then, mammals fall into two groups: those lacking and those possessing the X-element in the male germ-cells. Under the first group five[2] mammals can be classified; under the second, twelve. Both groups include higher as well as lower mammals. Measured by no other criterion known to me can these mammals be similarly grouped. Presence of heterochromosomes obviously bears no relationship to natural affinities or evolutionary levels of mammals. The proportion of 12 to 5 among examined and recorded cases of mammals in favor of those possessing heterochromosomes suggests that in those forms apparently lacking them they have simply eluded detection. They might presumably be so small as to escape recognition, or lack the peculiar morphological marks by which they are usually characterized, or be too labile to be identified.

Regarding a similar condition in *Culex*, Stevens (1911, 1912) suggests that here, "where no heterochromosome differentiation of any kind has been detected, the members of a pair of chromosomes may differ by a sex unit or some other character unit, and the difference in size comes within the probable error of most careful observation" (p. 165).

The observation of the attachment of the accessory chromosome to the parasynaptic spireme (figs. 28, 29, and 40) controverts the plausibility of Stevens's (1912) suggestion that "the condensed condition of the odd chromosome and the unequally paired heterochromosomes of the growth stage of the first spermatocytes might be due to their unpaired or unequally paired condition preventing them from joining with the other bivalent chromosomes to form a spireme, especially in cases of parasynapsis" (p. 166).

It would seem to be required, then, for a proper grounding of later hypotheses, that all uncertainty be disposed of, first with respect to the possible presence in some form or at some stage of an X-element in those animals in which it seems to be wanting; and second, with respect to possible confusion with a persisting plasmosome in those instances where an X-element is believed to obtain. Though the above order would seem to be the more logical, the best approach to the argument and the proof is perhaps by way of the second point, though in fact they sustain a reciprocal relationship.

---

[1] Gutherz (1912) confirms Guyer's (1910) observation respecting the presence of a heterotropic element in man, but interprets it as a pair of equal idiochromosomes undergoing neither heterokinesis nor giving rise to a dimorphism of spermatozoa as described by Guyer.

[2] This must be a tentative grouping; only four mammals can now be temporarily placed in this group.

Regarding a possible confusion between plasmosomes and accessory chromosomes, or X-elements, it must be noted first that in the stain employed (Heidenhain's iron-hematoxylin; checked in doubtful instances by Auerbach's methyl-green-acid-fuchsin stain) the plasmosome when present (as in spermatogonia and occasionally in primary spermatocytes) is always in properly decolorized preparations considerably less deeply stained than the X-element. Moreover, the latter is frequently attached to the spireme or one of its segments, and generally holds a position close to the nuclear wall and close to the point where the idiosome lies. Again, it is frequently bilobed or compound. In certain instances, *e. g.*, mouse more particularly, one of the first-division chromosomes occasionally passes to the pole in advance of the mass; but in no instance could the X-element be followed with any satisfaction or certainty beyond the early prophase. At this stage, however, it is in at least a number of instances clearly recognizable among the pale, mossy chromosomes as the body earlier identified as the X-element. The evidence would seem amply adequate to support the interpretation here as a typical X-element.

Heterotropic nuclear elements must be identified by other criteria than staining reaction. At best, staining capacity can only give confirmatory evidence. Morphological marks would seem to be the most certain grounds for basing distinctions. The complete nuclear history is of course necessary for full certainty. Chromosomes undergo alterations in their chromaticity and consequent staining capacity at different phases of the nuclear cycle. Again, true chromatin-nucleoli occur in certain forms (*e. g.*, oöcytes of *Asterias forbesii*, Jordan, 1908; oöcytes of *Echinaster* and *Cribrella*, Jordan, 1910), whose function at least in part is to contribute chromatic material to the chromosomes just before they enter the first maturation spindle. The plasmosomes of certain forms may thus be of true chromatic nature. Moreover, true nucleoli never assume—except perhaps very exceptionally and atypically—the characteristic bilobed and split forms of the chromosome-nucleoli during the growth stages. Degenerating nucleoli become ragged of outline, frequently fragment, and undergo karyolysis, but never show the series of phenomena characteristic of heterochromosomes: sharp contour, deep basophily, frequently split form, frequent attachment to spireme, and usual location close to the nuclear membrane. A presumptive chromosome-nucleolus may meet the test of basophilic staining reaction in a differential dye, but if it does not meet at least the majority of the above structural and spatial tests it very probably is simply a chromatic plasmosome; on the other hand, if it answer to the latter tests, confirmatory—but perhaps not crucial, in view of the undoubted chemical changes which chromosomes undergo—evidence accrues from a chromatic reaction to a "specific" stain.

Regarding the first stated point of possible doubt, then, nothing further can be said than that in the five forms enumerated as lacking an X-element, the tissue was similarly well preserved and stained, but notwithstanding careful search, not the slightest evidence of such an element in its usual morphological form and peculiar behavior with reference to spireme and idiosome could at any stage be detected; but this negative evidence obviously can not remove all uncertainty with respect to this first point.

Heterochromosomes (allosomes, Montgomery) in mongoose, and other forms showing like growth-stage conditions, may possibly have disappeared by close union with one of the ordinary chromosomes and thus forced into the usual behavior of the autosomes during auxocyte phases. Transition stages in such process of disappearance are apparently shown in certain orthoptera (McClung, 1905) and amphibia (*e. g.*, *Necturus*, King, 1912).

Militating further against the objection of mistaken identity is the fact that in this group the plasmosome has almost invariably disappeared[1] before synapsis, when the X-element first exhibits its characteristic behavior. If plasmosome could be confused with X-element in mammals, a group of five, with no relatively closer affinity than obtains among the contrasted group, could hardly be expected to give consistent and unequivocal evidence in favor of complete absence. Moreover, if the plasmosome generally disappears before or about the time of synapsis in a relatively no more closely related group of five forms, it seems quite legitimate to infer that it disappears at about the same time in six other—and as closely related—forms, and thus leaves little opportunity for confusion. And the above deduction is supported to some extent by direct observations (exception: man).

Having disposed of these objections as far as possible within the limitations of microchemical technic, it remains to consider further bearings and implications of the facts established. The observation of an X-element in the ovary of young cats (fig. 42) by Winiwarter and Sainmont (1909) has important significance in this connection. If my negative evidence for the male germ-cells in the cat can be regarded as equally certain with the positive evidence of these investigators for the female germ-cells, then it would seem that in those forms in which the males lack a typical X-element this is possessed by the female.[2] An analogous instance from the invertebrate group is that of certain sea-urchins reported by Baltzer (1909). Here the female possesses a pair of idiochromosomes, while the male lacks any indication of such. The above hypothesis for mammals must be tested by examination of the young ovaries of those forms in which the male appears to lack the accessory.

This hypothesis would be somewhat weakened if cases were known in which both male and female germ-cells possessed typical[3] X-elements. The meager evidence available is contrary to such a hypothetical condition. Wilson (1905, 1906) was unable to find a chromosome nucleolus in certain genera among the insects, including *Euchistus*, in which he was confirmed by Foote and Strobell (1909). Buchner's (1909) evidence with respect to *Gryllus*—the only presumptive contradictory evidence known to me—

---

[1] A delayed disappearance occasionally occurs, more especially in cat and man.

[2] Presumably by approximately half of the ova.

[3] That is from the standpoint of behavior during the growth stages.

judged from his illustrations, seems far from conclusive. In fact, the hypothetical so-called X-element ("accessory body") in the ovary lacks much of being similar in structure and behavior to the undoubted X-element in *Œdipus* (described and figured in the same paper) and the male *Gryllus*. Moreover, Gutherz (1910) has shown that the two X-chromosomes, characteristic of the female, are both present in the metaphase plates of the oögonia, in addition to the outlying "accessory body." As is now established beyond any doubt the accessory, for example, of the male germ-cells passes into all females. Its homologue is present in both males and females; but the additional male accessory, at any rate, would seem to be able again to comport itself during the growth stage of the maturing oöcyte as it originally behaved in the growing spermatocyte; and similarly with respect to its female homologue, since that in the male, coming originally also from the egg, behaves again in typical "accessory" fashion. It seems fairly well established that the female homologues of the male accessory do not behave in the growing oöcytes as does the X-element in the spermatocyte.

As indicated by observation on the cat, the reverse of the usual relationship here obtains: the oöcytes are probably dimorphic with respect to an accessory; the spermatocytes apparently monomorphic. Here, then, as in certain sea-urchins, the female is apparently digametic, the male apparently homogametic. Further investigations must establish the fact whether the same reverse condition obtains with respect to an X-element in the case of the remaining four mammals of the first group.

Male and female sex (together with secondary sexual characters) appear to be hereditary in a manner similar to other organic characters, and may be regarded as a pair of "unit characters." Since the femaleness is associated with, or determined by, the presence of X-elements, the female (containing a pair of homologous X-elements) is presumably homozygous,[1] the male heterozygous for sex; or, in accordance with a more recent terminology, the female represents a duplex (but apparently recessive like a nulliplex) condition, the male a simplex (dominant) condition. Maleness is accordingly characterized by the absence, femaleness by the presence of a "determiner" (presumably an inhibitor), the X-element. The former is the negative or minus (lacks accessory, contributed to female at fertilization), the latter the positive or plus, condition. Sex inheritance conforms thus to the Mendelian scheme, in which maleness represents the DR and femaleness the RR condition; or, stated in terms of the presence (+) and absence (−) of an inhibiting accessory, or X-element, maleness is + −, and femaleness the + + condition. Femaleness may therefore be plus or positive in an inhibiting sense; a germinal plus condition prevailing in the female, inhibiting the appearance of a positive somatic condition or male sex.

This modified Mendelian interpretation is suggested in part by an analogy with conditions in crosses between horned and hornless cattle, where the positive character (horns) is recessive to the negative or hornless

---

[1] That is, in the group where the male germ-cells contain an X-element.

character; meaning, according to the general interpretation, that hornlessness is determined by the presence of some determiner which prevents the development of horns. Similarly, femaleness may be due to the presence of the X-element, preventing the development of maleness.[1] It would be immaterial whether it were contributed by the male or by the female gamete. This idea is further suggested by, and seems in perfect accord with, the numerous observations indicating that femaleness is undeveloped maleness, *e. g.*, embryological facts; relatively female characteristics of male infants; the assumption of male secondary characters after spaying, or after the menopause; etc.

SUMMARY AND CONCLUSIONS.

Among the forms examined, including mongoose, cat, squirrel, pig, rabbit, white mouse, sheep, horse, mule, bull, and dog, heterochromosomes are apparently lacking in the male germ-cells of the first five, and present in the remainder. The available evidence favors more the interpretation in terms of a bipartite univalent or compound X-element than of an associated X and Y group (idiochromosomes).

In view of the fact that heterochromosomes have recently been reported in man (Guyer, double X-element; Gutherz, equal pair of idiochromosomes, or X- and Y-elements), rat (Guyer), armadillo (Newman and Patterson), guinea-pig (Stevens), and opossum and bat (Jordan), the evidence indicating similar elements in the above-enumerated group of six common mammals would seem to warrant the conclusion that sex-chromosomes are very generally present in mammals. Universality of presence seems vitiated for the present by the fact that in another group of five mammals, carefully studied, such elements seem apparently lacking. It might be assumed that such elements are actually present in the male germ-cells, but are so small or labile as to elude detection by ordinary methods, or do not present the usual morphology of heterochromosomes during the prophase stages. The unmistakable presence, however, of a "split-accessory" in the female germ-cells (primary oöcyte) of the cat, as recorded by Winiwarter and Sainmont, and the absence of any X-element in the male (confirmed by Gutherz, 1912), suggests very forcibly that sex-chromosomes are present in all mammals, generally in the male, exceptionally in the female. The same result would follow (that of numerical sex-equality) whether present in one or the other sex. If this hypothesis can be further sustained, it would seem cogently to reinforce the evidence for an essential sex-determining function of heterochromosomes. Interpreted in terms of Mendelian heredity-formulæ, in those mammals in which an X-element is present in the male, the female sex is homozygous, the male heterozygous. The facts would seem to fit the hypothesis that the accessory chromosome acts as a deterrent to the develop-

---

[1] However, in the case of horn-heredity, the inhibitor, according to this explanation, is dominant; in sex-heredity, recessive. In cases where the female is the heterozygote, the condition might be parallel to that of horn-heredity. In these instances the female would be simplex, the male nulliplex. Recession of a duplex condition seems a contradiction in terms. The suggestion can have significance in only an approximate or general sense.

ment of maleness; or more accurately, and in keeping with a quantitative interpretation of sex in a final analysis, the accessory with its egg-homologue (two X-elements) inhibits male-sex development, the single egg-homologue in males being insufficient to counteract the male tendency, thus giving origin to male individuals. In those instances where the female can be shown to be the heterozygote, one X-element, according to the hypothesis, may be assumed to be able to counteract the male tendency.

ADDENDUM.

The opportunity recently presented itself for the study of very favorable human material. I am indebted to Dr. H. T. Marshall, professor of pathology at the University of Virginia, for the specimen, a thin slice of testicle fixed in Zenker's fluid, and obtained at autopsy from a negro aged 38 years, who died as the result of drinking wood alcohol. The material is in excellent state of preservation. It was stained for study with iron-hematoxylin. Primary spermatocytes in early postsynaptic phases (text-figs. 1 to 9) are especially abundant and clear. Mitoses, however, both in spermatogonia and spermatocytes, are infrequent, and, though a sufficient number can be found at metaphase in the latter cells to furnish a fairly satisfactory opportunity for attempting chromosome counts, I can come to no definite conclusion concerning the actual number. My specimens of primary spermatocyte mitoses, however, compare very favorably with the illustrations given by Guyer and by Gutherz, every one of which I can practically duplicate.

An impartial judge of the figures must admit, I believe, that certainty is impossible at least within an error of two—and two makes all the difference between the presence of an accessory as urged by Guyer and denied by Gutherz. The inherent difficulty of an accurate count is indicated by the fact that the diploid chromosome number of the male cells has been given as 22 (Guyer), 24 (Flemming, Duesberg, Branca, Gutherz), 16 (Bardeleben), 18 (Wilcox), 33 or 34 (Wieman), and 47 (Winiwarter). It is significant, however, that Guyer, Gutherz, Duesberg, and Branca agree on 12 as the haploid (reduced) number; but Guyer, in contrast to the others, regards 2 of these as univalent accessories; also Guyer, Gutherz, and Winiwarter agree in claiming the presence of a heterochromosome; and Guyer and Winiwarter both report a dimorphism of spermatozoa, the former giving the number of chromosomes as 10 and 12, and the latter as 23 and 24.

It seems clear that a heterochromosome of some valency is present; it is equally clear that the true nature of this body can not yet be established on the basis of numerical relationships; the count is still uncertain as regards at least 2 chromosomes. Study of my material convinces me that the reduced number is not less than 12, but perhaps several more. As regards conclusions respecting the presence of an accessory chromosome drawn from a study of side views of metaphase spindles, it may be pointed out that Guyer's and Gutherz's figures are substantially alike; but Guyer interprets the appearance as demonstrating, Gutherz as contradicting, the presence of an accessory. My own figures occasionally show a double chromosome at one pole in advance of the main complex, and the evidence favors Guyer's interpretation rather than Gutherz's, but there is here nothing so striking as one sees in certain insects (*e. g.*, the phasmid, *Aplopus mayeri*) and the opossum. Strong evidence for the presence of a heterochromosome in man is given by Gutherz in his illustrations of early postsynaptic nuclei (text-figs. 2 to 6). But neither he nor Guyer seems to offer satisfactory evidence as to its composition from chromosome counts and behavior at metaphase. Both, moreover, regard it as a double structure. My own evidence confirms the findings of Guyer and Gutherz in so far as pertains to the actual presence and bipartite nature of a heterochromosome or X-element, and it emphasizes the additional points of similarity between this and undoubted sex-chromosomes, namely, frequent connection with the diplotene thread and close spatial relationship to nuclear wall (exception, text-fig. 3).

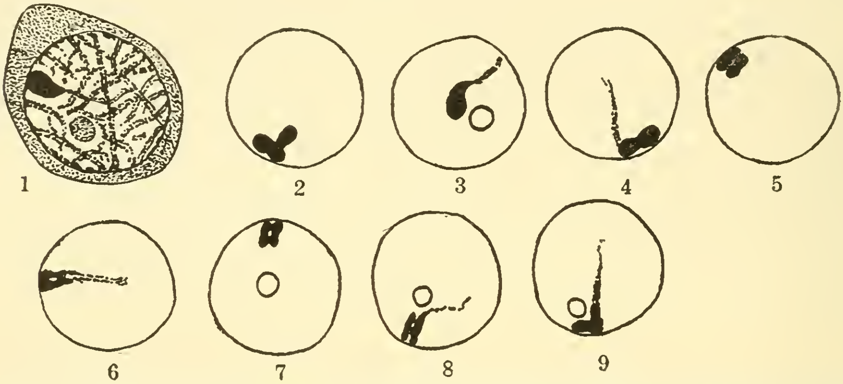


Fig. 1.—Human primary spermatocyte; nucleus in early diplotene post-synaptic phase, showing a deeply staining oval chromatin (chromosome) nucleolus on the nuclear wall and attached to one of the threads; the true nucleolus is a spherical, less deeply staining body, and only very rarely placed close to the nuclear wall. The cytoplasm is homogeneous, finely granular.

Figs. 2 to 9.—Outlines of nuclei at same stage to show the general form and location of the heterochromosome. It is almost invariably bipartite and attached to one of the threads, and on the nuclear membrane. The nucleolus when present is indicated in outline.

Judging from the illustrations, Winiwarter (1912) has had the advantage of possessing by far the best human material. His illustration (fig. 25) is practically a duplicate of my own of the postsynaptic diplotene (passing into the pachytene) phase. However, the later history of the accessory element as traced by Winiwarter is not at all stages perfectly clear. But figures 39 and 40 show pairs of sister spermatids, one pair with, the other without, a deep-staining nuclear body (accessory chromosome?). If this spermatid element actually represents, as seems very probable, the postsynaptic nuclear bipartite body, or heterochromosome, then cogent additional evidence here also accrues favoring the legitimate interpretation as a heterochromosome of the similar (structurally and tinctorially) peculiar postsynaptic nuclear element wherever found in mammals.

LITERATURE.

Baltzer, F. 1909. Die Chromosomen von *Strongylocentrotus lividus* und *Echinus microtuberculatus.* Arch. f. Zellf., Bd. ii, Heft 4.

Buchner, P. 1909. Das accessorische Chromosome in Spermatogenese und ovogenese der Orthoptern, zugleich ein Beitrag zur Kenntnis der Reduktion. Arch. f. Zellf., Bd. iv, Heft 2.

Duesberg, J. 1910. Nouvelles recherches sur l'appereil mitochondrial des cellules séminales. Arch. f. Zellf., Bd. vi, Heft 1.

Foot and Strobell. 1909. The nucleoli in the spermatocytes and germinal vesicles of *Euchistus variolatus.* Biol. Bull., vol. xvi, No. 5.

Gross, J. 1912. Heterochromosomes and sex-determination. Zool. Jahrb., vol. xxxii.

Gutherz, S. 1909. Wird die Annahme einer Beziehung zwischen Heterochromosomen und Geschlechts bestimmung durch das Studium der Gryllus-oogenese wiederlegt? Sitzungsber. d. Gesellsch. Naturforsch, Freunde, Nr. 9.

——— 1912. Ueber ein bemerkenswertes Structurelement (Heterochromosom?) in der Spermiogenese des Menschen. Arch. f. Mikr. Anat., Abteilung ii, 79, 2.

Guyer, M. F. 1910. Accessory chromosomes in man. Biol. Bull., vol. xix, No. 4.

Jordan, H. E. 1908. The spermatogenesis of *Aplopus mayeri.* Carnegie Institution of Washington Pub. No. 102. Abstract in Anat. Anz., vol. xxxii.

——— 1908. The relation of the nucleolus to the chromosomes in the primary oocyte of *Asterias forbesii.* Carnegie Institution of Washington Pub. No. 102.

——— 1910. The relation of nucleoli to chromosomes in the egg of *Cribrella sanguineolenta* Lütken. Arch. f. Zellf., Bd. v, Heft 3.

——— 1911. The spermatogenesis of the opossum (*Didelphys virginiana*), with specia reference to the accessory chromosomes and the chondriosomes. Arch. f. Zellf., Bd. vii, Heft 1.

——— 1912. Notes on the spermatogenesis of the bat. Anat. Anz., Bd. xl.

King, Helen Dean. 1912. Dimorphism in the spermatozoa of *Necturus maculosus.* Anat. Record, vol. vi, No. 10.

Kirillow, S. 1912. Die Spermiogenese beim Pferde. I. Arch. f. Mikr. Anat., Bd. lxxix, Abteilung ii, Heft 3.

Leplat, G. 1910. La Spermiogénèse chez le Chat. Arch. de Biol., Tome xxv, Fasc. 2 and 3.

McClung, C. E. 1905. The chromosome complex of orthopteran spermatocytes. Biol. Bull., vol. ix.

Mollè, J. van. 1906. La Spermiogénèse dans l'écureuil. La Cell. Tome xxiii, Fasc. 1.

——— 1907. Les Spermatocytes dans l'écureuil. Ibid. Tome xxiv, Fasc. 2.

Montgomery, T. H. 1910. On the dimegalous sperm and chromosomal variation of *Euchistus,* with reference to chromosomal continuity. Arch. f. Zellf., Bd. v, Heft 1.

Morgan, T. H. 1909. A biological and cytological study of sex determination in phylloxerans and aphids. Jour. Exp. Zool., vol. vii, No. 2.

Newman, H. H., and J. T. Patterson. 1910. The development of the nine-banded armadillo from the primitive streak to birth, with special reference to the question of specific polyembryony. Jour. Morph., vol. xxi, No. 3.

Payne, F. 1909. Some new types of chromosome distribution and their relations to sex. Biol. Bull., vol. xvi, Nos. 3 and 4.

Poll, H. 1911. Mischlings Studien V: Vorsamenbildung die Mischlingen. Arch. f. Mikr. Anat., Abteilung ii, Bd. lxxvii, Heft 2.

Regaud, C. 1909–1910. Etudes sur la Structure des Tubes Séminifères et sur la Spermatogénèse chez les Mammifères. Arch. de Anat. Micr., Tome xi. Paris.

Schoenfeld, H. 1902. La Spermatogénèse chez le taureau, et chez les Mammifères en général. Arch. de Biol., Tome xviii, Fasc. 1.

Stevens, N. M. 1909. An unpaired heterochromosome in the aphids. Jour. Exp. Zool., vol. vi, No. 1.

——— 1911. Further studies on heterochromosomes in mosquitoes. Biol. Bull., vol. xx.

——— 1912. Heterochromosomes in the guinea-pig. Biol. Bull., vol. xxi, No. 3.

Wieman, H. L. 1913. Chromosomes in man. Am. Journ. Anat. 14: 4.

Wilson, E. B. 1905a. The chromosomes in relation to the determination of sex. Science, n. s., vol. xx, 564.

——— 1905b. The behavior of the idiochromosomes in Hemiptera. Studies on Chromosomes, I. Jour. Exp. Zool., vol. ii, No. 3.

——— 1905c. The paired microchromosomes, idiochromosomes, and heterotrophic chromosomes in Hemiptera. Studies on Chromosomes, II. Ibid., vol. ii, No. 4.

WILSON, E. B. 1906. The sexual differences of the chromosome groups in Hemiptera, with some considerations on the determination and heredity of sex. Studies on Chromosomes, III. Ibid., vol. III, No. 1.

——— 1909A. The accessory chromosome in *Syromastes* and *Pyrrhocoris* with a comparative review of the types of sexual differences of the chromosome groups. Studies on Chromosomes, IV. Ibid., vol. VI, No. 1.

——— 1909B. The chromosomes of *Metapodius*. A contribution to the hypothesis of the genetic continuity of chromosomes. Studies on Chromosomes, V. Ibid., vol. VI, No. 2.

——— 1910. The chromosomes in relation to the determination of sex. Science Progress, vol. IV, No. 16.

——— 1911. The sex chromosomes. Arch. f. Mikr. Anat., Bd. LXXVII, Abteilung II, Heft 2.

——— 1912. Observations on the maturation phenomena in certain Hemiptera and other forms, with considerations on synapsis and reduction. Studies on Chromosomes, VIII. Ibid., vol. XIII, No. 3.

VON WINIWARTER, H. 1912. Etudes sur la spermatogenèse humaine. Arch. Biol. Tome XXVII.

VON WINIWARTER, H., and G. SAINMONT. 1909. Nouvelles recherches sur l'ovagénèse et l'organogénèse de l'ovaire des Mammifères (chat). Arch. Biol., Tome XXIV, Fasc. 2 and 3.

DESCRIPTION OF PLATE.

Fixation: Flemming's strong solution. Stain: Heidenhain's iron hæmatoxylin.
Magnification: 1500 diameters.

MONGOOSE.

1. Spermatogonium; the nucleus contains three small plasmosomes.
2. Spermatogonium; the nucleus is in process of amitotic division.
3. Primary spermatocyte; the nucleus contains a centrally located plasmosome; the delicate chromatic reticulum consists of an apparently continuous single thread; leptotene-nucleus.
4. Bouquet stage; the slightly thickened spireme has aggregated in a close-meshed mass at the idiosome pole of the nucleus; the cytoplasm surrounding the idiosome contains pale mitochondria; synizesis, polarized amphitene.
5. Synapsis: the disentangling threads are pairing side by side; the nucleus is still approximately of the same size as in the resting spermatocyte, hence synizesis and synapsis signify activity (motion) on the part of the nuclear reticulum; synaptene-nucleus.
6. Postsynapsis; early prophase; diplotene-nucleus.

7 and 8. Later prophases; at no stage do heterochromosomes appear.

9 and 10. Side and polar views respectively of metaphase plates; no chromosome is conspicuous for unusual size or behavior; the number of chromosomes is approximately twenty-four, the haploid group.

11. Resting secondary spermatocyte.

12 and 13. Side and polar views respectively of metaphase plates; the number of chromosomes is approximately twelve, forming a hemioid group.

14. Spermatid; the cytoplasm has become filled with pale mitochondria.

15. Appearance of "sphere" and centrosome.

16 and 17. Appearance of axial filament and middle piece.

18 and 19. Formation of spiral filament by coalescence of mitochondria.

20 and 21. Face and profile views respectively of mature, living spermatozoa.

WHITE MOUSE.

22. Spermatogonium.

23. Primary spermatocyte, nucleus at leptotene phase; the bilobed nucleolus may be a pair of heterochromosomes.

24. Synapsis, polarized amphitene, bouquet or synaptene phase; the heterochromosome is apparently single.

25. Postsynapsis; early prophase; heterochrome (or accessory) conspicuous; pachytene-nucleus.

26 and 27*a*. Early and late prophase groups respectively, both including conspicuously the pair of heterochromosomes almost invariably situated on the nuclear wall and close to the idiosome; 26, diplotene-nucleus.

27*b*. Metaphase; one of the chromosomes has moved in advance of the others to one pole; this has a tetrad form and is still clearly bivalent; accordingly, it fails to divide in this mitosis and may represent the "accessory" of the growth stages.

SHEEP.

28. Resting primary spermatocyte, showing the accessory at the idiosome pole; perhaps postsynaptic "confused stage" of Wilson.

29. Bouquet (synapsis) stage; the accessory chromosome is attached to a double thread, and invariably lies close to the nuclear wall.

30. Postsynapsis; early prophase, showing a bipartite accessory (or pair of heterochromosomes).

HORSE.

31. Primary spermatocyte; the nucleus contains two irregular karyosomes and a bilobed chromatic nucleolus, probably a pair of heterochromosomes.

32. Synapsis stage, showing the heterochromosomes among the pairing threads close to the nuclear wall.

33. Postsynapsis, showing a tripartite X-element, the heterochromosome group; pachytene-nucleus.

MULE.

34. Resting primary spermatocyte, showing a divided, or paired, heterochromosome.

35. Synapsis stage, showing a heterochromosome.

36 and 37. Early and late prophase stages respectively, showing a pair of heterochromosomes.

BULL.

38. Postsynapsis, showing an accessory chromosome among the bivalent threads, close to wall and idiosome; diplotene-nucleus.

DOG.

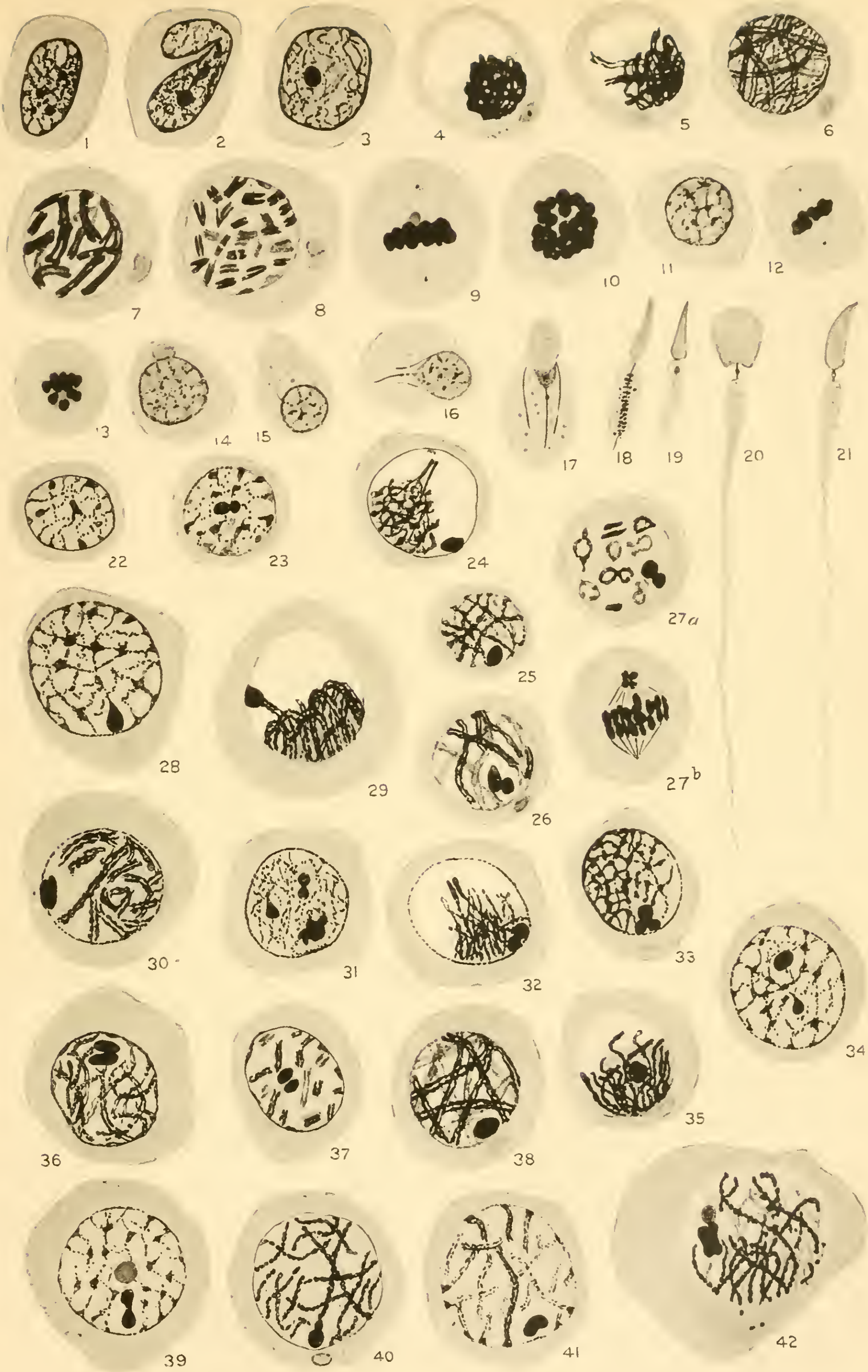
39. Primary spermatocyte; presynaptic resting phase, showing plasmosome and bilobed monosome.

40. Postsynaptic phase, pachytene-nucleus; monosome attached to one of the threads.

41. Early prophase, diplotene-nucleus; chromosomes in form of long bivalent threads; monosome close to nuclear wall.

42. Oöcyte from ovary of 23-day cat. Synapsis. True nucleolus; monosome divided longitudinally (after H. von Winiwarter et G. Sainmont, fig. 43).

JORDAN PLATE 1



XI.

THE BRYOZOA OF THE TORTUGAS ISLANDS, FLORIDA.

BY RAYMOND C. OSBURN.

Twenty-three text-figures.

THE BRYOZOA OF THE TORTUGAS ISLANDS, FLORIDA.

By Raymond C. Osburn.

In the summer of 1908 the writer had the privilege of spending the month of June at the Carnegie Institution Laboratory for Marine Biology, located on Loggerhead Key of the Tortugas Islands. Owing to the short time at my disposal the entire period was devoted to a close search for the bryozoa inhabiting the shallow waters about the reefs, on the piles of the old government dock on Garden Key, in the moat of old Fort Jefferson on the same key, and in dredging the shallow waters about the islands down to 22 fathoms. For much of the work a skiff or a small launch was used, and for the deeper dredging (10 to 22 fathoms) the schooner *Physalia* was employed. The Tortugas Islands are islets of a coral atoll and in the diversified bottom afforded by such a region a rather abundant bryozoa fauna was found.

Comparatively little work has been done on the bryozoa of the Florida and West Indian regions. Smitt's papers on the Florida bryozoa (1872–73) deal with 87 species collected by Count L. F. de Pourtales and afford the only extended record of the bryozoa of this region. Pourtales (1867), in a paper entitled "Distribution of the Fauna of the Gulf Stream at Great Depths," listed and described as new 7 species of bryozoa, 2 of which have been proved to be synonyms. Verrill, in his Bermuda papers, has listed 21 species from the Bermuda Islands. Levinsen, in his important work, "Morphological and Systematic Studies on the Cheilostomatous Bryozoa" (1909), records 6 species from the West Indian and Florida region, describing two of them as new. Otherwise this vast region remains untouched. As the collections of Pourtales were made in the deeper waters of the Florida region, it was presumed that careful collecting in the shallow waters would disclose the presence of a somewhat different fauna, a presumption well borne out by the results of my collecting. There is, indeed, a remarkable disparity between the list given by Smitt and that forming the basis of the present paper. Not only did 41 of the species described by Smitt fail to appear in the shallow waters, but 40 others, whose presence was not hitherto suspected in the Florida region, and many of them not even in America, were taken. This brings the list of the species at present known from Florida and West Indian waters up to 127.

By comparing with lists from other regions where the bryozoa have been carefully worked, it will be seen that the bryozoa fauna of the Tortugas and of the Florida-West Indian regions is fairly rich in species and fairly representative of tropical and semi-tropical regions. Careful collecting for a number of years in a limited region about Woods Hole, Massachusetts, and extending down to about 20 fathoms, yielded 83 species (see Osburn, 1912). Waters (1909–10) listed 73 species from the Red Sea. Norman (1909) records 139 species from Madeira and neighboring islands. This latter list is of special interest for comparison, since the Madeira bryozoa have been collected with some care for about 50 years and it may be supposed that it is fairly complete. In making comparison, however, it must be noted that the dredging about Madeira extended down to 200 to 300 fathoms, while those of the present list go only to 22 fathoms, so that to properly compare the Florida with the Madeira fauna the present list of shallow-water forms should be combined with that of Smitt.

The Tortugas bryozoan fauna (shallow water) presents a very different facies from that of Woods Hole at the same depth, since the two lists of 76 and 83 species, respectively, have only 13 species in common. The Woods Hole fauna is distinctly northern, while that of the Tortugas, at least for the shallow waters, is distinctly tropical. This is readily understood when we recall that the Tortugas are within 0.5 degree of the tropics, and that these islands receive, directly along their shores, the warm waters of the Gulf Stream which sweep up from the Caribbean Sea.

It is interesting to note in this connection that, of the 40 species here added to Smitt's list, 33 are limited entirely or chiefly to a tropical distribution.

The arrangement of the bryozoan species, genera, and families has undergone so much alteration in recent years, as a result of the studies of Norman, Waters, Calvet, and Levinsen, as to be wholly unintelligible to anyone except the systematist familiar with the changes of the last ten years. It is impossible that this should be otherwise, since the older classification was based almost entirely upon the structure of the skeleton of dead and dried material, without reference to the general morphology.

In the following list I have followed as far as possible the classification adopted by Levinsen (1909). In the cases of a few imperfectly understood species the older genera have been retained as "catch-alls." Thus the genera (?) *Lepralia* and *Phylactella* have been used in the old Hincksian sense for certain species which, with more complete knowledge, must undoubtedly go elsewhere.

The figures were drawn by Mr. S. Shimitori, except figures 7, 11, 22, and 23, which are the work of Mr. H. Murayama.

ENTOPROCTA.

GENUS PEDICELLINA Sars, 1835.

Pedicellina cernua (Pallas).

OSBURN, 1912, p. 213, Synonymy and previous records of the occurrence of this species on the American coast.

Apparently not common, but several small colonies were taken on the piles of docks and dredged at 10 fathoms.

GENUS BARENTSIA Hincks, 1880.

Barentsia discreta (Busk).

BUSK, 1886, p. 44 (*Ascopodaria discreta*).—JULLIEN, 1888, p. 13 (*Pedecellina australis*).—(?) VERRILL, 1900, p. 594 (*Barentsia timida* sp. nov.).—WATERS, 1904, p. 99.—OSBURN, 1912, p. 214.

This species, first described from Tristan da Cunha in the *Challenger* reports, is now known to be widely distributed, as follows: Tristan da Cunha, 100 to 150 fathoms (Busk); China Sea, 27 fathoms (Kirkpatrick); Cape Horn, 26 fathoms (Jullien); Ile Londonderry, Magellanes, Chile (Waters); Woods Hole, Massachusetts (Osburn); Beaufort, North Carolina (Osburn); Tortugas, Florida (Osburn).

If Verrill's *Barentsia timida* from the Bermudas is the same species, as I strongly suspect, this will add another locality. Verrill states in regard to his *B. timida* that it is closely allied to *B. discreta*, but that the latter has a shorter and more annulated basal cylinder and also several annulations of the stem below the base of the cup. In my experience, the annulations of the stem are of little importance, if any, as there is much individual variation which may represent only differences in contraction at this point.

The individuals are small and the species may readily escape observation. It appears only once in my collection made at the Tortugas, being dredged in 18 fathoms directly north of the island on a bottom of coral mud; several fragments of colonies attached to shells.

CYCLOSTOMATA.

GENUS CRISIA (PART) Lamouroux, 1816.

? Crisia denticulata (Lamarck).

LAMARCK, 1816, p. 137 (*Cellaria denticulata*).—STIMPSON, 1853, p. 18.—SMITT, 1872, p. 4 (*Crisia eburnea*).—JELLY, 1889, p. 73.—HARMER, 1891, p. 136.—VERRILL, 1879, p. 28; 1900, p. 592.—WHITEAVES, 1901, p. 110.—OSBURN, 1912, p. 216.

Numerous small colonies were taken at from 10 to 15 fathoms in various places about the island, attached usually to sponges and shells. Smitt records the species as *C. eburnea* from 7 to 60 fathoms. Stimpson (1853), Verrill (1879), and Whiteaves (1901) have recorded it from New England to Canada, though these records are questionable on account of failure to consider the oœcia, and the writer has recorded it questionably from Woods Hole, Massachusetts (oœcia wanting). Verrill has reported it as common at Bermuda.

Harmer (*l. c.*), referring to Smitt's Florida record, states: "I do not feel certain that the form described is really identical with *C. ramosa*, although it can hardly be regarded as *C. denticulata*," and suggests that it may be Stimpson's *C. cribraria*. It does not seem to agree with the latter species, however, in any essential point (see Osburn, 1912, p. 215, for redescription of *C. cribraria*), nor does it agree with *C. ramosa*, in which the radical fibers have long internodes with yellow or colorless joints. It does agree with *C. denticulata* in having short internodes in the radical fibers and the joints of these fibers, as well as those of the zoarium, conspicuously jet-black. As the form of the colony and of the zoœcia agree fairly with *denticulata*, I retain that name for the species. It is unfortunate that ovicells are wanting, so that it is impossible to make a positive determination, for, in spite of the number of times the species has been recorded from North America, there seems to be not one of these records based on an unquestioned identification.

GENUS LICHENOPORA Defrance, 1823.

Lichenopora hispida (Fleming).

FLEMING, 1829, p. 530 (*Discopora hispida*).—JELLY, 1889, p. 134, synonymy.

A very minute specimen was taken on an alga at 2 fathoms and placed with some question in this species. A well-developed colony taken by Dr. Paul Bartsch at Biscayne Key, Florida, has recently been examined, and after comparison there seems to be no doubt as to the identity of the Tortugas specimen. The species hitherto has not been noted in the Florida or West Indian regions.

CHEILOSTOMATA.

GENUS AETEA Lamouroux, 1812.

Aetea truncata (Landsborough).

LANDSBOROUGH, 1852, p. 288 (*Anguinaria truncata*).—JELLY, 1889, p. 5, synonymy and references.—CORNISH, 1907, p. 75.—NORMAN, 1909, p. 283.

Common in shallow water and down to 5 fathoms, creeping over shells and seaweed. It has been recorded at Canso, Nova Scotia (Cornish, *l. c.*).

Aetea sica (Couch).

COUCH, 1844, p. 102 (*Hippothoa sica*).—JELLY, 1889, p. 5 (*Ætea recta*) synonymy and references.—WATERS, 1909, p. 129 (*Ætea recta*).—NORMAN, 1909, p. 283.

Tortugas at 10 fathoms on shells. Not previously noted in American waters.

Some authors prefer to consider this only a variety of ***Ætea anguina.*** The latter has not been taken in the Florida region, though it is common northward from Beaufort, North Carolina.

GENUS BUGULA Oken, 1815.

Bugula neritina (Linné).

LINNÉ, 1758, p. 38 (*Sertularia neritina*).—VERRILL, 1878, p. 304 (*Acamarchis neritina*); 1900, p. 588.—ROBERTSON, 1905, p. 266.—WATERS, 1909, p. 135.

This widely distributed warm-water species is abundant in the shallow water, growing on piles, shells, seaweed, etc. Colonies 1.5 inches in height with oœcia abundantly developed were taken on the bottom of a skiff which had been in the water only from May 1 to June 23.

Verrill has recorded the species for the Bermuda Islands and from Fort Macon, near Beaufort, North Carolina. Otherwise it has not been noticed on the American side of the Atlantic. Robertson found it common on the Pacific coast as far north as Monterey Bay, California.

Bugula neritina var. minima Waters.

WATERS, 1909, p. 136.

One small colony with ovicells abundantly developed and with numerous avicularia (as described by Waters in Red Sea specimens) was taken at a depth of 8 fathoms. Previously known only from the type locality. This variety is distinguished from the typical *neritina* by the smaller size of its zoœcia and by the presence of avicularia situated near the lower end of the zoœcia.

Bugula flabellata (Gray).

GRAY, 1847, p. 106 (*Avicularia flabellata*).—SMITT, 1872, p. 18.—VERRILL AND SMITT, 1873, p. 711.—VERRILL, 1879*b*, p. 189; 1880, p. 29 (*Bugula flustroides*).—OSBURN, 1912, p. 225.

A single small colony of this species, attached to *Retepora atlantica*, was taken at a depth of 12 fathoms. The ovicell is more widely opened than in Woods Hole specimens. A very widely distributed species, occurring northward on our coast to Maine. Miss Robertson found it at San Diego, California.

Bugula microœcia n. sp. (Figs. 1 to 3.)

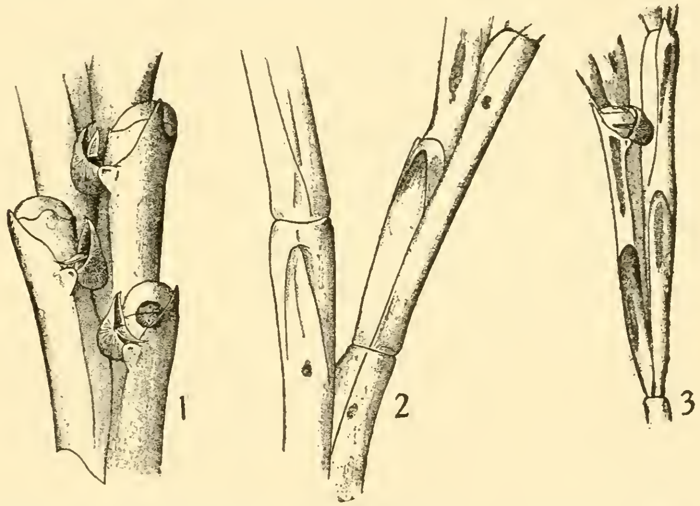


FIG. 1.—*Bugula microœcia* n. sp. Front view of portion of branch, showing details. Upper two oœcia not quite complete. Lower one complete with embryo.
FIG. 2.—The same. Portion of main branch showing joints. Degenerate polypides are present.
FIG. 3.—The same. Portion of stem higher up, showing less-modified zoœcia. Remains of degenerate polypides within.

Zoarium delicate, composed of a central stalk with long, narrowly flabellate branches arising in an irregular dichotomous fashion from the main stem. The stalk, as well as its branches, consists of very much elongated and modified zoœcia arranged biserially. That these are really zoœcial in character is shown by the fact that they contain polypides and occasionally one of them even bears an avicularium. Notwithstanding this, definite joints appear at the bifurcations of the main and all the accessory branches. These conditions show an interesting connecting link between the *Bugula* and *Stirparia* types of stems. From the lower stem zoœcia arise numerous, strong, radical fibers.

The ordinary zoœcia, which are arranged biserially, are long and slender and expand but little toward the tip; the frontal aperture extends almost to the base and faces somewhat toward the axis of the branch; a strong spine is situated at the distal outer edge; near the distal end, at the point where the outer wall curves farthest over the frontal area, is situated a short, stout avicularium with a strongly decurved beak; the avicularium is set upon a stalk so short as to be almost wanting.

The oœcium is hemispherical, very small, and set very low down, partially hidden by the spine, so as to be very inconspicuous; it is thin and transparent, with a slightly arched aperture. Many of these contain embryos in various stages of development.

Taken at 18 fathoms on a bottom of coral mud, several colonies attached to shell fragments; the largest 2.5 inches in height. Small fragments were also found decorating the legs of crabs (*Hyas* sp.?) at the same depth.

Bugula caraibica Levinsen.

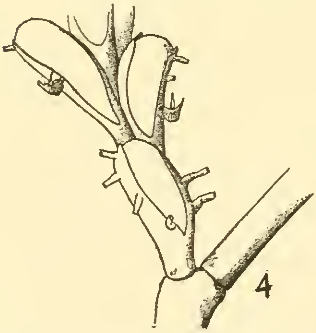
Levinsen, 1909, p. 104, pl. III, figs. 2a–2n.

This species, recently described from St. Croix, Danish West Indies, is common at the Tortugas on the piles of the government docks, and colonies 1.5 inches high were taken on the bottom of a skiff which had been in the water only from May 1 to June 23, 1908.

It is one of the most conspicuous species of the region, growing in loose tufts of a fine purple color to the height of 4 to 6 inches. Levinsen does not recognize *Stirparia* as a separate genus, but if the species with a jointed stalk are to be separated, *caraibica* will fall in that genus.

Bugula armata Verrill. (Figs. 4 and 5.)

Verrill, 1900, p. 588 (*Bugula* [*Caulibugula*] *armata* n. sp.).



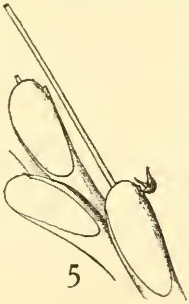


Fig. 4.—*Bugula armata* Verrill. Modified zoœcia at base of branch, showing arrangement of spines and position of avicularia.

Fig. 5.—The same. At tip of same branch, showing character of spines and position of avicularium.

Verrill has described from Bermuda a species which I take to be the same as one occurring at Tortugas. His description is as follows:

> A much more delicate, white *Bugula*, consisting of diverging, fan-like branches attached to the alternate sides and to the tip of slender jointed stems, sometimes having alternately a long joint and a very short joint, but more frequently the short joint is lacking and the end of the joint is swollen, as in *Stirparia*. There are usually 2 or 3 annulations at the base of each main branch and these arise just below the internodes. Many of the cells have a slender, distal vibraculum or sometimes two. It should doubtless form the type of a new genus or subgenus (*Cauli-*

bugula) intermediate between *Bugula* and *Bicellaria* on account of its articulated spines or vibraculum, and related to *Stirparia* by its jointed stem. It may be named *Bugula* (*Caulibugula*) *armata*. Its zoœcia are oblong and biserial, alternate. The pedicellariæ are on short pedicels, large, lateral not numerous.

Verrill in the above description overlooked some interesting and important points. He makes no mention of radical fibers which originate at the lower ends of the internodes of the stalks. He does not mention the oœcium, which is subglobose with a rather wide opening directed toward the zoœcial axis. The oœcium is attached by a narrow stalk to the outer edge of the zoœcial aperture near the distal extremity and is turned sidewise at a right angle to the zoœcial axis.

The avicularia ("pedicellariæ" of Verrill) show a peculiar distribution. The basal zoœcium bears no avicularium, but the zoœcia immediately above have the avicularia situated on the side about half-way along the aperture. The next few cells in order have the avicularium farther and farther removed toward the distal end, and in all zoœcia farther out on the branches the avicularium is on the distal outer edge of the aperture. This is a feature which I have never seen exhibited by any bryozoa. There are one or two ong spines, jointed at the base, on the distal end of the zoœcium (sometimes wanting). Verrill errs in calling these "vibracula," a term which should be applied only to modified avicularia with elongate mandibles. The basal zoœcium of the main branches arising from the stem differs from the others in having usually 6 spines surrounding the aperture, 4 on the outer, 2 on the inner edge, a feature exhibited by *Stirparia occidentalis* (Robertson, 1905, pl. XIII, fig. 73).

I can see no reason for erecting a new genus for this species. The jointed stalks, swollen at the nodes, seem sufficient to place it in *Stirparia* if that name were to be maintained for the Bugulas with jointed stalk. The jointed spines do not necessarily relate the species to *Bicellaria*, as this feature is present in some species of *Bugula* and *Stirparia*.

Taken on a number of occasions at 8 to 10 fathoms, growing in a sprawling fashion over sponges. Found also on the legs of spider crabs at 10 to 18 fathoms, and dredged on a bottom of coral mud at a depth of 18 fathoms.

GENUS BEANIA Johnston, 1838.

Beania mirabilis Johnston.

JOHNSTON, 1847, p. 372.—JELLY, 1889, p. 17, for further reference.—ROBERTSON, 1905, p. 276.

Several fragments of colonies on the legs of a crab (*Hyas* sp.) taken at 18 fathoms. This striking and well-known species has not before been noticed on the American side of the Atlantic.

Beania intermedia Hincks.

HINCKS, 1881*a*, p. 133 (*Diachoris intermedia*).—WATERS, 1906, p. 15; 1909, p. 137.

At 5, 10, and 15 fathoms, sprawling over hydroids and other bryozoa, and on shells. Very small colonies consisting of only a few cells. The simple, spineless character of the zoœcium easily serves to distinguish it from others of the genus.

The species is entirely southern in its distribution, being recorded from Tasmania (type locality), Australia, Chatham Island, Ganjam coast, and the Red Sea. The present record therefore adds the species to the Atlantic fauna and greatly increases the known range.

Hincks described the species as having spines on each side. Waters (1909) remarks that they are absent in Red Sea specimens, but sometimes present in those from Chatham Island. There is no indication of them in my material.

Beania cupulariensis n. sp. (Figs. 6 and 7.)

Small, straggling colonies growing attached to the under side of *Cupularia guiniensis*. The individual cells are fairly large (about as in *B. mirabilis*). On each side of the flattened frontal area there are about 6 (5 to 7) slender marginal spines which curve somewhat over the area. At the distal end 2 smaller spines project forward. At each side of the aperture is placed an avicularium situated on a short stalk on margin of cell; as far as observed, these are always paired. The form is short, the beak strongly decurved. The zoœcium arises from the preceding one of the series, near the distal part of the dorsal surface, by a tubular stalk so short that the top of one zoœcium projects over the base of the next in series. A branch arises about midway of the zoœcium near the lateral margin. Here again the tubular portion is very short and, as far as observed, only one branch arises from a zoœcium—never in pairs. There seem to be no other processes arising from the zoœcium and many of the cells have no tubes, branches, or other processes arising from them, except that of the zoœcium next in the series and a dorsal process for attachment.

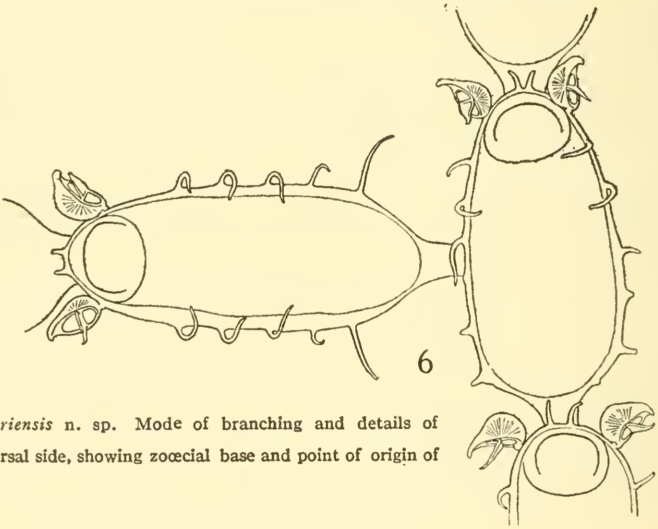


FIG. 6.—*Beania cupulariensis* n. sp. Mode of branching and details of zoœcium.
FIG. 7.—The same. Dorsal side, showing zoœcial base and point of origin of dorsal fiber.

The colony appears to be very loosely attached to the *Cupularia* by processes from the dorsal sides of the cells. The species occurred at various depths—in fact, wherever this species of *Cupularia* was found, at from 10 to 22 fathoms, but was found nowhere else. Usually only a single colony was found on one *Cupularia*, but occasionally on a large specimen two or three colonies would occur.

GENUS SYNNOTUM Hincks, 1886.

Synnotum aviculare (Pieper).

PIEPER, 1881, p. 43 (*Gemmellaria avicularis*).—HINCKS, 1886, p. 257.—ROBERTSON, 1905, p. 286.

This well-known species is abundant about the islands, growing especially on shells and sponges at a depth of 8 to 10 fathoms. It has not before been recorded from North America, except on the Pacific coast, where Miss Robertson found it at San Pedro and San Diego, Southern California. Hincks (1886) described the sessile avicularia as alternating on Adriatic specimens. Robertson states that they appear on every pair in specimens from California. In the Florida material in my collection the alternate condition is the rule, but occasionally sessile avicularia appear on successive pairs of zoœcia. Besides the above localities the species is now known from the Mediterranean and Red Seas, South Africa, Australia, and the Andaman Islands.

GENUS NELLIA Busk, 1852.

Nellia oculata Busk.

BUSK, 1852, p. 18.—LAMARCK, 1816, p. 135 (*Cellaria tenella*).—SMITT, 1873, p. 3.—JELLY, 1889, p. 94 (*Farcimia tenella*, references and synonymy).—WATERS, 1909, p. 167 (*Farcimia oculata*).—LEVINSEN, 1909, p. 120 (*Nellia tenella*).

Abundant at 10 to 18 fathoms, frequently attached to sponges or occasionally to shells. The usual height of the colonies is 0.5 to 1 inch. One large, branched colony was taken, measuring 4 inches across and of equal height. Smitt recorded the species from 13 to 138 fathoms. It has also been recorded from Texas and St. Thomas, West Indies (Levinsen), and is widely distributed in the Atlantic, Pacific, and Indian Oceans down to a depth of 550 fathoms.

Waters (1909, p. 167) objects to the use of Lamarck's name *tenella* on the ground that the short description given by Lamarck is not diagnostic and "might be applied to several species or even genera."

GENUS SCRUPOCELLARIA van Beneden, 1844.

Scrupocellaria cornigera (Pourtales).

POURTALES, 1867, p. 111 (*Canda cornigera*).—SMITT, 1872, p. 14 (*Cellularia cornigera*).—JELLY, 1889, p. 61 (*Cellularia cornigera*).

One small specimen of this species was taken at 10 fathoms and several others at 15 fathoms. The radical fibers are characteristically armed with stout, retrorse spines, as figured by Smitt. This alone is not sufficient for determining the species, as Busk has noticed serrate radicals in *S. ferox*

Busk and *S. macandrei* Busk, and Waters has named a species from the Red Sea *S. serrata* on account of this character. Florida specimens of *S. cervicornis* Busk show similar spines occasionally on the basal radicals. *S. cornigera* is a very delicate species and the radical fibers are transparent and thread-like, and this fact alone will serve to distinguish it from *S. cervicornis.*

Pourtales took the species at 270 fathoms, so it has a rather wide range in depth and temperature.

Scrupocellaria cervicornis Busk.

Busk, 1852, p. 24.—Smitt, 1872, p. 14 (*Cellularia cervicornis*).—Verrill, 1900, p. 594.

Occurs commonly about the islands, from low water to 18 fathoms, growing on piles of docks, attached to stems of gorgonias, etc. Colonies about 0.5 inch in height, with oœcia containing eggs, were taken from the bottom of a skiff on June 23, which had been in the water only since May 1. Recorded by Smitt from 7 to 17 fathoms.

The radical fibers, which are abundant at the base of the colony, are usually smooth, but in a few cases they bear retrorse spines like those of *S. cornigera.* In such cases the species are easily distinguished by the fibers alone, as they are much coarser in *cervicornis.* The cervicorn spines on the outer distal extremity of the zoœcia are well marked.

Genus Canda Lamouroux, 1816.

Canda caraibica Levinsen.

Levinsen, 1909, p. 142.

This species has been recently described by Levinsen, who gives no further indication of its distribution than is embodied in his remark "plentiful material of a West Indian species." Levinsen suggests the probability that this species is identical with *C. simplex* Busk, but being unable to determine this point he gives a new name to the West Indian material.

Several colonies were taken by the writer at the Tortugas at a depth of 15 fathoms, attached to shells. The largest of these was not much over 0.25 inch in height and no ovicells nor avicularia were present. The absence of an opercular spine and the length of the membranous frontal area (two-thirds of the whole zoœcium) show this form to be that described by Levinsen. The vibraculum in some cases is longer than the width of the branch.

The other Florida species of this genus, *C. retiformis* Pourtales (1867, p. 110), which Levinsen wrongly attributes to Smitt, is quite distinct from *C. caraibica,* since it possesses a broad opercular spine, the membranous area is but little more than half as long as the zoœcium, and there are differences in the vibracula. *C. retiformis* was not found at the Tortugas.

GENUS MEMBRANIPORA Blainville, 1834.

Membranipora membranacea (Linné).

LINNÉ, 1766–68, p. 1301 (*Flustra membranacea*).—PACKARD, 1867, p. 274.—ROBERTSON, 1908, p. 267.—NORMAN, 1909, p. 286.

One colony on the bottom of a skiff. In every respect this colony agrees with European specimens in my collection, except that there is a very slight extension of the calcification over the area at the base of some of the zoœcia. This is so slight, however, that I can not consider it of specific value. The species was not listed for Floridian waters by Smitt, nor was it taken by the writer at Woods Hole, Massachusetts, in several years collecting.

Packard recorded it from the Labrador coast. It is a common European species, occurring as far south as Madeira (Norman). It is also found in Australia and New Zealand, and Miss Robertson (1908) states that on the Pacific coast of North America it occurs from California to Alaska.

? Membranipora lacroixii (Audouin).

AUDOUIN, 1826, p. 240 (*Flustra lacroixii*).—BUSK, 1852–4, vol. 2, pl. 1.—DAWSON, 1859, p. 256.—PACKARD, 1867, p. 8.—SMITT, 1873, p. 18.—JELLY, 1889, p. 162 (*M. reticulum*).—WATERS, 1898, p. 697.—WHITEAVES, 1901, p. 97.—ROBERTSON, 1908, p. 261.—OSBURN, 1912, p. 227.

Taken in drift incrusting the carapace and legs of a large crab, and at 8 fathoms on shell. The specimens taken at Tortugas are much more heavily calcified than those from Massachusetts and between the zoœcia are numerous, roughly triangular prominences with triangular, membranous areas, as figured by Busk (l. c., pl. 1), while these are almost wanting in the Massachusetts specimens. Examination of the reverse side of the zoœcium, however, reveals the transparent circles and the irregular projections described by Waters (l. c.).

There has been much difference of opinion concerning this species and there can be but little certainty in regard to many earlier records, such, for example, as those of Dawson and Packard. Smitt's figures of Florida specimens seem, without question, to represent the same species as my own, though the dorsal surface is not shown. The range on the eastern coast of North America is from Florida to the Gulf of St. Lawrence, or to Labrador, if Packard's record is valid. Elsewhere it is known from Europe, New Zealand, and from California northward to Alaska.

Membranipora tehuelcha (d'Orbigny).

D'ORBIGNY, 1839, pl. 17 (*Flustra tehuelcha*).—BOSC, 1802, p. 118 (*Flustra tuberculata*).—JELLY, 1889, p. 167 (*M. tehuelcha*) and p. 168 (*M. tuberculata*).—WATERS, 1898, p. 674.—VERRILL, 1900, p. 594 (*Biflustra dentata*).—NORMAN, 1909, p. 286 (*Membranipora tuberculata*).—OSBURN, 1912, p. 231.

This species is found on *Sargassum bacciferum* (gulfweed) wherever it floats. It is abundant at the Tortugas. Verrill notes its occurrence at Bermuda, under the name of *Biflustra dentata*, as "common on Sargassum found upon the beaches." Smitt did not record it for the Florida region.

Norman prefers to use Bosc's older name for this species on the ground that, while his description means nothing, Bosc stated that it occurs "en immense quantité sur les fucus nageans dans l'Atlantique." As I am not aware that, under the rules of nomenclature, the habitat alone is considered a sufficient diagnosis, I prefer to follow Waters in using d'Orbigny's name.

Membranipora irregularis d'Orbigny.

D'Orbigny, 1839, p. 17, pl. viii, figs. 5 and 6.—Smitt, 1873, p. 8, pl. ii, fig. 63.—Jelly, 1889, p. 151, for synonymy.—Waters, 1904, p. 31.

Incrusting shells at 8, 15, 18, and 22 fathoms. Smitt's figure is very satisfactory and there can be no doubt that the present species is the one which he figured as taken at 60 fathoms. The granulation of the border varies with the amount of calcification. Oœcia are present in some numbers. In younger stages these are quite prominent, but with later calcification they become included in the general crust.

Membranipora savartii (Audouin).

Audouin, 1826, p. 240 (*Flustra savartii*).—Smitt, 1873, p. 20 (*Biflustra savartii*).—Waters, 1909, p. 137.

One small, branching specimen 0.5 inch in height was collected at a depth of 10 fathoms. The broad, internal, basal denticle figured by Waters for Red Sea specimens is the best means of determining the species. Recorded by Smitt, 29 fathoms.

GENUS CUPULARIA Lamouroux, 1821.

Cupularia guiniensis Busk.

Busk, 1854, p. 98.—Busk, 1859, p. 87 (*C. canariensis*).—Smitt, 1873, p. 10 (*Membranipora canariensis*).—Norman, 1909, p. 289, synonymy.

Abundant at 10 fathoms, especially on soft bottom with algæ. The umbrella-shaped disks range in size from 0.125 to 0.75 inch in diameter. The color of living colonies is horn brown, due mainly to the chitinous bristles which form the mandibles of the avicularia. When touched the bristles stand erect for some time.

Recorded by Smitt from Pourtales's collections from 10 to 44 fathoms. Smitt listed this species under *Membranipora* because of the character of the zoœcium, holding the zoarial characters as of no importance. Just why he should have retained the related *C. lowei* and *C. doma* in *Cupularia* is not certain, but probably on account of the greater amount of calcification of the front wall.

The under surface of the colony is usually clear and free of any attached animals or plants, except that in numerous cases there occurs, closely attached, a new species of *Beania*, which I have named *B. cupulariensis*.

Cupularia lowei Busk.

Busk, 1854, p. 99.—Smitt, 1873, p. 14 (*C. umbellata* Manzoni).—Verrill, 1878, p. 305 (*C. umbellata*).—Norman, 1909, p. 290.

Only two specimens, both dead, were taken, one at 12 and the other at 22 fathoms, in company with *C. guiniensis*. Each was about 0.25 inch in diameter.

Recorded by Smitt for 29 fathoms and also in 7 fathoms off the mouth of the Cape Fear River. Smitt regarded *C. johnsoni* Busk (syn. *C. doma* d'Orbigny) as a highly calcified form of *C. lowei* (*umbellata*), but later investigations do not support this view.

Verrill (l. c.) recorded the species with doubt from one worn specimen taken at Fort Macon, near Beaufort, North Carolina. As the writer has taken specimens at the same locality, Verrill's record may be considered good.

GENUS CRIBRILINA Gray, 1848.

Cribrilina floridana (Smitt).

SMITT, 1873, p. 23 (*Cribrilina figularis* and local variety *floridana*).—JELLY, 1879, p. 66 (calls attention to fact that *C. figularis* of Smitt is not Johnston's species, and lists *C. floridana* as a distinct species).

A number of small colonies of this species taken at 5 to 15 fathoms on shells. Smitt recorded it from 29 to 42 fathoms. It is not known to occur outside of the Florida region.

No oœcia nor avicularia are developed on my specimens. The posterior margin of the orifice is straight, and the orifice is completely filled by the semicircular operculum, which is well chitinized and of a brownish color. There are two short, stout oral spines and in young zoœcia there is frequently a third median spine.

There is a possibility that this species may belong to the genus *Puellina* of Jullien as amended by Levinsen (1909, p. 159), but the immature colonies in my collection seem rather to belong to *Cribrilina* in the strict sense.

GENUS ARACHNOPUSIA Jullien, 1888.

Arachnopusia monoceros (Busk).

BUSK, 1854, p. 72 (*Lepralia monoceros*).—JELLY, 1889, p. 67, synonymy.—LEVINSEN, 1909, p. 160 (discusses relationship and adopts Jullien's genus *Arachnopusia* with emendations).

A single specimen of this widely distributed species was taken at 5 fathoms, incrusting a shell. The colony was small, measuring only 0.125 inch across, but the zoœcia ranged in development all the way from the ancestrula to adults with ovicells and from these to marginal individuals in various conditions of calcification. The species has not before been taken in North American waters.

GENUS SMITTIPORA Jullien, 1881.

Smittipora abyssicola (Smitt).

SMITT, 1873, p. 6 (*Vincularia abyssicola*).—JELLY, 1889, p. 253, synonymy and references.—HINCKS, 1881, p. 155; 1887, pp. 161 and 164.

Found at low water and down to 15 fathoms on shells, bases of gorgonias, etc. Smitt recorded two specimens taken by Pourtales, one at 68 fathoms, the other at 450 fathoms. The bathymetrical range of the species, from low water down to nearly 0.5 mile, is worthy of note.

Only the incrusting phase was seen, with no evidence of the erect stems described and figured by Smitt in one colony. The family relations of this genus are very uncertain. Hincks (1881, p. 155) placed it in the Microporidæ, but later (1887, p. 154) he removed it from this family on account of "the double layer of the ectocyst," and placed it in the Steganoporellidæ. As we understand the latter family at present, this genus can not be included in it. It will require a careful study of sectioned material to determine the real position of the genus.

GENUS STEGANOPORELLA Smitt, 1873.

Steganoporella magnilabris (Busk).

BUSK, 1854, p. 62 (*Membranipora magnilabris*).—SMITT, 1873, p. 15 (*Steginoporella elegans*).—VERRILL, 1900, p. 594 (*Steginoporella elegans*).—HARMER, 1900, pp. 279–286 (revision, synonymy, and detailed description).—LEVINSEN, 1909, pp. 167–168 (discussion of family and genus).

Common in low water to 15 fathoms. Beautifully convoluted, frill-like colonies were taken on piles and on shells, sponges, coral, etc., at 12 to 15 fathoms. The erect frill-like extensions are sometimes 2 inches high and 3 inches broad. These are bilaminate and are sometimes tubular in form. The color in life varies from pink to reddish brown.

Smitt recorded the species in Pourtales's collections from 15 to 37 fathoms; Bermuda (Verrill); other distribution given by Harmer (l. c., p. 280).

Steganoporella connexa Harmer.

HARMER, 1900, p. 254.

Dead colonies of what appears to be this species were taken incrusting shells at a depth of 12 fathoms. The opercula are all lost from the colony, so it is impossible to make use of this important structure for identification. The character of the calcification, with the junction of the median process with the sides of the zoœcium to form a pair of opesiulæ or foramina, is similar to that described and figured by Harmer. Since this connection of the median process with the zoœcial walls is known only in *S. connexa*, I refer my specimens to that species. The other points, as far as I can make them out on the dead specimens, agree with *connexa*, except perhaps in the matter of size, since the zoœcia in my specimens are smaller than described by Harmer. There is much variation in the matter of size, however, a condition also stated by Harmer to occur in *connexa*. Only one form of zoœcium can be distinguished.

The species is known from a single locality, "John Adams Bank," the location of which is somewhat in doubt, but Harmer seems to feel satisfied that it is south of Abrolhos Island off the coast of Brazil.

GENUS THALAMOPORELLA Hincks, 1887.

Thalamoporella rozierii (Audouin).

AUDOUIN, 1826, p. 239 (*Flustra rozierii*).—(?) SMITT, 1873, p. 16 (*Steginoporella rozierii*).—LEVINSEN, 1909, p. 181 (discusses at length, with five varieties).

Found on shell in drift and at 10 fathoms on sponges. Only small, unilaminar colonies without oœcia were taken. Smitt found only a single, small specimen in Pourtales's collections. His description of this specimen is brief and his figure (pl. 4, fig. 102) does not show the avicularium nor the spicules, so I include it in the above synonymy with some doubt. I have received from Professor A. E. Verrill a fine, erect, convoluted, bilaminate colony taken on the west coast of Florida. Levinsen (l. c., p. 183) records the variety *labiata* from Jamaica and my Florida specimens agree fairly closely with this variety.

Thalamoporella granulata Levinsen.

LEVINSEN, 1909, p. 188.

In the drift were found several dead specimens incrusting shells and calcareous algæ. The sinuated character of the orifice with the strong lateral denticles; the nearly equal opesiulæ reaching the marginal wall and with granulated edges; the dorsal opesiular outgrowths; the granulated character of the zoœcial walls; the form of the large, spatulate avicularian mandible, and the character of the spicules, all approach closely to *T. granulata*. The only difference to be observed is in the basal portion of the avicularian chamber. When completely calcified this structure becomes closed by a calcareous lamina up to the hinge denticles of the mandible, leaving only two openings similar in appearance to the opesiulæ of the ordinary zoœcia, except that they are much smaller and are removed from the lateral wall.

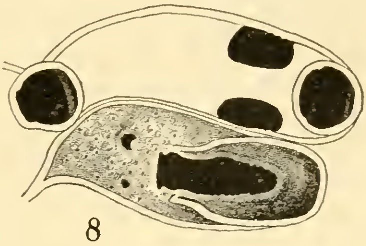


FIG. 8.—*Thalamoporella granulata* Levinsen. The variety in which the avicularium chamber is closed basally, except for two opesiulæ.

Thalamoporella falcifera (Hincks).

HINCKS, 1880*b*, p. 380 (*Steganoporella rozieri*, form *falcifera*).—LEVINSEN, 1909, p. 186.

A single specimen of this species, which is distinguished by the falcate mandible of the avicularium, was taken in shallow water growing on algæ. Apparently this species grows only on algæ, if one may judge from the comparatively small number of records. It has a wide distribution and is recorded from Campeche Bank, Yucatan; Java Sea; Geographe Bay, Australia, and from latitude 23° 30′ N., longitude 40° W.

GENUS SAVIGNYELLA Levinsen, 1909.

Savignyella lafontii (Audouin).

AUDOUIN, 1826, p. 242 (*Eucratea lafontii*).—JELLY, 1889, p. 93 (synonymy under *Eucratea lafontii*).—NORMAN, 1909, p. 295 (*Catenaria lafontii*, later synonymy and discussion of relationships).—WATERS, 1909, p. 131 (*Catenaria lafontii*, later synonymy and discussion of generic name).—LEVINSEN, 1909, pp. 213 (note) and 274 (*Savignyella*, new genus and reasons for change in generic name).

This widely distributed tropical species is abundant about the islands from low water down to 10 fathoms on shells, piles, and sponges, in company with *Amathia*, *Bowerbankia*, etc. Oœcia with eggs in various stages of development are common. A number of colonies with oœcia containing eggs were on June 23 taken from the bottom of a skiff which had been in the water only since May 1. The color in life is dark brick-red, which makes the colonies quite conspicuous against the background in spite of their small size. The presence of this species in American waters has hitherto escaped notice.

While there has never been any question as to the validity of this species, there has been great confusion as to its generic position ever since its discovery. This has been sufficiently discussed by Norman (l. c.), Waters (l. c.), and Levinsen (l. c.). Waters remarks "though it certainly never ought to have been placed under *Catenaria*, it seems best to leave it here," but Levinsen solves the problem by the erection of a new genus *Savignyella*. This seems the only proper course, since the species does not have generic relationship with any of the older genera (*Catenaria*, *Eucratea*, *Alysidium*, *Catenicella*) in which it has been placed by previous authors.

GENUS HIPPOTHOA Lamouroux, 1821.

Hippothoa distans MacGillivray.

MACGILLIVRAY, 1868, p. 130.—JELLY, 1889, p. 112 (*Hippothoa flagellum*), references.—WATERS, 1904, p. 54, synonymy and references.

This minute species occurs abundantly at the Tortugas from low water to 12 fathoms, spreading over the inside of dead shells. Oœcia are abundantly developed. The "short processes arising from the side of the zoœcium, below the lateral tubular branches," described and figured by Waters (l. c.) as occurring on specimens from Sydney, New South Wales, are developed on many of the zoœcia. I am unable to add anything to Waters's description of this organ, except that it is constricted at the base where it is attached by a movable joint to the zoœcium.

The species is very widely distributed in European seas, New Zealand, Australia, Pacific Ocean, Cape Horn, etc., but has not hitherto been noticed on the American side of the Atlantic.

GENUS TRYPOSTEGA Levinsen, 1909.

Trypostega venusta (Norman).

NORMAN, 1864, p. 84 (*Lepralia venusta*) and 1909, p. 299.—GABB and HORN, 1862, p. 127 (*Lepralia inornata*).—SMITT, 1873, p. 37 (*Gemellipora glabra, forma striatula*) and p. 61 (*Lepralia inornata* Gabb and Horn).—JELLY, 1889, p. 233 (*Schizoporella striatula*), p. 237 (*S. venusta*) and p. 128 (*Lepralia inornata*).—LEVINSEN, 1902, p. 23, and 1909, p. 281 (*Trypostega venusta*).

On shells, *Steganoporella* and *Oculina*, at 5 to 15 fathoms. Smitt recorded it as *Gemellipora glabra forma striatula*, incrusting nullipores at a depth of 68 fathoms, one colony, and as *Lepralia inornata*, two colonies from 26 and 60 fathoms. After careful study of the material at hand, I am unable to distinguish more than one species, or to separate it from the *venusta* of Norman, even as a variety. The form of the aperture, the umbonate knob below, the puncturing, the character of the dwarf zoœcia and their relation to the oœcia, all appear to me to be identical. Levinsen (see above) has recently made this species the type of a new genus, *Trypostega*, characterized especially by having the oœcia covered by dwarf zoœcia with scattered pores and a minute orifice.

This species is widely distributed, but on the American coast is known only from the Florida region. Levinsen (p. 281) included Gabb and Horn's and Smitt's records for *Lepralia inornata*, but failed to include Smitt's *Gemellipora glabra forma striatula* as a synonym. Smitt (pp. 61–62) separated the species on the following ground: "The most characteristic difference, which has caused us to place them in different families, depends on the shape of the zoœcial aperture," and his figures show some differences, but these may be accounted for by variation. In a single colony in my possession the variation is as great as that shown by Smitt's two specimens.

GENUS ADEONA Busk, 1884.

Adeona violacea (Johnston).

JOHNSTON, 1847, p. 325 (*Lepralia violacea*).—(?) REUSS, 1847, p. 85 (*Cellepora heckeli*).—SMITT, 1873, p. 30 (*Porina violacea* and *Porina plagiopora* Busk).—JELLY, 1889, p. 184 (*Microporella heckeli*), synonymy.—VERRILL, 1901, p. 54 (*Porina plagiopora*).—NORMAN, 1909, p. 296 (*Reptadeonella violacea*).—LEVINSEN, 1909, p. 283, discusses genus and species.

Taken from 5 to 18 fathoms. Both the typical form and the nominal variety *plagiopora* (Busk) occur and in some colonies the avicularia are intermediate in position between that of *violacea* and *plagiopora*. Occasionally the characters of both "varieties," together with intermediate conditions, may be observed in the same colony. The usual color is purple, varying to nearly black, or through pale bluish to white.

Smitt recorded the species "from the depth of 35 fathoms W. off Tortugas" (*Porina violacea*), and "at a depth of 60 fathoms W. off Tortugas" (*Porina plagiopora*), and Verrill has noted the form *plagiopora* at Bermuda. Otherwise the species has not been recorded from American waters.

Levinsen (1909, p. 282) has returned to the use of Busk's family Adeonidæ, thus again breaking up the arrangement established by Hincks in his family Microporellidæ. The latter family was based on the presence of a frontal pore (ascopore) as the principal character; but, as Levinsen has shown, this brought together a number of forms which are separated by more fundamental characters.

GENUS BRACEBRIDGIA MacGillivary, 1886.

Bracebridgia subsulcata (Smitt).

SMITT, 1873, p. 28 (*Porina subsulcata*).—VERRILL, 1901, p. 54 (*Porina subsulcata*).—HINCKS, 1880*a*, p. 76 (*Microporella subsulcata*).

Abundant from 10 to 12 fathoms. Branching colonies reach a height of 2 inches or more. The color in life varies from yellowish pink to orange; when dead, white. Smitt recorded the species from 10 to 48 fathoms and a dead specimen from 471 fathoms. Verrill has recorded it from Bermuda, but otherwise it is known only from the Florida region.

I have placed this species in the genus *Bracebridgia* with some hesitation, since, as this genus is understood, it possesses no ascopore (Levinsen, 1909, pp. 283, 289). In *subsulcata* a minute pore is usually present below the suboral avicularium; a similar pore appears above the basal avicularium when this organ is present. This latter pore was not figured nor mentioned by Smitt. I have not been able to determine positively the nature of this structure and it may be, from the fact that it is often wanting and also because of its presence in connection with the basal avicularium, that it is not an ascopore at all, or that it represents this organ in a vestigial condition.

The nature of the colony and the zoœcia with the marginal and other ribs, the form of the orifice, the presence of a line of special independent avicularia on each edge of a branch, all seem to agree with *Bracebridgia*. *B. pyriformis* (Busk) has a flattened area below the orifice where the avicularium is located in *subsulcata*, but the fact that MacGillivray found a single avicularium in this position in one colony of *B. pyriformis* is sufficient to show the relationship. Moreover, in the rare cases in which the oral avicularium is wanting in *subsulcata* there is a flattened area similar to that of *pyriformis*.

GENUS RETEPORA Smitt, 1867.

Retepora marsupiata Smitt.

SMITT, 1873, p. 67.—BUSK, 1884, p. 116 (*Retepora atlantica*).—GABB AND HORN, 1862, p. 138 (*Phidolophora labiata*).—JELLY, 1889, p. 212 (Jelly adopts Busk's name *atlantica* for this species, but Smitt's publication of the name *marsupiata* clearly has priority).

Taken on a number of occasions at 10 to 18 fathoms. The largest colony measured about an inch in height. The color in life is a delicate pink. Smitt records the bathymetrical distribution as 16 to 262 fathoms.

GENUS RHYNCHOZOON Hincks, 1891.

Rhynchozoon tuberculatum n. sp. (Fig. 9.)

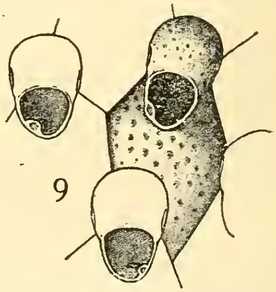


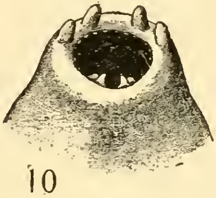
FIG. 9.—*Rhynchozoon tuberculatum* n. sp. Showing characters of zoœcium, orifice, peristome, and ovicell.

Zoœcia small, rather evenly swollen, separated by slightly raised marginal walls; the surface, except in young individuals, strongly tuberculate. Pores are wanting, except for occasional very minute ones at the margin. Orifice ovate, the broader distal border often somewhat straight; at one side near the proximal border a strong pointed tooth extends often more than half-way across the orifice and curves backward; on the opposite side a minute projection sometimes appears, but is often entirely absent. The peristome is thin and raised high above the primary orifice, usually erect at the sides, but flaring slightly backward behind the orifice; above the large tooth the peristome appears to bear a minute, short-elliptical avicularium, but I am not able to distinguish a mandible in my specimen.

The ovicell is globose, at first smooth, but later tuberculate like the zoœcium; on either side at the widest part and near the base is a rounded thin area appearing membranous; in complete calcification the peristome rises over the front of the ovicell and fuses with the outer layer, leaving a thin, somewhat triangular area on the front.

One colony at 18 fathoms, incrusting a shell with a single layer of zoœcia.

Rhynchozoon solidum n. sp. (Figs. 10, 11, and 12.)



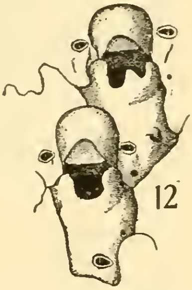


Fig. 10.—*Rhynchozoon solidum* n. sp. Enlarged, showing primary aperture, spines, two pairs of denticles, and the beaded vestibular arch.
Fig. 11.—The same. Operculum.
Fig. 12.—The same. Fully calcified, showing avicularium, peristome, and ovicell.

Zoœcia small, little swollen, rather broad, closely set in a continuous crust, thick-walled, the surface smooth or irregularly traversed by very fine lines. As a rule only three pores are seen, one at the posterior margin and the others on either side of the orifice at the margin. Orifice evenly rounded, a little broader than long, with a rounded sinus in the proximal border. This sinus is really double, being formed by two sets of denticles, the lower pair equal in size and inclosing a semicircular sinus much like that of many *Schizoporellas.* Immediately above them is another pair of denticles, more pointed and a little longer than the lower ones, and often one of them is a trifle larger than the other; they are turned inward more than the lower pair, so as to inclose a narrower and more nearly circular sinus. The operculum is well chitinized, yellowish in color, the dots showing attachment of muscles situated nearly half-way from the circumference toward the center. Through the operculum can be seen a beaded vestibular arch very similar to that figured by Levinsen (1909, pl. XXIII, fig. 4*e*) for *R. angulatum.* In young cells there are four short, stout spines about the anterior margin of the orifice. The peristome is high and thick, extending upward and forward on the sides into thick, lappet-like processes, usually a little unsymmetrical; posteriorly the peristome extends upward and over the orifice in the form of a broad mucro, though sometimes this is but little developed.

Small avicularia, sometimes a pair, frequently only one, are placed posteriorly not far from the margin, with the triangular beak pointing laterally.

The oœcia are globose, raised, smooth, without pores; a thin extension of the peristome runs upon the top and fuses with the outer layer of the ovicell, leaving a thinner area upon the front.

One small colony incrusting a shell at 8 fathoms.

ARBORELLA, NEW GENUS.

Zoarium erect, dichotomously branched, with flexible corneous joints at the bifurcations. Zoœcia arranged in pairs, back to back, each pair facing at right angles to the preceding pair of the series, giving a somewhat quadrangular appearance. Front wall porous, but without special enlarged pores. Fertile zoœcia shorter than the infertile. Orifice with a distinct sinus. Ovicell external, but inserted partly under the front of the zoœcium, its orifice closed by the zoœcial operculum. Spines and avicularia absent. A clear, chitinous, uncalcified ectocyst covers the zoœcium and ovicell.

The relationships of this genus can not as yet be stated positively. The general appearance of the colony and especially the character of the joints and the membranous ectocyst seem to relate it to *Tubucellaria*, but the character of the oœcium and the manner of origin of the zoœcia at the tips of the branches, together with the absence of a special median frontal pore, distinctly separate it from this genus. It may be necessary to erect a new family to accommodate it. Sectioned material will be studied to determine the points necessary for a more complete understanding of the relationships.

Arborella dichotoma n. sp. (Figs. 13 to 15.)

Zoarium erect, dichotomously branching, with hinged, flexible joints at the points of bifurcation; internodes consisting of 8 to 18 pairs of zoœcia, each pair set slightly in advance and at right angles to the preceding pair of the series, facing in four directions. Zoœcia broad fusiform, wedge-shaped at the base where they are inserted between the preceding pair. The front wall evenly arched, cryptocyst well calcified, porous, with no specialized, larger pores. Ectocyst uncalcified and covering the calcareous wall as a clear layer. The orifice is evenly rounded in front and on the sides, somewhat straighter on the posterior margin, with a broad, shallow, but very evident sinus. The operculum is compound, well chitinized, with an arched rib on either side, extending inward and upward from the hinge denticle. Avicularia and spines are wanting. The fertile zoœcia are somewhat different in form from the ordinary ones, being shorter and somewhat broader, and the oœcium incloses nearly all of the orifice. The oœcium is rounded in outline, large and prominent, the aperture looking upward and closed by the zoœcial operculum. The oœcial wall is porous like that of the zoœcium and is covered by the clear ectocyst.

The colony was evidently broken off in dredging and no description can be given of the base or the mode of attachment.

One colony 0.5 inch high, composed of 24 internodes, taken at 10 fathoms on a sponge bed between Loggerhead and Garden Keys, Tortugas.

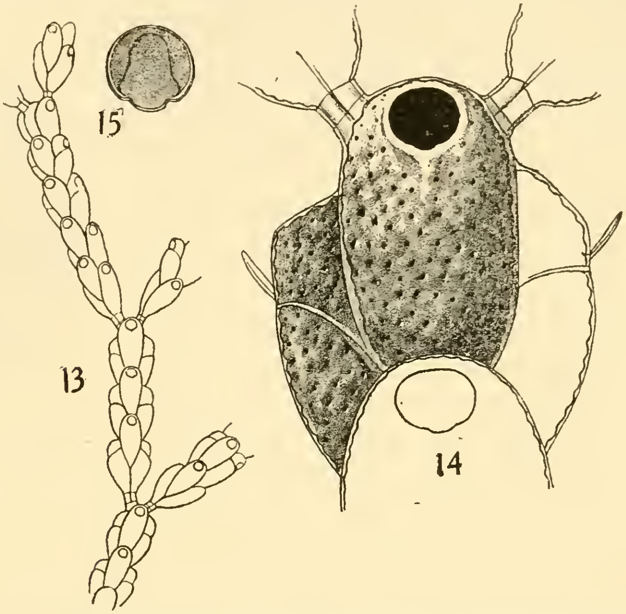


FIG. 13.—*Arborella dichotoma* n. sp. Portion of colony, showing mode of growth.
FIG. 14.—The same, showing details.
FIG. 15.—The same, operculum.

GENUS TUBUCELLARIA d'Orbigny, 1850–52.

Tubucellaria cereoides (Solander).

SOLANDER, 1786, p. 26 (*Cellaria cereoides*).—WATERS, 1907, p. 129.—LEVINSEN, 1909, p. 305.

One small colony about an inch in height was taken at a depth of 15 fathoms. This species has not before been taken on the American side of the Atlantic.

Waters makes *T. opuntioides* Pallas a synonym of *cereoides*, but Levinsen believes that they should be kept separate. This difference of opinion, which has existed since the discovery of the form, does not seem likely to reach a settlement soon. The single specimen taken by me at the Tortugas is not sufficient to decide the point. It agrees closely with specimens of *cereoides* of the same size taken at Naples, but *cereoides* has hitherto been limited to the Mediterranean by those who separate the species, while Atlantic specimens are considered to be *opuntioides*.

GENUS ESCHARELLA (PART) Gray, 1848.

Escharella costifera n. sp. (Fig. 16.)

Zoœcia of moderate size, rather regularly ovoid in form, evenly swollen, nearly hyaline. Around the margin is a row of rather large pores, between which rise strong, conspicuous ribs which converge regularly toward the central portion of the front wall. They fade out, however, before they reach it, leaving a smooth central area devoid of ribs. The orifice, which is placed far forward, is rounded in front, more straight on the posterior border, and the hinge denticles are rather conspicuous. A few zoœcia seem to show a slight median denticle, but I can not be certain of this. The peristome, which is very thin, rises in front and on the sides into a short tube, and is beset with six or eight long spines which are jointed at intervals. Posteriorly the peristome rises into a high, pointed mucro which projects forward over the orifice. This mucro is flat and thin, with a strong rib on each edge, looking as though it originated from two spines fusing at the tip, leaving an open space between. The development of the mucro, however, shows that this is not the case. The thin area forming the middle of the mucro is rounded below and pointed above and looks as though it were meant to harbor an avicularium, but no such structure is present.

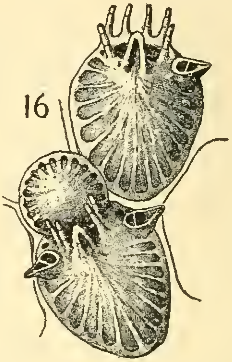


FIG. 16.—*Escharella costifera* n. sp. Details of front wall, mucro, avicularium, jointed spines, vestibular arch (in upper figure), and ovicell (in lower figure).

Avicularia are present on the zoœcium, usually situated near the margin on either side of the mucronate process. Occasionally only one is present. The avicularium is comparatively large, the mandible long triangular, projecting sidewise or a trifle backward and pointing strongly upward, The oœcium is rounded in outline, prominent, imperforate, smooth on the upper surface, or with fine, radiating lines. Around the margin is a strong, raised rib, within which there is a row of large pores with strong ribs running upward as on the zoœcial wall. The anterior pair of spines is inclosed within the ovicell.

Two small colonies, the largest scarcely over 0.125 inch across, incrusting algæ, at 2 fathoms. In spite of the small size nearly every cell is adult, with a complete oœcium.

I am a little uncertain as to the generic position of this species. *Escharella* as amended by Levinsen (1909, p. 315) includes only forms without avicularia. In spite of this difference the species seems to fit better into *Escharella* than into any related genus. The absence of zoœcial and oœcial pores, except the marginal ones, the well-developed vestibular arch, the very thin operculum, the character of the orifice and peristome, and the nature of the jointed spines, seem to locate the species in *Escharella*. In many respects it resembles *E. diaphana* MacGillivray, as figured by Levinsen (l. c.), except for the presence of the avicularia and the strong development of the ribs, which are wanting in *diaphana*.

Genus Schizoporella Hincks, 1880.

Schizoporella unicornis (Johnston).

Johnston, 1847, p. 320 (*Lepralia unicornis*).—Desor, 1848, p. 66 (*Lepralia variolosa*).—Leidy, 1855, p. 10 (*Escharina variabilis*).—Smitt, 1873, p. 44 (*Hippothoa isabelleana*).—Verrill and Smith, 1873, p. 713 (*Escharella variabilis*).—Verrill, 1875*b*, p. 41 (*Hippothoa variabilis*); ibid., p. 41, pl. III, fig. 1 (*Hippothoa reversa*, n. sp.); 1878, p. 305 (*H. variabilis*); 1879*b*, p. 193, and 1880, p. 30 (*Escharina isabelliana* d'Orbigny, *E. reversa* Verrill and *E. ansata* Gray); 1900, p. 592 (? *Schizoporella isabelliana*).—Levinsen, 1909, p. 323.—Osburn, 1912, p. 236.

Abundant from low water to 10 fathoms, in the drift and growing profusely on the piles of docks, incrusting shells, and coral rocks, and rising into branched, finger-like processes about worm-tubes and the stems of hydroids, or occasionally growing free. Masses nearly as large as a man's head were dredged. The color varies from white or pale pink or purple in young, rapidly growing colonies, to a dark purplish red or sometimes nearly black. Colonies 1.5 inches in diameter were found incrusting the bottom of a skiff that had been in the water only from May 1 to June 23.

Smitt recorded the incrusting form "growing in a single layer of whitish and yellowish hue on *Oculina* and *Nullipora* at the depth of 42 fathoms," and, "a more compound colony, composed of several concentric layers of a purplish-blue tint, around an axis of foreign matter," at a depth of 17 fathoms.

Schizoporella floridana n. sp. (Figs. 17 and 18.)

Primary characters of the zoœcium much like those of *S. unicornis* (Johnston) but with a slightly more V-shaped sinus; avicularia situated far forward, often in advance of the middle of the orifice, and with the mandible usually strongly curved toward the zoœcial axis; large vicarious avicularia with long-pointed, straight mandibles on hemispherical cells raised high above the surface of the colony.

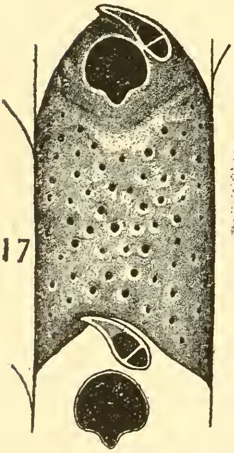
The naked-eye appearance of the colonies is very similar to that of *S. unicornis* (Johnston) and the general characters of the zoœcia are not very different from that species. It does differ remarkably, however, in the presence of the large, vicarious avicularia, which are sometimes very abundant. These are raised high above the surface of the colony as rounded, knob-like prominences; the mandibles, while broad at the base, are very much narrowed and elongated distally. These are turned in all directions on the colony without any apparent arrangement. *Schizoporella ampla* Kirkpatrick, from Mauritius, and *S. viridis* Thornley, from the Red and Mediterranean Seas, also have vicarious avicularia.

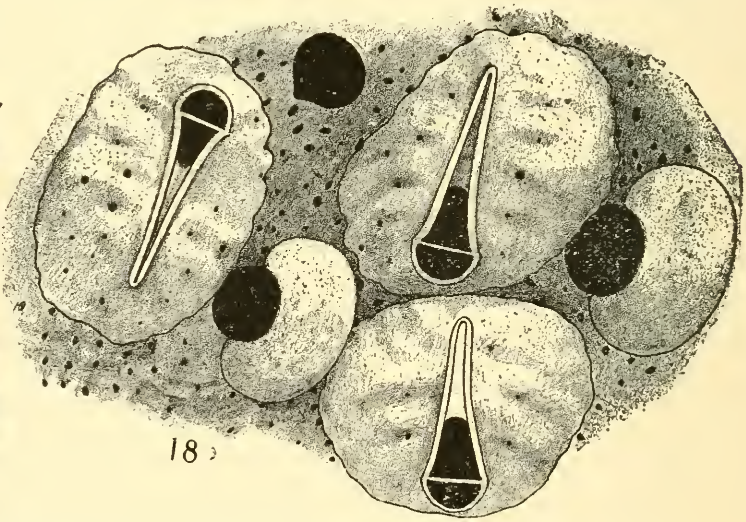
The ordinary avicularia are situated at the side of the orifice and the mandibles are curved toward the axis of the zoœcium so as to nearly conform to the curve of the margin of the orifice. There is much variation in this avicularium and the mandible is occasionally straight instead of curved, and it may be directed backward or sideways. It is usually situated well forward near the anterior border of the orifice, but may be placed farther back, occasionally behind the orifice. The zoœcia are swollen about as in *unicornis*, the punctures are similar to that species, and the form of the orifice (with the sinus) might readily pass for that species. No oral spines have been observed. In the very young stage a low, raised margin separates the cells, but this is soon obscured by the secondary calcification. An umbo is developed below the orifice, apparently only by secondary calcification. In young colonies, where the vicarious avicularia are not yet developed, this species may readily be mistaken for *S. unicornis*, but the more anterior position and the curved form of the avicularia will serve to distinguish it even in this condition.

The oœcium differs from that of any *Schizoporella* with which I am acquainted. It is comparatively small, very short (about two-thirds as long as wide), very high and prominent, smooth, and imperforate.

This well-marked species, which appears to be undescribed, was dredged in 15 to 18 fathoms, incrusting shells and hard sponges, and, in one case, forming an erect nodular growth nearly an inch in height and about half an inch in diameter around some foreign matter as a center. The color ranges from pure white to dark purplish-red.

17





18

FIG. 17.—*Schizoporella floridana* n. sp. Details of young zoœcium.
FIG. 18.—The same. Highly calcified condition, showing ovicells and the long, independent avicularia mounted on large, swollen cells.

Schizoporella sanguinea (Norman).

NORMAN, 1868, p. 222 (*Hemeschara sanguinea*).—JELLY, 1889, p. 233, synonymy.

Taken at 15 fathoms on a *Vermetus* shell; one colony with ovicells.

Reported by Smitt from Pourtales's collections at 60 fathoms, southwest of Tortugas.

Schizoporella biaperta (Michelin).

MICHELIN, 1841–2, p. 330 (*Eschara biaperta*).—SMITT, 1873, p. 46 (*Hippothoa biaperta*) and p. 47 (*Hippothoa divergens* n. sp.).—VERRILL, 1875*b*, p. 41 (*Hippothoa biaperta*); 1878, p. 305, 1879*b*, p. 30, and 1880, p. 193 (*Escharina biaperta*).—HINCKS, 1880, p. 258 (*S. biaperta* var. *divergens*).—NORMAN, 1909, p. 303 (*S. biaperta* var. *divergens*).—LEVINSEN, 1909, p. 323 (discusses and amends genus).—OSBURN, 1912, p. 237.

A few colonies of this species were taken at various depths from low water to 22 fathoms. The appearance is characteristic and the specimens compare very well with those from the Woods Hole region, but never reach such a luxuriant development.

Recorded by Smitt (under *Hippothoa biaperta*) from 9 to 60 fathoms, and (under *H. divergens* new species) from 135 fathoms "*forma typica*," and 120 fathoms "*forma laxa*."

Smitt's "*H. divergens*" has been ranked by Hincks and Norman as a variety of *biaperta*, and recorded by them from the British Isles and Madeira. All specimens examined by the writer belong to the typical *biaperta*.

Schizoporella spongites (Pallas).

PALLAS, 1766, p. 45 (*Eschara spongites*).—SMITT, 1873, p. 42 (*Hippothoa spongites*).—VERRILL, 1900, p. 592 (*Hippothoa* or *Schizoporella spongites*).—LEVINSEN, 1909, p. 324 (full discussion of the species).

One of the most characteristic species of the region; abundant from low water to 18 fathoms; incrusting shells, coral, rocks, and growing on the surface of harder sponges; also on piles. The very large oœcia serve to distinguish this species at a glance from any related forms. In life the color varies from translucent white or yellow to bright brick-red.

Recorded by Smitt from Pourtales's collections from 13 to 35 fathoms and by Verrill (l. c.) from Bermuda. Levinsen (l. c.) records it from St. Thomas and St. John, West Indies, and from Malacca (with some differences).

GENUS ESCHARINA (PART) Milne-Edwards, 1838.

Escharina pesanseris (Smitt).

SMITT, 1873, p. 42 (*Hippothoa pes anseris*).—JELLY, 1889, p. 141 (*Mastigophora dutertrei* var. *pesanseris*).—WATERS, 1909, p. 169 (*Schizoporella pesanseris*).—NORMAN, 1909, p. 302.—LEVINSEN, 1909, p. 326 (discusses genus, amended, and species fully).

One small dead specimen, composed of about a dozen zoœcia, was taken at a depth of 8 fathoms. The vibracula characteristic of the species were broken off. Oœcia present.

Smitt described this species from "two small colonies growing on a *Nullipora*, west of Tortugas" at 42 fathoms. It occurs also at Madeira in 70 fathoms (Norman), the Island of Mauritius (Kirkpatrick), the Red Sea (Waters), and Siam (Levinsen).

GENUS MICROPORELLA (PART) Hincks, 1877.

Microporella ciliata (Pallas).

PALLAS, 1766, p. 38 (*Eschara ciliata*).—SMITT, 1873, p. 26 (*Porellina ciliata*).—PACKARD, 1867, p. 270 (*Lepralia ciliata*).—VERRILL, 1879*b*, p. 29 (*Porellina ciliata*); 1875*c*, p. 53; 1880, p. 190, and 1879, p. 29 (*Porellina stellata* for a form of this species).—OSBURN, 1912, p. 233 (*M. ciliata*), and p. 234 (the variety *stellata* Verrill).—LEVINSEN, 1909, p. 328 (discusses genus).

From 5 to 18 fathoms on shells, corals, etc. One fine colony growing on an egg case of a large mollusk. Smitt records it at various depths from 7 to 60 fathoms. It is one of the most widely distributed of all bryozoa and occurs in all oceans.

Levinsen (l. c.) places this genus in family Escharellidæ.

GENUS SMITTINA NORMAN, 1903.

Smittina trispinosa (Johnston).

JOHNSTON, 1838, p. 280 (*Lepralia trispinosa*).—DAWSON, 1859, p. 256 (*Lepralia trispinosa*).—PACKARD, 1867, p. 67 (*Lepralia trispinosa*).—SMITT, 1873, p. 59 (*Escharella jacotini*), and p. 60 (*E. spathulata*).—VERRILL, 1879*b*, p. 31; 1880, p. 195 (*Mucronella jacotini*); 1875*a*, p. 514, 1878, p. 305, and 1879*b*, p. 30 (*Discopora nitida*).—WHITEAVES, 1901, p. 106 (*Smittia trispinosa*).—NORMAN, 1903, p. 120 (*Smittina* nom. nov. for *Smittia* preoccupied in Diptera).—OSBURN, 1912, p. 246 (*Smittia trispinosa*).

One of the most abundant and characteristic species in the Tortugas region from low water to 12 fathoms. A cosmopolitan species and distributed all along the Atlantic coast northward to the Arctic region. Smitt recorded it from 13 to 44 fathoms in Florida waters.

Smitt states (p. 60) "For the peculiarity of the development of the avicularia, the Floridan form, as a distinct variety, I propose to be named *Escharella spathulata*." But variation in the secondary characters of this species here as in many other regions occurs to a bewildering extent. The typical form with the large, pointed avicularia, common in northern waters, is rare, but these are occasionally observed. One beautiful colony growing on the under side of *Cupularia guiniensis* at 10 fathoms is an almost pure example of Smitt's *spathulata*. Even the smaller, triangular avicularia figured by Smitt (pl. x, fig. 200) are not represented, but in a few cases very elongated pointed avicularia occupy the place of the long-spatulate form figured by Smitt. Another colony found in the drift is more like Verrill's *nitida* in the character of the avicularia, which are small, short-pointed, and short oval in form, very much like specimens from the southern New England coast. In a few cases very large spatulate avicularia, as long as the whole zoœcium, were observed. In one colony short-triangular avicularia were rather regularly disposed in pairs below the orifice with the mandibles pointing outward. Occasionally the avicularia are almost wanting from a colony, a condition seen in many New England specimens that bear evidence of very rapid growth in a single layer.

The oœcia vary much with the state of calcification. In younger stages they are coarsely and sometimes very irregularly punctured. This layer may be entirely covered by secondary calcification, when the oœcia present a smooth, shining appearance or are variously roughened. The secondary layer usually grows irregularly over the primary layer, but in some cases it forms a rather regular raised border with a rounded area of the primary layer exposed on the top.

This form resembles closely the variety *protecta* Thornely, as figured by Waters (1909, pl. 17, fig. 5), but the large avicularia are evenly rounded at the tip instead of being divided into points. The peristome also varies greatly. In some cases it is scarcely raised; in others it takes the form of a tall, broad, median projection, often forked at the tip and projecting so far over the orifice as to nearly obscure it from above. All sorts of intermediate conditions are observed. The peristome also occasionally shows raised lappet-like projections at the side of the orifice, as seen commonly in specimens from Massachusetts (Osburn, 1912, pl. XXVII, fig. 65*a*, 66). In spite of all these variations in secondary characters there is a remarkable constancy in the primary orifice, denticle, oral spines, and the primary zoœcial walls.

Another variation, and one which I am at a loss to explain, is this: Some colonies consist of zoœcia, the secondary characters of which are all of one type or with little variation, while other colonies will show not only zoœcia representing two or more of the so-called varieties, but all sorts of intergradations as well.

Genus Lepralia (part) Johnston, 1847.

Lepralia audouinii (d'Orbigny).

D'Orbigny, 1850–2, p. 401 (*Cellepora audouinii*).—Smitt, 1873, p. 56 (*Escharella audouinii*).

This species, which is known from the Red and Mediterranean Seas, occurs at the Tortugas from low water to 10 fathoms. Colonies taken from the bottom of a skiff which had been in the water from May 1 to June 23 were an inch in diameter, with oœcia containing embryos. In life the colonies are translucent white, but the oœcia often appear light pink when embryos are present.

Smitt's record was based on a single colony growing on a nullipore at 37 fathoms, west of Tortugas.

Lepralia porcellana Busk.

Busk, 1860, p. 283, pl. 31, fig. 3.—Smitt, 1873, p. 62 (*Lepralia cleidostoma*).—Norman, 1909, p. 305, synonymy.

Taken at 5 to 15 fathoms on shells and on other bryozoa, such as *Steganoporella magnilabris* and *Holoporella turrita*. The key-hole form of the orifice, the pointed avicularia with elongate mandibles, and the absence of pores except occasional ones at the margin serve to distinguish the species readily. Oœcia present. In one case there is a vicarious avicularium, somewhat larger than the usual type, mounted on a smooth, swollen chamber. A low, smooth, umbonate process is sometimes present below the orifice.

Recorded by Smitt from Pourtales's collections from 30 to 120 fathoms.

Lepralia uvulifera n. sp. (Figs. 19 and 20.)

Zoœcia small, the surface shining and covered by small, smooth knobs. Pores are wanting except for 3 to 5 large, marginal pores. Usually these are placed as follows: One on either side near the orifice, one on either side about half-way back, and a single pore at the posterior end. The orifice is slightly broader than long, evenly rounded anteriorly, nearly straight on the posterior border, hinge teeth scarcely noticeable. Peristome slightly raised anteriorly and beset with about six slender spines. Posteriorly the peristome rises into a strong, mucronate process, which in complete calcification is divided at the tip into three sharp spines. A small avicularium is present on one zoœcium, situated somewhat behind the orifice near the lateral border, with the pointed mandible pointing backward and outward. The oœcium is comparatively large, heavily calcified, and covered with knobs like those of the zoœcium; a high umbonate process rises on the top, and there is a single large pore on either side of the oœciostome near the base; the oœcial orifice is wide and high, with a calcified projection extending nearly vertically downward into the orifice and bearing a close resemblance to the uvula of the human palate, except that it is a little more truncate at the tip.

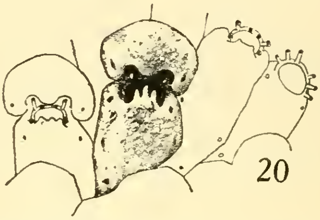


FIG. 19.—*Lepralia uvulifera*, n. sp.
FIG. 20.—The same. Portion of colony showing at the right the orifice of a young zoœcium.

One small colony of perhaps three dozen zoœcia incrusting the under side of a *Cupularia guiniensis* at 10 fathoms.

This species is certainly closely related to *L. watersi* Calvet (1906, p. 412, pl. XXVII, fig. 11) from the Cape Verde Islands, but it differs in having the umbo strongly trifid instead of merely pointed; in the more open form of the ovicell, which partially incloses the anterior part of the peristome, instead of being placed in front of it as in *L. watersi;* and also in lacking the complete lower border of the oœciostome shown in the figure of *L. watersi.* Calvet's figure also shows the oral spines situated slightly outside of the oral border, while in *uvulifera* the spines are on the border.

Lepralia cucullata Busk.

BUSK, 1854, p. 81.—WATERS, 1909, p. 150, synonymy and references.—JULLIEN ET CALVET, 1903, p. 141 (*Schizoporella cucullata*).

Common in shallow water at the Tortugas. In life the color of the colony is dark brownish-purple, sometimes almost black, and the polypides in the young zoœcia at the edge of the colony have a fine carmine color. A number of colonies more than an inch in diameter were found on the bottom of a skiff that had been in the water only from May 1 to June 23.

The generic position of this well-known species is very unsettled. A majority of authors have agreed in placing it in *Lepralia*, others in *Smittia*, and still others in *Schizoporella*. The reason for this difference of opinion lies in the general simplicity of the zoœcia, which lack characters usually considered as diagnostic. The form of the orifice is somewhat intermediate between that of *Lepralia* and *Schizoporella*. There is a very shallow curve on the posterior border, which may be interpreted as a sinus, as Calvet has done (l. c.), or as merely the space between the hinge denticles. In the absence of any means of settling the controversy, I place the species tentatively in *Lepralia*, in which genus it was described by Busk.

Distribution: Mediterranean, Red, and Arabian Seas; Azores Islands; Cape Verde Islands; South Africa, and Cape St. Lucas, Lower California. Not before noted on the Atlantic side of America.

Lepralia rostrigera (Smitt).

SMITT, 1873, p. 57 (*Escharella rostrigera*).—WATERS, 1885, p. 298; 1887, p. 61.—JELLY, 1889, p. 126 (under *L. depressa*).

The *Escharella rostrigera* of Smitt has been made a synonym of *L. depressa* Busk by Miss Jelly (l. c.), but in the opinion of the writer it represents a distinct species. Smitt recognized a relationship between the species, but indicated that the differences are constant. The study of material taken by me at the Tortugas confirms this view. The form of the zoœcial aperture is quite different, being well rounded at the posterior margin, as figured by Smitt, and there is never more than a faint indication of a constriction of the sides. The avicularia are characteristically placed far forward, alongside of the anterior part of the orifice, or frequently entirely in front of it. Busk's figure of *L. depressa* (1854, pl. 91, figs. 3 and 4) shows no indication of pores. In *rostrigera* there are numerous small pores in the frontal wall in younger stages, and large, marginal pores are present in all stages. The larger zoœcia with the broad aperture described and figured by Smitt (pl. X, fig. 205) are occasionally present in my specimens. Smitt's specimens were taken by Pourtales in 35 and 43 fathoms. Mine were taken at 10 and 15 fathoms on coral and shells. A fine colony at 10 fathoms incrusted the base of a living *Cladocora arbuscula*.

Lepralia contracta Waters var. serrata Osburn.

WATERS, 1899, p. 11.—NORMAN, 1909, p. 306.—OSBURN, 1912, p. 242 (*Lepralia serrata*).

Several colonies incrusting shells at 5 to 18 fathoms. This variety was described by me as *Lepralia serrata* n. sp., from the Woods Hole region (1912, p. 242, pl. 26, fig. 57).

After a careful study of the Florida specimens I am of the opinion that this can be only a variety of *L. contracta* Waters, described from Madeira (1899, p. 11). Waters's description is brief and his figures small, but Norman (l. c., pl. 41, fig. 56) has refigured the species. The differences seem to be largely in the secondary calcification, which appears to be much greater in American specimens; also there are six oral spines in Madeira specimens, while usually only four are to be observed in American material. The avicularia in Florida specimens are much more abundantly developed and are frequently raised high above the front of the zoœcium on small mammillary processes. Also, the lateral oral denticles are much more prominent than they appear in the figures of Madeira specimens and are strongly bifid; however, Norman figures one such bifid denticle. In one of my specimens the spatulate avicularia are extremely elongated, fully as long as the zoœcium, and, while usually directed forward, are sometimes reversed in position. The zoœcial wall appears to be much more thickened than in the Madeira specimens, to judge by the figures of Waters and Norman. Notwithstanding these differences I believe they are closely related. The form of the oœcium with the peculiar membranous area and the serrated character of the primary zoœcial orifice are identical and are so unique that I believe them to indicate the same species. Specimens from southern New England are much more highly calcified than Florida specimens, which seem in some respects to be intermediate between those from New England and Madeira.

Lepralia edax (Busk).

BUSK, 1859, p. 59 (*Cellepora edax*).—SMITT, 1873, p. 63 (*L. edax formæ typica* and *calcarea*).—HINCKS, 1880, p. 311.—VERRILL, 1909, p. 54.

One colony taken at 18 fathoms, forming a cylindrical mass more than 0.25 inch in diameter and many layers in thickness, which originally surrounded a branched structure of some sort, and one colony taken at 8 fathoms incrusting a shell fragment. Smitt's figures and description of this species are very complete. I have compared these specimens with one from the English Channel sent me by Dr. S. F. Harmer. English specimens are said to be found only on certain species of gastropod shells. While Florida specimens have not been taken in such situations, I can distinguish no differences of any importance. My Tortugas specimens belong to what Smitt calls the *forma calcarea*, but it can scarcely be considered a distinct variety.

The large, pointed, vicarious avicularia described and figured by Smitt are abundantly distributed over the colony. The ovicell has a peculiar membranous area on the upper surface, a feature also possessed by *L. contracta* Waters, though in the latter species this area is much nearer the zoœcial aperture.

Smitt records the species from Pourtales's collections from 49 to 79 fathoms. Verrill records it for the Bermudas in shallow water.

Lepralia janthina (Smitt).

Smitt, 1873, p. 63 (*Lepralia edax forma janthina*).

This, I believe, must be separated from *edax* as a distinct species. The form of the orifice, a character to which Smitt gave undue importance, is similar, but in *janthina* the orifice is not only much larger, but relatively wider and shorter, with less space behind the hinge denticles. The avicularia are all pointed and are situated on a prominence behind the orifice with the mandible turned forward and frequently slightly outward. There are no vicarious avicularia. The color is a deep blue-black or violet, entirely different from any specimens of *L. edax* I have seen. The zoœcia are considerably larger than those of *L. edax.* Ovicells are wanting.

One colony 0.25 inch in diameter taken at 6 fathoms incrusting a shell. Smitt records one specimen from 13 fathoms on coral.

The *Cellepora janthina* of Waters (1899, p. 14) from Madeira can not be the *L. edax* var. *janthina* of Smitt, as Norman (1909, p. 311) points out in renaming Waters's species *C. rotundora.*

Genus Phylactella Hincks, 1880.

Phylactella labrosa (Busk).

Busk, 1854, p. 92 (*Lepralia labrosa*).—Jelly, 1889, p. 204.—Norman, 1909, p. 308.

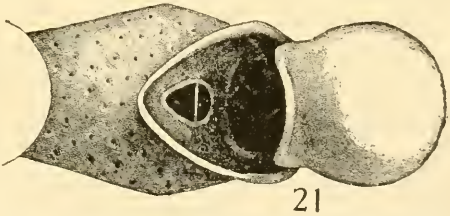
Dredged at 22 fathoms on shells and hard sponges. Ovicells are lacking. There is no median denticle on the proximal margin of the orifice, nor are the zoœcia disposed in radiating lines, but form a solid crust. However, Norman (l. c.) has shown that both of these characters are variable.

Phylactella collaris (Norman) var. aviculifera nov. (Fig. 21.)

Norman, 1866, p. 204 (*Lepralia collaris*); 1909, p. 309.—Jelly, 1889, p. 203.—Robertson, 1908, p. 307.

This species has not heretofore been recorded from the Atlantic side of North America, though Miss Robertson records it from southern California, and it is found on the European side of the Atlantic Ocean as far south as the Madeira Islands.

At the Tortugas, growing on shells at from 1 to 15 fathoms, occurs the variety which I have here called *aviculifera*. In all respects this appears to agree fully with *P. collaris*, except that there is a rather large avicularium situated within the collar immediately below the orifice, with a triangular mandible pointing upward, or very rarely sidewise. This appears on every zoœcium of the colonies studied. Norman has described a rounded avicu-



21

Fig. 21.—*Phylactella collaris* (Norman) *aviculifera*, var. nov. Viewed partly from in front and showing avicularium.

larium on the lower lip of occasional zoœcia of *L. labrosa* from Madeira (1909, p. 309).

GENUS CELLEPORA Linné, 1767.

Cellepora dichotoma Hincks.

HINCKS, 1862, p. 304.—SMITT, 1873, p. 53, pl. IX, fig. 193–198 (*C. avicularis*).—JELLY, 1889, p. 51, gives synonymy and also, p. 46, includes Smitt's references in *C. avicularis* Hincks.—(?) VERRILL, 1878, p. 305 (*C. avicularis*); (?) 1901, p. 54 (*C. avicularis*).

Two well-developed specimens, 0.5 inch or more in height, taken at a depth of 10 fathoms; one was attached to a hydroid stem. There can be no doubt that these specimens belong to *C. dichotoma* instead of *C. avicularis*, as I have compared them with authenticated material from England. Smitt's figures, which he refers to *C. avicularis*, undoubtedly are *C. dichotoma*, as Hincks (1880, p. 404) has already pointed out. Smitt indicates the bathymetrical distribution as from 9 to 111 fathoms.

Verrill's records for *C. avicularis* at Fort Macon, North Carolina (1878), and Bermuda (1901) in all probability apply to *dichotoma*, though it is possible that the former should be *C. americana* Osburn (1912, p. 238), which Verrill at another time (1879B) listed as *avicularis*. *C. americana* and *C. dichotoma* have been taken at Beaufort, North Carolina, by the writer.

Cellepora verruculata Smitt.

SMITT, 1873, p. 50.—BUSK, 1884, p. 150 (*Escharoides verruculata*).—JELLY, 1889, p. 60.—CALVET, 1906, p. 444.

A number of colonies taken on shells and in similar situations from low water to 15 fathoms. Smitt described the species from a single specimen taken by Pourtales west of the Tortugas in 42 fathoms. Recorded by Busk (l. c.) off Heard Island at 75 fathoms, and by Calvet (l. c.) for the Mediterranean Sea, "Naples, côtes de Corse, Cette."

The zoœcia undergo a remarkable change in appearance with advancing calcification.

GENUS LAGENIPORA Hincks, 1877.

Lagenipora ignota Norman.

NORMAN, 1909, p. 309, pl. 42, figs. 10–13.

A colony taken at Tortugas in 12 fathoms on a dead colony of *Mucronella bisinuata* and another at 10 fathoms on a *Vermetus* shell seem to be identical with Norman's species. They differ in not rising into rounded branches, but the small size of the colonies easily accounts for this. The character of the zoœcium, with the pair of oral avicularia, is identical, and the oœcia also. The large spatulate avicularia, said by Norman to be present in extraordinary numbers, are but sparsely represented.

Hitherto known only from the Madeira Islands, where it was taken at 70 fathoms (Norman).

GENUS HOLOPORELLA Waters, 1909.

Holoporella albirostris (Smitt).

SMITT, 1873, p. 70 (*Discopora albirostris*).—BUSK, 1881, p. 346 (*Cellepora albirostris*).—JELLY, 1889, p. 45 (references under *Cellepora albirostris*).—WATERS, 1885, p. 304; 1887, p. 68 (*Cellepora albirostris*); 1909, pp. 159–161 (*Holoporella* gen. nov.).

This species, which is very characteristic of the region, occurs in abundance from low water to 15 fathoms. It grows on coral-rocks, corals, shells, and on the firmer sponges. Recorded by Smitt from Florida waters in 25 to 35 fathoms. It is readily distinguished from other species of this region by the presence of a towering, pointed white spine situated at one side of the proximal margin of the orifice. Except in the youngest stages the colony has a dark grayish or blackish color, against which the white spines stand out in sharp contrast. A very small avicularium is situated at the base of the spine, large spatulate avicularia are distributed over the colony, and vestigial, minute avicularia are occasionally present at the side of the orifice.

Waters in 1909 (l. c.) established the genus *Holoporella* to include, for the most part, those species of the old genus *Cellepora* in which the sinus is lacking and which have a rounded or straight posterior margin of the orifice, and in which also the opercular muscles are attached near the border. Levinsen (1909, p. 347) erected a new family, Holoporellidæ, to include this genus, thus farther removing it from *Cellepora*. This separation is based on the fact that in *Holoporella* the operculum is attached, sometimes by hinge teeth, to the lateral margins of the orifice, while in *Cellepora* the operculum is suspended at the edges of the sinus. Oral spines are often present in *Holoporella*, but are wanting in *Cellepora*. Rostra, with avicularia, may be present in both genera. Waters includes the following American species of the Florida region in *Holoporella: H.* (*Discopora*) *albirostris* (Smitt), *H.* (*Lepralia*) *turrita* (Smitt), and *H.* (*Discopora*) *pertusa* (Smitt). Levinsen adds *H.* (*Discopora*) *advena* (Smitt), which apparently completes the list of the described species of this region.

Holoporella pusilla (Smitt).

SMITT, 1873, p. 70 (*Discopora albirostris forma pusilla*).—BUSK, 1884, p. 436 (*Cellepora pusilla*).

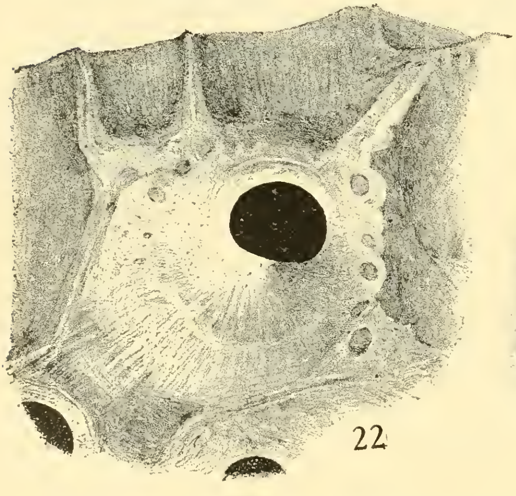
In the "Floridan Bryozoa" Smitt describes this species as a form of his *Discopora albirostris*, stating that their relationship is "incontestably proved by the very same form of the zoœcial aperture." Busk (l. c.) objects to placing *pusilla* as merely a variety of *albirostris*, giving it as his opinion that the two seem to him to be quite distinct. Although Busk possessed no material of *pusilla*, he was evidently correct in forming this opinion. If the single specimen taken by me at the Tortugas is identical, as I believe it to be, with Smitt's *pusilla*, it differs from *albirostris* in the entire absence of dark pigment; in the smaller size of the colony, the individual, and the orifice; in the presence of radiating lines of depressions and small wart-like prominences; in the smaller size of the oœcia; in the much slighter development of the rostrum, which never rises much above the avicularium; and in the more procumbent position of the rostrum, which projects forward over the orifice. The form of the orifice is, as stated by Smitt, very similar to that of *albirostris*, but (as Busk points out) this form is common to a number of species. Small hinge denticles are sometimes present. Smitt figures the species as having from 3 to 6 oral spines. There is scarcely any indication of these in the specimen in my possession. The oral avicularium is usually rounded, but occasionally the mandible is obtusely triangular. No other avicularia are present.

One colony 0.25 inch in diameter incrusting a shell at low tide.

Smitt records it from Pourtales's collections at 9 to 60 fathoms.

Holoporella magnifica n. sp. (Figs. 22 and 23.)

A very coarse species with very large zoœcia and orifices large enough to be distinguished readily by the naked eye. Taken at 10 fathoms incrusting a sponge and a very small colony on a dead shell at the same depth.



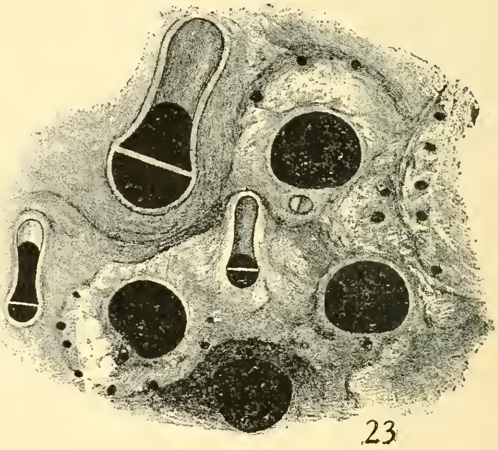


FIG. 22.—*Holoporella magnifica* n. sp. Young zoœcium at edge of colony, showing manner of growth. Rostrum and rostral avicularium not yet developed.

FIG. 23.—The same. Highly calcified portion near center of colony, showing one deeply immersed and three erect superficial zoœcia, independent avicularia of two sizes, and the rostral avicularium.

Zoœcia large, procumbent at the growing edge, erect and irregular at the center of the colony. Imperforate except around the edge, where there are large pores, often coarsely cancellated between the cells in the middle of the colony. Very heavily calcified, even in young cells. The orifice is much as in *H. albirostris*, except that it is much larger. The peristome is very thick and broad, slightly raised all around the orifice (when oœcia are present it extends over them in later stages of growth). The rostrum is small and low, projecting so slightly over the orifice as to scarcely hide the posterior margin in any case. On one side of the rostrum is placed a large avicularium with an elliptical mandible, black in color. Sometimes the rostrum is so slightly developed that the avicularium appears to be placed transversely behind the orifice. The operculum is heavily pigmented with dark brown, especially at the edge. Large, spatulate avicularia with brown or blackish mandibles are abundantly distributed over the colony. There is a slight amount of the brownish pigment in the zoœcial wall. In all the avicularia the pigment is confined to the mandible, which is thus strikingly contrasted with the colorless basal membrane. In the operculum also the color is limited strictly to the hinged portion and does not extend upon the base. The oœcia are, as in other species of this genus, shallow and widely open, and they are deeply immersed in the crust, except in the very young stage.

In addition to the specimens mentioned above, a large flat specimen, 2 inches across and many layers in thickness, which was apparently growing unattached, was taken by Dr. Paul Bartsch off Biscayne Key, Florida. It has not been possible to identify these specimens with any known species. The large size of the zoœcia and the orifice, the great thickness of the walls, even in young specimens, the straight proximal border of the orifice, the absence of a tall rostrum, and the large size of the oral avicularium, together with the elongate form of the mandible with its round tip in the vicarious avicularia, form a set of characters which serve to distinguish it.

Holoporella turrita (Smitt).

SMITT, 1873, p. 65 (*Lepralia turrita*).—WATERS, 1883, p. 438 (*Smittia turrita*); 1909 p. 161 (includes in *Holoporella*, new genus).—RIDLEY, 1881, p. 55 (*Cellepora turrita*).—JELLY, 1889, p. 253 (*Smittia turrita*).

A very common species at 12 to 15 fathoms, growing on shells, corals, and the firmer sponges. Recorded by Smitt from Pourtales's collections as not frequent, only a few specimens taken, at from 26 to 44 fathoms, growing on corals and nullipores.

Color in life bright pink to brick-red. Above the spreading incrustations rise knob-like projections, usually 0.25 inch or so in diameter, sometimes much larger. The younger zoœcia are separated by delicate, raised, white walls which are very conspicuous against the red color of the colony. The white points of the blunt spines are also strongly contrasted with the ground color.

GENUS PETRALIA MacGillivray, 1869.

Petralia bisinuata (Smitt).

SMITT, 1873, p. 59 (*Escharella bisinuata*).—LEVINSEN, 1909, pp. 350–51.

This well-marked species, which has not been noted outside of the Florida region, is common at the Tortugas on shells and sponges, from 10 to 18 fathoms. The color in life is bright vermilion. Smitt described the species from Pourtales's collections at 9 and 19 fathoms.

Levinsen (see above) has placed this species in MacGillivray's genus *Petralia* and has erected a new family, Petraliidæ, to include this genus.

CTENOSTOMATA.

GENUS BOWERBANKIA Farre, 1837.

Bowerbankia gracilis Leidy.

LEIDY, 1855, p. 142.—HINCKS, 1877, p. 215 (*Valkeria caudata*); 1880, p. 521 (*Bowerbankia caudata*).—VERRILL AND SMITH, 1873, p. 709 (*Vesicularia gracilis*), and p. 710 (*V. fusca*).—VERRILL, 1880, p. 28 (*Vesicularia gracilis*).—LEVINSEN, 1894, p. 82 (*Bowerbankia caudata*).—OSBURN, 1912, pp. 253–245 (synonymy); 1912*a*, p. 287.

Specimens of this species, which do not seem to differ from Woods Hole material, were taken in the moat at Fort Jefferson and on the piles of the docks, attached to shells, or creeping over the sea-weed, and covered to such an extent by coral mud as to almost obscure them. No erect branches were noted. Many individuals show the caudate process of the variety *caudata* (Hincks).

On the North American coast the species has been identified by the writer from Nova Scotia, Maine, Massachusetts, Connecticut, New Jersey, North Carolina, and Florida. Otherwise it is known from England and Denmark.

It is quite probable that the genus *Bowerbankia*, as Waters (1910, pp. 241 and 244) suggests, must be fused with *Zoobotryon*, but as Waters himself keeps them separate pending more thorough studies of the ctenostomes, the writer has not the temerity to combine them. The only marked distinguishing characters are the much greater softness and hyalinity of the stock and the absence of a creeping stolon in *Zoobotryon*. These characters will readily separate the one species of *Zoobotryon* from any *Bowerbankia* with which the writer is acquainted.

GENUS ZOOBOTRYON Ehrenberg, 1831.

Zoobotryon pellucidum Ehrenberg.

EHRENBERG, 1831, pl. III, fig. 10.—SONDER in Coll. Binder (*Ascothamnion trinitatis*).—WATERS, 1910, p. 243.

This species, first described from the Mediterranean, is common at the Tortugas, floating and attached, especially in the Fort Jefferson moat and about the piles of the dock. One colony 8 inches across was observed. The zoœcia in all cases were much obscured by a layer of white coral mud adhering to the ectocyst.

Not previously recorded for the Florida region. Sonder (see above) recorded it as a plant from the island of Trinidad, and according to Waters (see above) it is known from the Isle of Pines, South Australia, Zanzibar, the Red Sea, and the Cape Verde Islands.

GENUS CYLINDRŒCIUM Hincks, 1880.

Cylindrœcium giganteum (Busk).

BUSK, 1856, p. 93 (*Farrella gigantea*).—HINCKS, 1880, p. 535.

This species, which has been recorded from the British Isles, from various localities in the Mediterranean Sea, from the Red Sea, and from the Queen

Charlotte Islands, has not hitherto been noted on the American side of the Atlantic. It is abundant at the Tortugas from low water down to several fathoms, growing profusely over piles, shells, seaweed, and sponges. The zoœcial wall in all cases was thickly covered with a layer of coral mud. Occasional individuals showed the swelling at the side of the zoœciostome which forms the oœcium. Embryos in various stages of development were present.

GENUS ANGUINELLA van Beneden, 1844.

Anguinella palmata van Beneden.

VAN BENEDEN, 1844, p. 58.—BUSK, 1856, p. 95.—OSBURN, 1912, p. 253, pl. XXVIII, fig. 78.

This species occurs rather sparingly among algæ on the reefs in shallow water. It is very easily overlooked because its irregularly branched form gives it a marked resemblance to some of the smaller algæ. The species is now known to occur on the American coast from the Tortugas to Buzzard's Bay, Massachusetts (Osburn, 1912). At Beaufort, North Carolina, it is very abundant and grows much larger than at the localities mentioned above. It has not previously been noticed south of Charleston, South Carolina, where it was recorded by Busk (Harvey, coll.).

GENUS AMATHIA Lamouroux, 1812.

? Amathia goodei Verrill.

VERRILL, 1901, p. 329.—(?) SMITT, 1872, p. 4 (*Serialaria* sp. undet.).

Several colonies, growing attached to piles, seem to belong to this species, which Verrill described from the Bermudas. Verrill described the branches as "thick, soft and flaccid" and the zoöids as "numerous, arranged in large, dense elongated clusters composed of several close rows, which often nearly or quite surround the stem, but are scarcely at all spiral."

BIBLIOGRAPHY.

AUDOUIN, J. V. 1826. Explication sommaire des planches des mollusques, des annélides, des crustacés, des arachnides, des insectes, des échinoderms, des ascides de L'Egypte et de la Syrie, par G. C. Savigny. Paris.

BENEDEN, P. J. VAN. 1844. Recherches sur l'anatomie, la physiologie et le développement des bryozoaires qui habitent la côte d'Ostend. Nouveau Mémoires Académie Royale Belgique, t. XVIII, 1845. Bruxelles.

BOSC, L. 1802. Histoire naturelle des vers, vol. 3.

BUSK, G. 1852–4. Catalogue of the marine polyzoa in the collection of the British Museum. Chilostomata, part 1, 1852; part 2, 1854.

——— 1856. Zoophytology. Quarterly Journal of Microscopical Science, vol. 4, pp. 93–96, pl. 95–96.

——— 1859. The polyzoa of the Crag. Palæontographic Society.

——— 1860. Catalogue of the polyzoa collected by J. Y. Johnson at Madeira, etc. Quarterly Journal of Microscopical Science, vol. 8, pp. 280–285, pl. 30, 31.

——— 1881. Polyzoa collected by Capt. H. W. Feilden in the North Polar Expedition; with descriptions of new species. Journal of the Linnean Society, Zoology, vol. 15, pp. 231–241, pl. 13.

——— 1884. Report on the polyzoa collected by H. M. S. *Challenger*, pt. 1, *Cheilostomata*. Vol. X, pt. XXX, pp. (XXIV) 1–216, pl. I–XXXVI. London.

——— 1886. Idem, pt. 2, *Cyclostomata*, *Ctenostomata*, and *Pedicellinea*. Vol. XVII, pt. L, pp. (VIII) 1–47, pl. I–X.

CALVET, L. 1906. Expédition Scientifique des *Travailleur* et du *Talisman*. Pp. 355–495, pl. 26–30.

COUCH, R. Q. 1844. Cornish Fauna. Vol. 3.

DAWSON, J. W. 1859. Geological Survey of Canada for 1858. Polyzoa, pp. 255–257.

DESOR, E. 1848. Ascidioidian polyps or bryozoa (from Nantucket). Proceedings of the Boston Society of Natural History, vol. 3, pp. 66–67.

EHRENBERG, C. G. 1831. Symbolæ Physicæ, pt. 2, Evertebrata. Pages not numbered, pl. 3, fig. 10.

FLEMING, J. 1828. A history of British animals, exhibiting the descriptive characters and systematical arrangements of the genera and species of quadrupeds, birds, reptiles, fishes, Mollusca, and Radiata of the United Kingdom. First ed., 8vo, Zoophytes, pp. 505–554. Edinburgh.

GABB, W. M., and GEO. H. HORN. 1862. Monograph of the fossil polyzoa of the secondary and tertiary formations of North America. Journal of the Academy of Natural Sciences of Philadelphia, vol. 5, pt. 2, pp. 111–179, pl. 19–21.

GRAY, J. E. 1848. List of British Animals in the British Museum, part 1.

HARMER, S. F. 1891. On the British species of *Crisia*. Quarterly Journal of Microscopical Science, n. s., vol. 32, pp. 127–181, pl. 12.

——— 1900. A revision of the Genus *Steganoporella*. Quarterly Journal of Microscopical Science, n. s., vol. 43, pp. 225–297, pl. 12–13.

HINCKS, T. 1862. A catalogue of the zoophytes of South Devon and South Cornwall. Annals and Magazine of Natural History, ser. 3, vol. 9, pp. 303–310, pl. 12.

——— 1877. On polyzoa from Iceland and Labrador. Annals and Magazine of Natural History, ser. 4, vol. XIX, pp. 97–112, pl. X, XI. London.

——— 1880. British marine polyzoa. Vol. I, 601 pages of descriptive matter; vol. II, 83 pl. to accompany text. London.

——— 1880A. Contributions toward a general history of the marine Polyzoa. Annals and Magazine of Natural History, ser. 5, vol. 6, pp. 69–91, pl. 9–11.

——— 1880B. Same title, pt. 2 and 3, same journal, ser. 5, vol. 6, pp. 376–384.

——— 1881. Same title, pt. 4, same journal, ser. 5, vol. 7, pp. 147–162, pl. 8–10.

——— 1881A. Same title, pt. 8, same journal, ser. 5, vol. 8.

——— 1887. Critical notes on the polyzoa. Same journal, ser. 5, vol. 19, pp. 150–164.

JELLY, E. C. 1889. A synonymic catalogue of the recent marine bryozoa. 322 p. London.

JOHNSTON, G. 1838. History of British zoophytes. London. Bryozoa confused with other groups under *Ascidioida*. Pp. 238–324, pl. XXIX–XLIII.

——— 1847. Idem, 2d ed. Polyzoa, pp. 253–406, pl. XLVI–LXXIV.

Jullien, J. 1881. Note sur une nouvelle division des Bryozoaires *Cheilostomiens.* Bulletin Société Zoologique du France, vol. 6, pp. 271–285.

——— 1888. Mission Scientifique du Cap Horn. Bryozoaires. Tome 6, Zoologie, pp. 1–92, pls. 1–15.

Jullien, J., et L. Calvet. 1903. Bryozoaires provenant des campagnes de L'Hirondelle. Résultats des campagnes scientifique du Prince de Monaco, fasc. xxiii, pp. 1–188, pl. i–xviii. Monaco.

Lamarck, J. B. 1816. Histoire naturelle des animaux sans vertèbres, vol. ii, 1^{er} éd., Paris. Bryozoa scattered among "Polypes."

Landsborough, D. 1852. A popular history of British zoophytes. London. Polyzoa, pp. 265–386, pls. 15–20.

Leidy, J. 1855. Contributions toward a knowledge of the marine invertebrate fauna of Rhode Island and New Jersey. Journal of the Academy of Natural Sciences of Philadelphia, ser. 2, vol. 3 (Polyzoa on pp. 9–11).

Levinsen, G. M. R. 1894. Mosdyr (Polyzoa eller Bryozoa). In: Schiodte, J. C., Zoologica Danica, 4de bd., 1ste afd., pp. 1–105, pl. i–ix. Kjobenhavn.

——— 1909. Morphological and systematic studies on the cheilostomatous bryozoa. 364 pages, 24 plates. Copenhagen.

Linne, C. 1758. Systema naturæ, ed. 10, vol. 1. Lithophyta and zoophyta, pp. 789–821. Holmiæ.

——— 1767. Idem, ed. 12, vol. 1, pt. 2. Lithophyta and zoophyta, pp. 127–1337. Holmiæ.

MacGillivray, P. H. 1869. Descriptions of some new genera and species of Australian Polyzoa, etc. Transactions and Proceedings of the Royal Society of Victoria, part 2, vol. 9, pp. 126–148.

Michelin, H. 1841–2. Iconographie zoophytologique . . . des polypiers fossiles de France, . . . xii, 348 p., atlas of 79 pl. Paris.

Norman, A. M. 1864. On undescribed British hydrozoa, actinozoa, and polyzoa. Annals and Magazine of Natural History, ser. 3, vol. 13.

——— 1903. Notes on the natural history of East Finmark. Annals and Magazine of Natural History, ser. 7, vol. 12, pp. 87–128, pl. 8–9.

——— 1909. The Polyzoa of Madeira and neighboring islands. Journal of the Linnean Society, vol. xxx, pp. 275–314, pl. 33–42.

Orbigny, A. d'. 1839. Voyage dans l'Amérique méridionale. Vol. 5, pt. 4, Bryozoa, pp. 7–23, pl. 1–10. Paris.

——— 1850–2. Paléontologie française, Terrains crétacés. Vol. 5, pp. 1–1191, pl. 600–800.

Osburn, R. C. 1912. The bryozoa of the Woods Hole region. Bulletin of the United States Bureau of Fisheries for 1910, vol. 30, pp. 201–266, pls. 18–31.

——— 1912a. Bryozoa from Labrador, Newfoundland, and Nova Scotia, collected by Dr. Owen Bryant. Proceedings of the United States National Museum, vol. 43, pp. 275–289, pl. 34.

Packard, A. S. 1863. List of animals dredged near Caribou Island (Labrador). Canadian Naturalist and Geologist for 1863, pp. 406–412.

——— 1867. Invertebrate fauna of Labrador and Maine. Proceedings of the Boston Society of Natural History, vol. 1, pp. 66–69.

Pallas, P. S. 1766. Elenchus zoophytorum. Hagæ Comitum.

Pieper, F. W. 1881. Eine neue Bryozoe der Adria, *Gemellaria* (?) *avicularis.* Jahresber. Westfälischen Prov.-Vereins, vol. 9, pp. 43–48, pl. 1.

Pourtales, T. F. de. 1867. Contributions to the fauna of the Gulf Stream at great depths. Bulletin of the Museum of Comparative Zoology, vol. 1, No. 6 (Bryozoa on pp. 106 and 110–111).

Reuss, A. E. 1847. Die fossilen Polyparien des Wiener Tertiar-beckens. Wien.

Ridley, S. O. 1881. Account of the zoological collections made during the survey of H. M. S. *Alert.* Proceedings of the Zoological Society of London.

Robertson, Alice. 1905. Non-encrusting chilostomatous bryozoa of the west coast of North America. University of California Publications, Zoology, vol. ii, No. 5, pp. 235–322, pl. 4–16.

——— 1908. The encrusting chilostomatous bryozoa of the west coast of North America. University of California Publications, Zoology, vol. iv, No. 5, pp. 253–344, pl. 14–24.

Smitt, A. F. 1872–3. Floridan Bryozoa, collected by Count L. F. de Pourtales. Kongl. Svenska Vetenskaps-Akademiens Handlingar, pt. 1, 1872, in bd. 10, No. 11, pp. 1–20, taf. i–iv; pt. 2, 1873, in bd. 11, No. 4, pp. 1–83, taf. i–xiii. Stockholm.

Solander, D. 1786. Natural history of many curious and uncommon zoophytes, collected from various parts of the globe by the late John Ellis, systematically arranged and described by the late D. Solander. London.

STIMPSON, W. 1853. Synopsis of the marine invertebrata of Grand Manan. Smithsonian Contributions to Knowledge (Bryozoa, pp. 17–19, pl. 1).

VERRILL, A. E. 1875. Brief contributions to zoology from the Museum of Yale College, No. 32. American Journal of Science and Arts, vol. 9 (Bryozoa on p. 414).

——— 1875A. Idem, No. XXXIII. Results of dredging expeditions off the New England coast in 1874. Ibid., vol. X. Bryozoa, pp. 41–42, pl. III.

——— 1878. In: Coues and Yarrow, Notes on the natural history of Fort Macon, North Carolina, and vicinity. Proceedings of the Academy of Natural Sciences of Philadelphia. List of polyzoa by Verrill on pp. 304–305.

——— 1879. Preliminary check-list of the marine invertebrata of the Atlantic Coast from Cape Cod to the Gulf of St. Lawrence. Pp. 28–31. (Published privately, New Haven, Connecticut, April 1879.)

——— 1879A. Brief contributions to zoology from the Museum of Yale College, No. XLIII, Notice of recent additions to the marine fauna of the eastern coast of North America, No. 6. American Journal of Science and Arts, vol. XVIII, pp. 52–54. New Haven.

——— 1880. Notice of recent additions to the marine invertebrata of the Atlantic coast of America. Proceedings of the United States National Museum, vol. 2, 1879 (published 1880). Polyzoa, pp. 188–196.

——— 1900. Additions to the *Tunicata* and *Molluscoidea* of the Bermudas. Zoology of the Bermudas, vol. 1 (Bryozoa on pages 592–594, figs. 4 and 6 of pl. 20).

——— 1901. Additions to the fauna of the Bermudas from the Yale Expedition of 1901. Zoology of the Bermudas, vol. 1 (Polyzoa on p. 54).

——— 1901A. Review of recent papers relating to the fauna of Bermuda. American Journal of Science, vol. 11 (on page 29 in a footnote is a description of *Amathia goodei* n. sp.).

VERRILL, A. E., and S. I. SMITH. 1873. The invertebrate animals of Vineyard Sound and adjacent waters. Report of the Commissioner of Fish and Fisheries for 1871–2. (Bryozoa, pp. 707–714 and p. 747.) Washington.

WATERS, A. W. 1883. Fossil chilostomatous bryozoa from Muddy Creek, Victoria, etc. Quarterly Journal of the Geological Society, vol. 39, pp. 423–443, pl. 12.

——— 1885. Chilostomatous bryozoa from Aldinga and the River-Murray Cliffs, South Australia. Same journal, vol. 41, pp. 280–310, pl. 7.

——— 1887. On tertiary chilostomatous bryozoa from New Zealand. Same journal, vol. 43, pp. 40–72, pls. 6–8.

——— 1898. Observations on Membraniporidæ. Linnean Society Journal, Zoology, vol. XXVI, pp. 654–693, pl. 47–49. London.

——— 1899. Bryozoa from Madeira. Jour. Roy. Micros. Soc., pp. 6–16, pl. 3.

——— 1904. Resultats du voyage du S. Y. *Belgica*. Bryozoa, pp. 1–103, pl. 1–9.

——— 1906. Bryozoa from Chatham Island and d'Urville Island, New Zealand. Annals and Magazine of Natural History, ser. VII, vol. XVII, pp. 12–23, pl. 1.

——— 1907. Tubucellaria: Its species and ovicells. Linnean Society Journal, vol. XXX, pp. 126–133, pl. 15, 16.

——— 1909. Reports on marine biology of the Sudanese Red Sea, etc., XII, Bryozoa *Cheilostomata*, part 1, Linnean Society Journal, vol. XXXI, pp. 123–181, pl. 10–18.

——— 1910. Same title, XV, Bryozoa *Cyclostomata*, *Ctenostomata*, and *Endoprocta*, pt. II, same journal, vol. XXXI, pp. 231–256, pl. 24, 25.

WHITEAVES, J. F. 1901. Catalogue of the marine invertebrata of Eastern Canada. Geological Survey of Canada, Ottawa. Polyzoa, pp. 91–144.