BULLETIN

OF THE

Harvard University.

MUSEUM OF COMPARATIVE ZOÖLOGY

AT

HARVARD COLLEGE, IN CAMBRIDGE.

VOL. XXXIV.

(Geological Series, IV.)

CAMBRIDGE, MASS., U. S. A.
1899.

University Press:
John Wilson and Son, Cambridge, U.S.A.

CONTENTS.

June, 1899.

TABLE OF CONTENTS.

The Geology and Physical Geography of Jamaica: Study of a Type of Antillean Development. Based upon Surveys made for ALEXANDER AGASSIZ. By R. T. HILL.

INTRODUCTION.

JAMAICA presents a more favorable opportunity for detailed geologic investigation than any other tropical area. The authorities have constructed over 4,000 miles of macadamized highways and two lines of railroad across the island in different directions. Bridle paths have been cut to the highest peaks and other points of interest. These public works have made excellent exposures of the substructure, far better than can be seen in most tropical countries. Furthermore, many years ago the English government made, for its time, a most thorough reconnoissance geologic report, and map of the island, which served as guides for the present study, and relieved us of the preliminary drudgery of reconnoissance which ordinarily seriously detracts from the consideration of the higher geological questions in the tropics.

The geology of Jamaica has been studied *in situ* by several writers, the principal of which have been De la Beche,[1] Barrett,[2] Wall,[3] Brown,[4] and Sawkins,[4] all of whom except de la Beche were members of the Official Geological Survey.

De la Beche's conclusions upon the older formations of the island are noted elsewhere. His monograph contains many excellent observations concerning the Tertiary and later formations, which in a degree are more in harmony with the conclusions to be presented by us than the subsequent and more extensive reports of the official surveys which supplanted them.

---

[1] Remarks on the Geology of Jamaica, by H. T. de la Beche. Memoir. Transactions Geol. Soc. London, 1829.

[2] Quart. Jour. Geol. Soc. London, Vol. XVI. pp. 324–326, 1860.

[3] Ibid., Vol. XXI. pp. 1–14, 1865.

[4] Reports of the Geological Survey of Jamaica, London, 1869.

The studies of the island made by the official surveyors were comprehensive and began at least as early as 1859. The official report[1] is the present standard of reference.

The observations and material of the Jamaican survey have also been the bases of several independent papers on the geology of the island, by S. P. Woodward, Moore, Wall, Duncan, and others, which have appeared in the English serials, and which will be frequently cited later on.

Many individuals who have not personally observed the geology of the island have made paleontologic studies of material collected by the survey and others, and announced important conclusions. Among these may be mentioned Moore, S. P. Woodward, Duncan, Gabb, W. J. L. Guppy, Dall, Etheridge, T. Rupert Jones, and Jukes-Browne. So far as minute study and interpretations are concerned, the petrography and physical geography of the island have received little or no attention.

The writings of the authors mentioned have been valuable aids in the preparation of this book. In perusing this literature the reader is constantly impressed with the fact that these researches failed to solve the essential problems of the succession and age of the strata; this fact impaired the value of all subsequent deductions, and fundamental mistakes were made which have had wide bearing on the interpretation of Antillean history. The literature of no other region, especially that relating to paleontology, presents so many erroneous conclusions. To avoid constant corrections of these mistakes, it is best to point them out at the beginning. It is but fair to state that this unfortunate stratigraphic confusion was not the result of incompetence, but was due to an act of Providence. Mr. Lucas Barrett, the Scientific Director of the Official Survey, who alone knew the combined results of its several workers, and was able to correlate them, was drowned in a diving bell while carrying on his studies.[2] Conflicting endeavors to make posthumous interpretations of his opinions were the sources of the subsequent erroneous conclusions.

The official report is a peculiar and unfinished composite, Barrett's death having occurred before its publication. The introduction of two

---

[1] Entitled "Reports on the Geology of Jamaica, or Part II. of the West Indian Survey," by James G. Sawkins, with contributions by G. P. Wall, Lucas Barrett, Arthur Lennox, and C. D. Brown, and an Appendix by Robert Etheridge, Paleontologist of the Geological Survey of Great Britain, printed for Her Majesty's Stationery Office, 1869, 339 pages, with Maps and Plates. This work and its parts will be frequently referred to in this paper as the Jamaican Reports.

[2] December, 1862. See Obituary Notice in the Geologist, Vol. IV. pp. 60–62, 1863.

pages is by Sir Roderick I. Murchison. The first general summary of the island is by James Gay Sawkins. Individual reports of the different parishes are by Barrett, Wall, Sawkins, Lennox, and Brown. The Appendix contains a discussion and résumé of the paleontology and age of the rocks of the Caribbean Sea by Robert Etheridge, with paleontologic determinations by Duncan, Carrick Moore, T. Rupert Jones, and others.

In the reports upon the individual parishes each field worker used an independent and often conflicting nomenclature for the various formations described, and frequently expressed contradictory opinions concerning the age of the same formations. For instance, as has been pointed out by other writers[1] with respect to the age of the White limestone, "the reports of the surveyors are inconsistent with one another. In some places (as on pp. 23 and 149) it is called Miocene; in others (pp. 29 and 30), Pliocene, and in the tabular view at the end of the volume it is labelled Post-Pliocene." This confusion is equally apparent concerning all other formations discussed.

The report is deficient in local stratigraphic sections by which the discrepancies might be corrected. On the other hand, the parties who attempted to correlate and generalize the individual reports in the Appendix went to the other extreme, and reduced the nomenclature to a compact but an illogical arrangement. In general, the descriptive portions of the report are fair, but its conclusions concerning the classification, sequence, and age of the rocks leave the reader in a state of confusion.

We cannot point out all of these discrepancies; a comparison of the three summaries given in different parts of the volume will sufficiently exhibit them.[2] The chief confusion resulted from the attempt of those who wrote the summaries to include the various formations of the local observers under certain broad generic terms, such as the "White" or "Yellow" limestones, whereby the whole succession and age of these rocks, whose correct interpretation is most essential to an understanding of the geological history of the island and the Antilles, was confused.

These errors resulted from erroneously correlating the Eocene Yellow limestones with the Miocene (old usage) Bowden beds. The former occur at the base of the entire series of White limestones, and the latter

---

[1] Jukes-Browne and Harrison, Jour. Geol. Soc. London, No. 190, Vol. XLVIII. p. 219.

[2] Jamaican Report, pp. 128, 186–189, and table at end of volume.

near the top of the same.[1] Furthermore, in this mixture the erroneously combined group was given the stratigraphic position of the Yellow limestones below the White limestones, and the age position of the Bowden beds. This resulted in making all the White limestone, much of which is pre-Miocene, appear as overlying the Bowden Oligocene. As this error has had far reaching importance in obscuring Antillean geology and paleontology, we give a brief sketch of its origin and history.

The following section,[2] showing the sequence of the Jamaican formations, was published by Woodward in 1862, seven years before the appearance of the official reports in 1869, as a posthumous interpretation of Barrett's conclusions as he (Woodward) understood them. The names on the right are those to be used by us for the equivalent beds of the section. The sequence of the formations, as given in this section, corresponds more nearly with their true occurrence than any of the subsequent compilations to be noted.

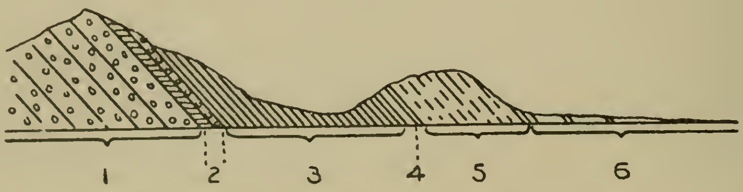


Figure 1. Woodward's Interpretation of Barrett's Section of the Jamaican Sequence.

Barrett's Section.	*Equivalent Nomenclature of this Paper.*
6. Pliocene Limestone and Marls,	Bowden and other Beds of the Coast Series.
5. Miocene Limestone,	*Oceanic Series.*
4. Orbitoidal Limestone,	*Cambridge Beds.*
3. Gray Shales,	*Richmond Beds.*
2. Cretaceous Limestone and Hippurites,	Blue Mountain Series.
1. Purple Conglomerate.	

This original section, supposedly by Barrett, in addition to giving the position of the Hippurites limestone, from which Orbitoides and Nummulinæ were reported, gave in its correct place, under the name of Orbitoidal limestone but without age designation, the beds called Yellow

---

[1] The Bowden formation, although one of the most important in the Jamaican sequence, and the one from which all of the alleged Miocene fossils of Jamaica have come, seems not to have been clearly defined or understood by these earlier writers, — probably because of their supposed identity with the Yellow limestone. See further details, pages 82–84 of this paper.

[2] The Geologist, London, 1862, Vol. V. p. 373.

limestone by Brown, which we shall call the Cambridge formation. Woodward, in the text, accidentally no doubt, omits to mention this important formation, and erroneously states[1] that the shales, No. 3 of the figure (our Richmond Beds), are followed by the White limestones of "Miocene age." For verification he refers to a previous article by Barrett,[2] in which we can find no mention of any such sequence.

Later, T. Rupert Jones also published an illustration of a geological section which he said had been given to him by Barrett, "whose unfortunate death had then recently occurred." This section, like that given by Woodward, shows the stratigraphic position of the Orbitoidal limestone, *b*, (called "Nodular Orbitoidal Limestone,"[3] — our Cambridge Beds), between the black shales (Richmond) and White limestones. In the legend of the section the age of the Orbitoidal formation is given by a bracket as the "Miocene." This is the first section in which the Orbitoidal limestone (our Eocene Cambridge Beds in part) was referred to the Miocene. In the same section the overlying White limestones, *a*, which we will show embraces formations of the Vicksburg Eocene (old usage, — called Miocene in Woodward's paper previously alluded to) is referred to the Pliocene. Jones states that "he understood Mr. Barrett to have referred the great "White limestone" to the Pliocene.[4]

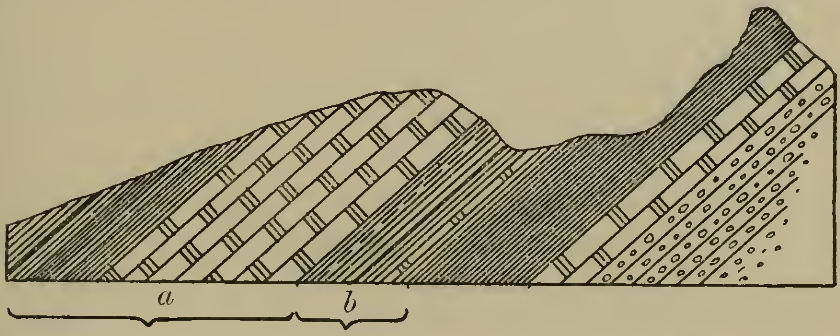


FIGURE 2. T. Rupert Jones's Interpretation of Barrett's Section of the Jamaican Sequence.

In 1864 Duncan and Wall wrongly correlated the Yellow Eocene Orbitoidal limestones at the base of the White limestones with the Bowden beds (Oligocene) which occur above them, and referred the

---

[1] The Geologist, London, 1862, Vol. V. p. 373.

[2] "On Some Cretaceous Rocks in Southeastern Portion of Jamaica." Quart. Jour. Geol. Soc. 1860, Vol. XVI. pp. 324–326.

[3] Quart. Jour. Geol. Soc. London, 1863, Vol. XIX. p. 515.

[4] Ibid., pp. 514, 515.

whole to the Miocene. They emphasized this conclusion by speaking[1] of Barrett's "determination of the Miocene age of the coralliferous sands and shales at the base of the great inclined limestone." We can find in literature no substantiation of this alleged assertion of Barrett, and it is not in harmony with his sections as given by Woodward and Jones. These writers were no doubt misled by the superficial resemblance of the upper beds of the Blue Mountain Series to the Bowden conglomerates into considering them identical.

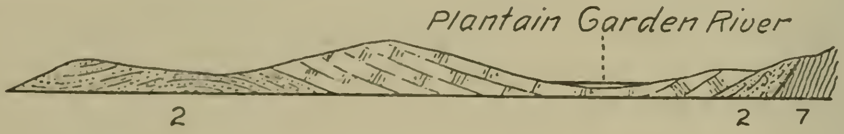


FIGURE 3. Duncan and Wall's Section of the Jamaican Sequence. 1. White Limestone. 2. Miocene Marls and Sands. 7. Altered Conglomerates and Cretaceous Rocks Mixed with Dikes.

In the same paper Duncan and Wall, by the figured section[2] reproduced herewith, completely obliterated all conception of the true position of the Bowden formation by erroneously making it stratigraphically continuous with the Cambridge Yellow limestone beds. In 1896 we personally restudied the section between Bath and Bowden, and found that the relations of the beds had been wrongly given by these writers, and that the Bowden beds, instead of being continuous with the Cambridge beds, were separated from them by all the lower White limestones as shown in the following section.

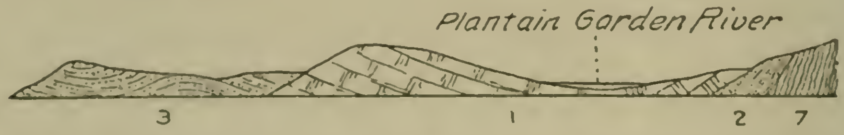


FIGURE 4. Correction of Duncan and Wall's Section of the Jamaican Sequence.

These errors, as published in the English serial literature between the dates of the official field work and the publication of the final report, were perpetuated by Etheridge in the Appendix of the latter work. On page 203, our Cambridge beds — which are so well described in the individual reports upon the western parishes under the heads of "Yellow Limestone" and "Calcareous Marls" — are correlated by him with the Bowden beds, and discussed with them (and perhaps other formations)

---

[1] Quart. Jour. Geol. Soc. London, 1865, Vol XXI p. 2.

[2] Ibid., p. 6.

as a single formation under the vague head of the "Miocene." Furthermore, the precedent of not specifying the locality from which the fossils came was followed in all the subsequent paleontologic literature of Guppy and others, and by Dall,[1] who referred the rocks of Jamaica, included by the others in the Miocene, to the Oligocene.

Thus the true sequence of the Jamaican strata was confused in early literature; the proper place of the Cambridge beds (the true Yellow limestones of the west), at the base of the White Limestone Series, appeared for a brief moment, next to be obliterated by erroneous correlation with the entirely different and higher Bowden beds of the east, and all conception of the position and age of a greater part of the great White limestones which mostly lie between them was destroyed. This confusion has become so confounded in the passing years that the present state of knowledge to be derived from the literature is chaotic. Not only after reading the geologic literature of Jamaica, but after going over the island with these reports in hand, the opinion already expressed by others[2] is emphasized, that "clearly there are many interesting questions in the geology of Jamaica which are awaiting further investigation, and the mutual relations of these white marls and limestones is not the least important of them." To straighten out this entanglement will be our earnest endeavor.

It is but justice to say concerning the volume of official reports, that, despite their discrepancies, they are full of valuable uncorrelated data. Although unintelligible to one who has not studied the island, we do not hesitate, after two years of careful study of its pages and the localities of which they treat, to say that by careful re-editing, including the correlation of the observations on the various parishes under a uniform and systematic nomenclature, and striking out much of the Appendix, the volume could be made a valuable guidebook of Jamaican geology. The writer appreciates the worth and value of the individual reports, and acknowledges that they represent important steps in the progressive research which contribute to the ultimate solution of the problems, and that the following pages would have been impossible without them.

In view of the complications presented, and in the light of additional knowledge in the present paper, the formations will be classified *de novo*, with proper credit wherever possible for all previous determinations.

---

[1] Proc. U. S. National Museum, Vol. XIX., Washington, 1896.

[2] Jukes-Browne and Harrison, Quart. Jour. Geol. Soc. London, 1896, Vol. XLVII. pp. 190, 221.

Our classification will differ from that of previous writers as follows. In accordance with modern usage, local geographic names will be used for formations instead of lithologic, chronologic, and paleontologic terms, so that where the age or relations of formations are not known, their identity is nevertheless preserved. Hence the terms "White Limestone," "Yellow Limestone," "Trappean Series," "Metamorphic Series," etc., will be abandoned.

Inasmuch as this paper will deal largely with the formations of the Tertiary period, it is necessary briefly to explain the nomenclature to be followed. Until very recently, after the example of Dana, the American Tertiary has been divided into three epochs, the Eocene, Miocene, and Pliocene. Dall has recently adopted the European nomenclature, which accepts a fourth epoch, the Oligocene, interpolated between the Eocene and Miocene, which includes the Vicksburg stage of the Upper Eocene (American usage) and the older beds of the Miocene. Throughout this paper Dall's four divisions, as accepted by him, will be used.

Investigations upon which the present report is based were made in two visits to the island in the winters of 1896 and 1897. These included over eight hundred miles of traverses, with studies of the typical localities of the previous observers, and examinations of excellent new exposures of structure afforded by recent railway construction. Careful study of material in the Museum of the Institute of Jamaica was made, embracing the typical collections of the official surveys. Collections of the rocks and fossils were made wherever possible, and permission was given by the officials of the Institute of Jamaica to borrow such specimens as were desired.

My thanks are due to their Excellencies Governor Sir Henry and Lady Blake, the Governing Board and Professor J. E. Duerden of the Jamaica Institute, Mr. L. Frank of the Jamaican Railway, Mr. Henry Vendryes, Captain Baker and sons, Mr. Arthur James, and many others, for their hospitable aid in our researches.

The following specialists have kindly assisted in a careful study of materials collected: Mr. Whitman Cross, in the study of the petrography of the igneous rocks; Mr. T. W. Stanton, in the study of the Cretaceous and Eocene Mollusca; Mr. R. M. Bagg, Jr., of the New York State Museum, in determining the fossil Foraminifera; Mr. G. B. Shattuck, of Johns Hopkins University, in studying the Cretaceous and Eocene Mollusca.[1] Special thanks are due to Mr. T. Wayland Vaughan for his

---

[1] Mr. Shattuck has been unable to complete these studies for publication in this Report. His results will be presented separately at a later date.

extensive, thorough, and painstaking studies of the fossil corals, including not only careful examination of all the material in hand, but also personal visits to nearly all the European Museums where the collections of previous workers are preserved. His determinations have been the chief reliance in the interpretation of many obscure points. His studies will be published elsewhere more *in extenso.*

PART I.

Geography and Physiography.

The island of Jamaica is situated between North Latitude 17° 40′ and 18° 3′ and West Longitude 75° 10′ and 78° 23′. Its northern shore lies almost due south of the western half of the Sierra Maestra coast line of Cuba, from which it is 65 miles (nautical) distant. Between these islands lies the eastward prolongation of the great Bartlett depression, 3,000 fathoms deep. The eastern coast is about the same distance from Cape Tiburon, the western point of the island of Haiti, and is separated therefrom by 1,000 fathoms of water. On the south lies a wide stretch of the Caribbean, 2,000 fathoms deep. Cape Gracias á Dios, the nearest Central American land on the western coast of Honduras, is 780 nautical miles distant. Between the Isthmian-Honduran continental littoral and Jamaica extends the Rosalind and Pedro Banks, less than 500 fathoms deep, which constitute an extensive shallow submarine platform, indented at one place by a narrow submarine strait of less than 1,000 fathoms.

Jamaica is almost the exact centre of the great American Mediterranean. By drawing straight lines through the island, as shown in Figure 5, from Galveston to the mouth of the Orinoco, from the southern point of Florida to the northern part of South America, from the eastern end of the Antilles (St. Thomas) to the western indentations of the Gulf of Honduras, and from the most northern Bahama to the Gulf of Atrato, the central position of the island will be apparent, for it will be found at the point of intersection of these radiating lines and about equidistant from their termini. This central position of the island is important from geographic, biologic, and geologic points of view, and makes it a typical base of study for one interested in Antillean problems. Like a measuring gauge set up in the middle of a stream to record the rise and fall of a river, it stands in the centre of the American Mediterranean, — a standard geological index of the great oscillatory changes of level which have taken place in the history of Tropical America, whose feebler amplitudes only are indicated in the perizonal continental borders.

The extreme length of the island is 144 miles, its greatest width is 49 miles, and its least width is 21½ miles, from Kingston to Annatto Bay. The longest axis lies in east and west directions. The outline of the island which encloses 4,207⅛ square miles,[1] about one eleventh the area of Cuba and 500 square miles greater than Porto Rico, is an elongated parallelogram whose corners have been obliquely truncated, resulting in a wide oblong central area from whose east and west ends project two broad peninsulas.

At first glance, the outline does not appear to have any peculiar meaning, but when analyzed in connection with the geologic structure and adjacent submarine topography, it is of great significance. An interesting feature of this outline is that, while the major trend of the north coast and the island as a whole is east and west, nearly one half the coast line is diagonal to this cardinal direction. The northwest and southeast trends are survivals of the earlier days of Antillean history. The predominant east and west directions are produced by a later geographic revolution.

Configuration. — The relief of Jamaica is dominantly mountainous, for the interrupted Coastal Plain constitutes only a narrow fringe around the island. The first distant view from the east shows a group of mountain summits rising above the expanse of sea in a tangled mass, apparently without systematic ridges or secondary types of relief features by which its configuration can be classified. The higher summits of this end are usually, if not always, veiled in clouds, so that only the lower half of their slopes is ordinarily visible. The mists are apparently forever present in the upper regions. As the coast is more closely approached and the island encircled, the configuration resolves itself into differentiated forms, presenting four distinct and easily recognizable major types and numerous secondary modifications, which will now be explained. Its chief features are: (1) the interior mountain ranges constituting the nucleus of the island; (2) an elevated limestone plateau which surrounds the interior mountains, and ends abruptly towards the sea; (3) the coastal bluffs or back coast border of the seaward margin of the plateau; and (4) a series of low, flat coastal plains around the periphery of the island between the sea and the back coast border. The relation of these features is shown in the various profiles and sections.

---

[1] As given by the Jamaican Land Department.

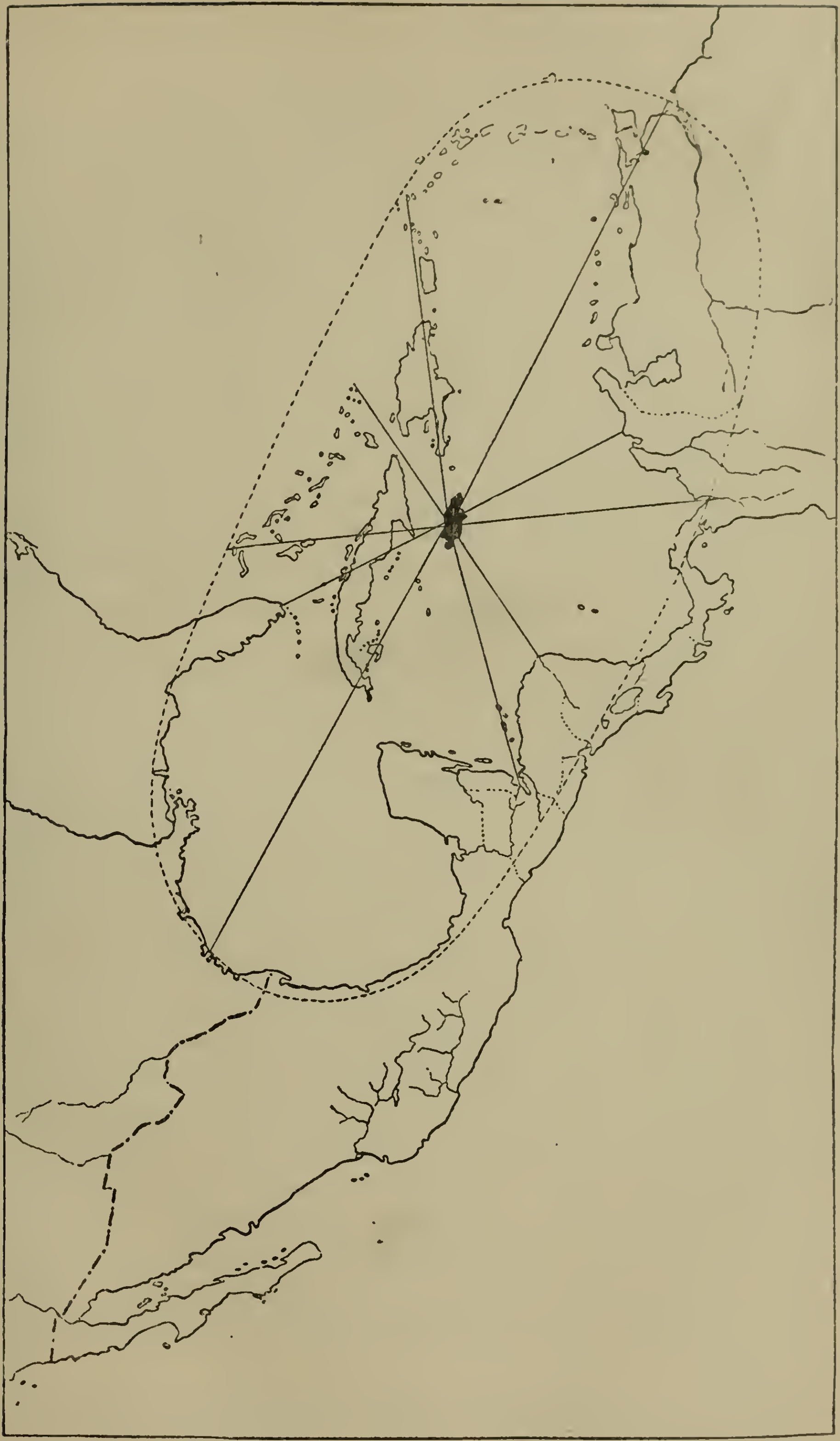


FIGURE 5. Diagram showing Central Position of Jamaica relative to the American Mediterranean.

The origin of this configuration, which is inextricably associated with the stratigraphic history and geologic evolution of the island, will be more fully explained in the later chapters of this report.

The main mass of the island is an elevated region of rugose relief, consisting of a nucleal mountain range surrounded by a high dissected plateau. The higher region does not slope gradually to the sea, but is terminated near the coast by very abruptly truncated bluffs, steep slopes or benches, usually, but not everywhere, separated from the sea by a narrow strip of plain, as if the original coast margins of the mountainous upland once extended much farther seaward and had been horizontally planed away by the sea's encroachment. The abrupt sea face of the mountainous upland is a marked topographic peculiarity, which we shall call the back coast border. This narrow ribbon of coastal plain is not a continuous belt, but is interrupted, and constitutes an important feature of the Jamaican topography. The secondary features are interior basins and valleys in the summit of the plateau, certain coastal benches and terraces carved out of the margin of the back coast border, and the drainage valleys.

Of these the interior mountains and the limestone plateau are by far the most conspicuous features, and will be first discussed.

The relation of the plateau region to the interior mountains is that of an elongated mesa or bench completely surrounding a higher sierra, the plateau having an outline somewhat like a child's bib, through the neck of which the mountains of the east protrude, surrounded by a narrow collar of plateau, while the main expanse or apron, which lies towards the west, presents occasional views of the buried mountain structure, through rents and holes made by water. The two types of relief of the upland regions are readily distinguishable, even from a great distance, by the entirely distinct physiognomy of their slopes. The interior mountains are marked by deeply etched knife-edged salients (cuchillas) and angular re-entrants which present the aspect of a crumpled handkerchief picked up by the middle, — an illustration used by Columbus in describing the mountains of the Indies to Queen Isabella. These peculiar escabradurate[1] slopes are shown in the illustrations on Plate VI. The corrugations of the Blue Mountain Ridge are plainly visible from Kingston. On the other hand, the hills of the limestone plateau, whether of peaked or flattened summits, present uncorrugated, densely wooded slopes.

---

[1] From the Spanish Escabradura, signifying the erosion scratches, — "Bad-land," relief of American usage.

The Mountains of the Interior. — These comprise the Blue Mountain Ridge, which dominates the topography of the eastern third of the island, and certain peculiar isolated summits to the west of the Blue Mountains proper, such as Jerusalem Mountain, Westmoreland, and the Clarendon (Bull Head) Mountains of Clarendon Parish. The isolated groups occur as limited inliers, surrounded and overlooked by hills of the limestone plateau.

The Blue Mountains form a sinuous divide with many bifurcating branches. They extend one third the length of the island, from near the eastern point towards Port Maria, and have a trend of north of west, parallel to the truncated northeast coast of the island. In general, this ridge marks the boundary between the eastern parishes of the north side (Portland and St. Mary) and those of the south (St. Thomas, St. Andrew, and St. Catherine). It presents a serrated crest line with radiating laterals whose summits culminate near the centre of the ridge in the Blue Mountain Peaks (alt. 7,360 feet).[1] West of these peaks the altitudes gradually decrease until they become lower than those of the surrounding limestone hills beneath which the mountain structure was buried in ancient times. Everywhere the ridge and numerous laterals which project from it at right angles present the profile of an inverted letter V, thus Λ. Its configuration is singularly free from benches, mesa tops, or vertical escarpments, the last seldom occurring except as the bluffs immediately adjacent to the present stream beds.

Imagination pictures no more exquisite scenery than that which attends the ascent of Blue Mountain Peak. With increasing altitude panorama after panorama of tropical landscape unfolds in rapid succession. At Gordontown, nine miles north of Kingston, where the interior margin of the Liguanea Plain meets the mountain front, the ascent through the red-colored cliffs of the Hope River Canyon begins, which here, at an altitude of 900 feet, debouches into the gravel plain through a boca. A thousand feet above, the white buildings of Newcastle Barracks look like doves upon a housetop, yet we climb so far above them that they seem like toy houses below. At 2,000 feet the Plain of Liguanea with its city and villages and the shipping of Kingston Harbor, grow smaller and smaller, and finally appear like a diminutive plaza below us. Sometimes our path clings to the side of steep declivities, with an apparently endless slope above and a bottomless chasm below. Again, it follows a knife edge from which we can see beyond, on both sides of the island, the waters of the Caribbean, so distant and

---

[1] Altitudes given in this report are mostly from the Jamaican surveys.

so far below that no horizon can be distinguished where the gray of the sea meets that of the sky. Still higher, the forest covered summits of the limestone plateau, with its rugged back coast border, appear below as an unbroken meadow.

Each step of the way is marked by wonders of the vegetal kingdom. At the foot is the semi-arid south coast chapparal with exogenous banana plants, cocoanut trees, native cactus, and acacias. Ascending Hope River Canyon the delicate deciduous flora of the island begins, while the cliffs are burdened with ferns — golden, silver, and delicate maidenhair — besides numerous little flowers which find foothold in the rocks. From 1,000 to 4,000 feet, plantations of coffee are numerous, finding congenial temperature and moisture. At 4,000 feet the government has found environment for its cinchona farm. Above 6,000 feet, in an atmosphere of perpetual humidity, tree ferns set in. In this tropical climate such alpine heights offer no obstacle to human environment, and to an altitude of 4,000 feet the slopes are well populated.

There are many other conspicuous peaks of the Blue Mountain Ridge, but few of them have received local names. Sugar Loaf Peak, which lies just east of Blue Mountain Peak, is a part of the latter. To the west are Sir John's Peak, John Crow Hill,[1] Silver Hill, and St. Catherine Peak (alt. 5,036 feet). These high summits are situated near the central portion of the main ridge, which is crossed by five passes with altitudes varying between 3,000 and 4,000 feet.

East of Kingston there are few practical openings through the Blue Mountain ridges which are passable on horseback. One of these is that of Cuna Cuna, between Port Antonio and Bowden, and traverses some of the most rugged and beautiful scenery on the island. Its altitude is 2,698 feet. A good highway crosses the island through a pass in the ridge cut by the waters of the Agua Alta (Wag Water) between Kingston and Port Maria.

Westward from St. Catherine Peak, almost due northeast of Kingston, the main ridge bifurcates; the southern and larger branch continues in a sinuous but generally northwestern course through St. Andrew, where it is known as the Ram's Horn Ridge, and "Above Rocks," and on between St. Mary and St. Andrew as Goddard Ridge, to the drainage divide of Rio Doro and Trumbell's River, near the line of the Port Antonio Railway. Several other ridges radiate from St. Catherine Peak to the northwest in palmate arrangement. All these branches,

---

[1] Not to be confused with the John Crow Mountain of the northeast coast.

representing the western end of the Blue Mountain ridges, terminate on the eastern side of the great basin of St. Thomas-in-the-Vale.

The mountains are composed of the friable or loosely consolidated shales, clays, and conglomerates of the Blue Mountain Series, with here and there an exceptional local bed of limestone or an occasional dike or mass of igneous rock usually decomposed, all of which are intensely plicated and folded. Their present configuration is due to the readiness with which they yield to erosion. When one considers how rapidly degradation is going on and has gone on, he can only conclude that the mountains were once of much greater altitude and extent. There is no reason why its summits in times past may not have extended as high as their kindred in the Sierra Maestra of Cuba, over 8,000 feet, or in San Domingo, over 10,000 feet.

These Blue Mountains are the highest of an extensive system of corrugations which were partially buried, especially west of the centre of the island, during a former period of subsidence, beneath the veneering of white limestone, and which has since been re-elevated to a height of 3,000 feet. Only the Blue Mountain ridges persisted as land during this epoch of subsidence, while the Clarendon and other westward groups were covered by the ocean's waters.

The old Blue Mountain structure and material reappear in many places in the great central valleys of St. Thomas-in-the-Vale, Clarendon Parish, Great River, and elsewhere to the west, where the later crust of the White Limestone Plateau has been worn away. It is also seen in the face of the back coast bluffs along the western half of the north side of the island below the limestone and above the narrow coastal benches. These were originally a part of the same grand system as the Blue Mountains, which were buried beneath the white limestones, and are now re-exposed by erosion of the latter. Let us examine some of these localities more closely.

The Clarendon Mountains. — The exact geographic centre of Jamaica is marked by a most interesting topographic feature, an anticlinal valley worn out of the crest of the low arch of the White Limestone Plateau. This is an elongated oval area, fifty miles in length, lying mostly in Clarendon Parish, but extending on the southeast into St. Catherine and on the northwest into Trelawney. This great amphitheatre is completely surrounded by the inward facing breaks of the Limestone Plateau, which rise 2,558 feet on the south and 3,000 feet on the west side. Most of the area of the valley is occupied by two parallel mountainous ridges with laterals and disconnected outliers. The most southern ridge

— the drainage divide of the Minho and St. Thomas — is known as the "Main Ridge." The other, which lies between the drainage of the Minho and Cave and Pindars Rivers, may be called the Santa Maria Ridge. It culminates eastward in Bull Head, an elongated summit. A view of the latter mountain is shown on Plate VII. These ridges consist of the same material as the Blue Mountain Ridge, present similar slopes with cuchillate salients, and differ only in their crests, which are not so serrated. They have a general north of west trend, parallel to that of the Blue Mountain Ridge. They are not continuous with the latter, whose west end terminates *en échelon* many miles northeast of where the former begin.

The present relief of these ridges, while greatly resembling that of the Blue Mountains, has been produced during late epochs by the deep erosion of the river valleys which are parallel to them. The heights of these mountains (Bull Head, 2,885 feet, and the main ridge, 2,542 feet) do not anywhere exceed that of the circumscribing White Limestone Plateau. It is our opinion that they are merely modern drainage divides, their summits representing an older floor of a former central basin valley like those described on later pages. Furthermore, the data indicate that this older and higher floor was once completely covered by the formations of the White Limestone Plateau.

In the southeast corner of Hanover Parish, in the valley of Great River, at Jerusalem Mountain in the north central portion of Westmoreland and along the northwest coast of Hanover, the Central Mountain rocks and structure are again exposed by denudation of the once overlying white limestone sheet as in the Clarendon district. Jerusalem Mountain is a hill 600 feet above the plain, surrounded by an amphitheatre of white limestone hills. The other exposures are usually shown in the valleys of streamways. Probably the Great River and Jerusalem Mountain localities represent exposures of a third line of old mountain folds lying south of the Clarendon trend.

In all the localities mentioned, the Central Mountain structure is intensely folded. In the east it is a crumpled anticline, and has evidently been subjected to the additional disturbance of a later intrusion of a great mass of granitoid porphyry, with many auxiliary dikes, which is now exposed by erosion on the north side of the west end of the ridges in St. Mary. Westward the structure is that of overthrown closed folds, as shown in Plate XXII., which is a view of the structure on the north coast near Lucea. The geologic section further exhibits the deformation which has produced the Blue Mountains of Jamaica.

In general, all the Central Mountain structure occurs along three lines of strike, probably representing the outcrop of two original lines of corrugation, whose ends overlap *en échelon*. One is the Blue Mountain Ridge proper; the others are represented by the buried summits of the west. The Blue Mountain Ridge is the most northern and eastern of these old corrugations, the Clarendon and Hanover exposures an intermediate one, and the Jerusalem the most southern and western.

While the mountain eminences of the Central type nowhere extend to the immediate coast, and are everywhere separated from it by the hills of the back coast country, the mountain structure itself is found in the bluffs on the north coast outcropping at the sea beneath the White Limestone Plateau. From this fact we conclude that, collectively, the Central Mountains of Jamaica represent an ancient mountainous topography, at one time occupying an area larger than the whole of the present island, and, for reasons stated in our final chapter, related to similar features of the other Great Antilles.

The Plateau Region. — This later addition to the original island of Jamaica is now a much dissected plain rising 3,000 feet. Its principal occurrence is west of the Blue Mountains, where it extends entirely across the island. In the east it constitutes a narrow collar or dado of limestone country around the coastward margin of the Blue Mountain Ridge. In all, it occupies fully four fifths of the total area.

As a whole, the profile of the plateau, could the irregularities of erosion be eliminated, would be a very gentle arch, from whose east and west axis the surface slopes towards the adjacent seas. The curves of this arch if continued would not reach the sea at the present truncated margin of the land, but intercept it quite a distance beyond either shore, as shown in Figure 6, indicating that the former borders of the now restricted island were extended. Thus in many places the margin of this plateau is marked by benches and terraces, constituting the back coast borders presently to be described.

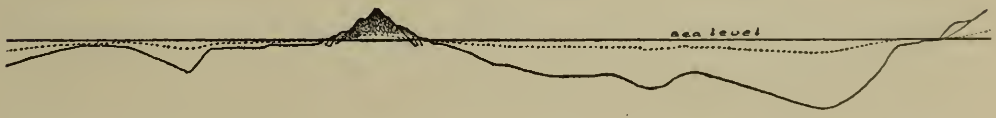


FIGURE 6. Showing Truncated Margins and former Seaward Extension of Jamaica. — Dotted line shows Natural Profile.

By tacit consent, the innumerable eminences of the plateau which rise to nearly 3,000 feet are called hills in Jamaica, to distinguish them from the Central Mountains. The highest summits of the plateau are found in the crests surrounding the Clarendon basin, near the centre of the island, which attain a maximum altitude of about 3,000 feet or less than one half that of the highest Blue Mountain peaks. The highest of the plateau remnants is Mount Diablo, which forms the divide between the two coasts as well as between St. Thomas and Clarendon valleys. It is reported to be 3,053 feet in altitude. Altitudes exceeding 2,000 feet continue southward from the west end of the Clarendon Valley almost to the southern coast of Manchester and St. Elizabeth. Some of these are given by the official surveys as follows: Mocha, 2,558 feet; Cabbage Hall, 2,983 feet; Drayton, 2,210 feet; Sedburg, 2,269 feet; Mason's Run, 3,000 feet; Craig Head, 2,619 feet; Aboukir, 2,019 feet; and Water Mount, 1,844 feet. Don Figuera Mountains, over 2,400 feet, Mile Gully Mountains, 2,514 feet, and Carpenter's Mountain of Manchester, 2,400 feet, are also remnants of this old plateau level, near the south coast of the central region. On the east the John Crow Ridge (alt. 2,110 feet), an elongated summit extending parallel to the coast, may be either a remnant of the old summit level or the oldest and highest of the base level plains cut out of its marginal topography. On the south side of the Blue Mountain Ridge the highest summit of Yallahs Mountain (alt. 2,254 feet) is the sole surviving remnant of the old summit topography of that side of the island. These elevations indicate that the region of maximum altitude of the plateau was in the widest part of the island from near the south coast of Manchester to and just across the boundary of St. Ann.

In places along the south coast there are isolated white limestone remnants of the plateau, which are separated from the main body by the wide indentations of the lower lying Coastal Plains. The Port Henderson and Healthshire Hills of St. Catherine, and the Braziletto Mountains and Portland Ridge of Clarendon, are of this type.

The materials of the plateau and its outliers are soluble limestones, — old sheets of calcareous oceanic sediments now chalky or subcrystalline in texture, which were deposited upon and around the bases of the Central Mountains and attained their present altitude by a subsequent elevation. These white limestones are described elsewhere in this paper under the names of the Montpelier, Moneague, and Cobre formations. The details of the configuration are largely due to the peculiar solvent character of the limestone. These hills, especially in the interior, owe their configuration largely to the agency of solution, while the forms of the Central Mountains are due entirely to denudation. So important and wide reaching are the influences of solution that it must be constantly considered in a discussion of the region.

The summit of the plateau is a roughly serrated hilly country, indented by cockpits (sinkholes), subcircular basin valleys, and deep drainageways leading to the sea. In many places the surface is marked by jagged honeycombed rocks, between which grows a dense tropical foliage. Knife-edged lateral salients, like those which characterize the Central Mountains, are missing from this topography. Steep bluffs, undermining benches, caverns, and sinkholes abound.

The Cockpit Country. — The origin of the ragged summit topography of the White Limestone Plateau, and the evolution of the numerous interior basin valleys of which they are antecedent, can be best illustrated by a description of "the cockpit country," as it is locally called; this, with its modifications, includes the whole of the high interior portions of the parishes of St. Ann, Trelawney, St. James, Hanover, Westmoreland, Manchester, and St. Elizabeth, to the west and north of the Clarendon ridges, although the cockpits are limited to a rough district embracing the corners of Trelawney and St. James. In the interior of the western half of the island the hills are sharply rounded conical points. Towards the coast there are long flat-topped ridges with steep slopes, such as the John Crow Ridge of Portland, Yallahs Ridge of St. Thomas, Long Mountain of St. Andrew, the Healthshire Hills of St. Catherine, the Portland Hills of Clarendon, and others. Still another type are flat-topped circular mesas with steep walls, such as occur in parts of Westmoreland and Hanover.

The cockpits are primarily deep funnel-shaped sinkholes, from which the drainage percolates downward into the cavities and fissures of the underlying rocks. The steep acclivities of these holes ascend into pointed conical hills. Their origin and evolution is shown upon the accompanying figure. The pits vary in depth from shallow circular basin-like depressions surrounded by low mammillary hills (Fig. 7, I) which mark the youthful stage of their formation, to deep-sided sinks often 500 feet in depth, denoting the acute stage of development (Fig. 7, II). Both these types are common on the summit region, where there is no surface drainage, the water settling in pools and penetrating down into the soluble and open textured substructure, carrying with it lime in solution and leaving behind as soil and in the cavities of the limestone a blood red residuum of iron and clay, as may be seen in many fine vertical sections cut along the line of the newly constructed Montego Bay Railway.

The two foregoing stages of the cockpit topography are always developed in the upper part of the white limestones. Below these is another limestone formation of more even texture, still soluble but less pervious than the former, which forms a temporary resistance plane to the progress of degradation. Still below the latter are the nodular limestones, clays, and conglomerates of the older insoluble and impervious formation whose close texture stops the further downward progress of the lime-charged waters which must then find passage in sub-horizontal directions.

When the bottoms of the cockpits reach the temporary resistance layers of the second group of limestone beds (Fig. 7, III) their perimeters begin to expand laterally, thereby forming peculiar round or oval valleys with steep sides, commonly known in Jamaica as light-holes (Plate IX. Fig. 2). The downward process continues below the lower limestone, first dissecting it into flat-topped remnants, as shown in Figure 7, IV and V, and finally removing it entirely.

When the insoluble beds of the older nucleal mountain material are reached, the cockpit topography enters a period of decadence. Downward degradation by solution ceases; the valleys expand by lateral erosion (Fig. 7, VI) and extensive circular enclosed basin valleys result. Furthermore, great springs of water break out at the contact of the limestones and clays, and establish corrasive drainage, absent in the higher limestone districts, which etches the floor of these basins into miniature mountain forms, thus reviving the ancient antecedent topography. The barriers between these valleys and the coastal drainage are ultimately captured by the latter, and in this manner some of the valleys have become connected with the Coastal Plains of the Liguanea type to be described. Such is the evolution of the topography of the cockpit country and the origin of the interior basin valleys of Jamaica.

The Interior Basin Valleys. — The many basin-shaped depressions occurring throughout the plateau region constitute some of the most interesting physiographic features of the island. Although varying in dimensions, these are all of a uniform type, consisting of deep depressions in the summit of the plateau, enclosed by rugged limestone walls, and having a floor established upon the rocks of the Blue Mountain Series, and are covered by accumulations of alluvium or residual soils. The valleys differ from one another chiefly in area and irregularities of the relief of the basin bottoms which seldom exceed 400 feet in altitude above sea level, while the perimeters of surrounding hills rise from 1,200 to 2,500 feet above them, the height varying in different localities. In

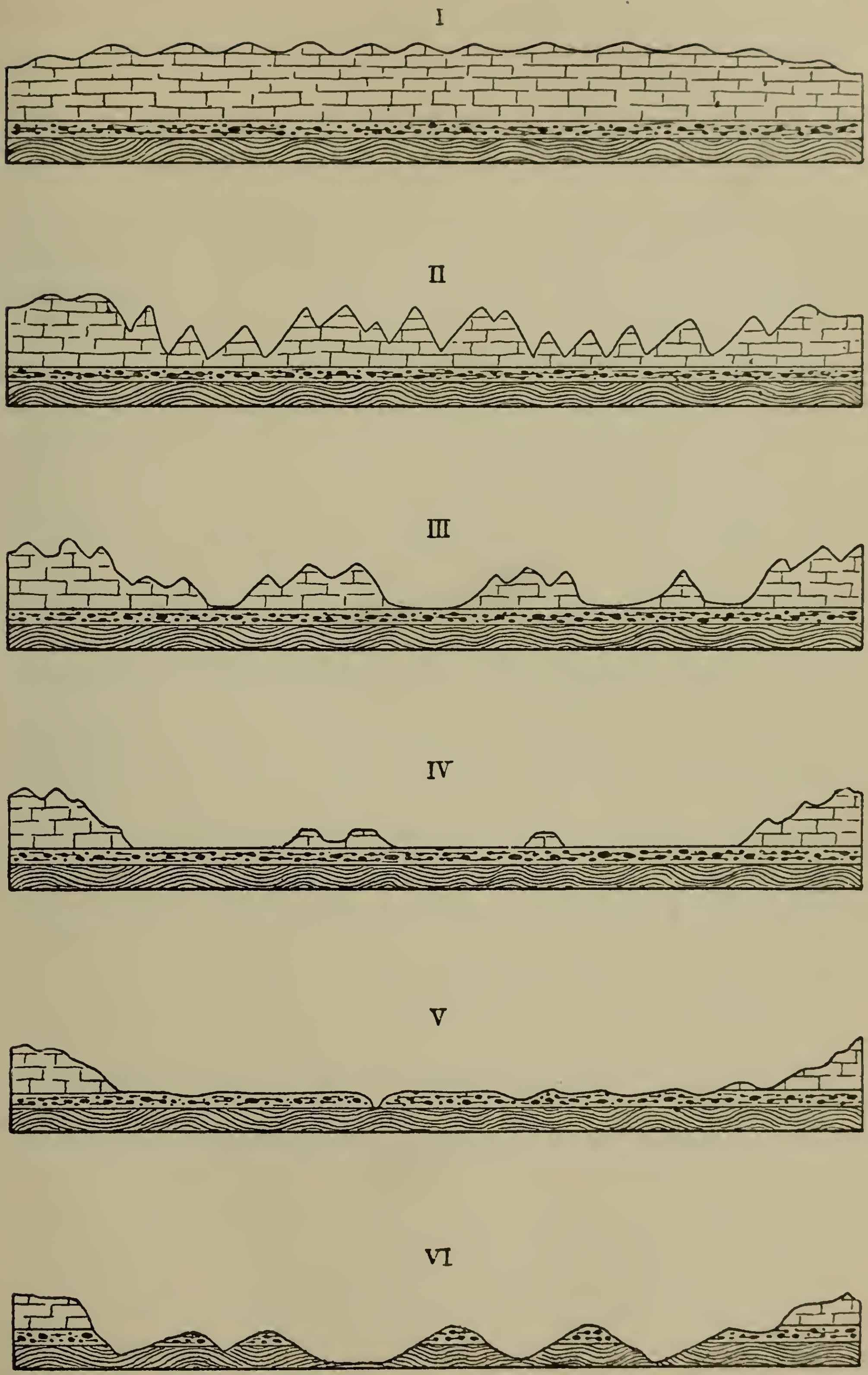


FIGURE 7. Evolution of the Cockpit Topography.

many cases these valleys have no superficial outletting drainage, while in others the barriers have been partially eroded away, and they are drained by rivers leading to the sea.

The largest of these depressions are those of St. Thomas-in-the-Vale, the great Vale of Clarendon, surrounding the Clarendon Mountains, the Hector River Basin in northern Manchester, and the Niagara River Valley along the boundary of St. Elizabeth and St. James. Montpelier Valley along Great River in Hanover, and Morgan's Gut Valley in Westmoreland, are similar basins which have had drainage gaps cut through their surrounding barriers. The latter now constitutes an interior embayment of the great plain of Savanna-la-Mar.

The valley of St. Thomas-in-the-Vale is almost circular in outline and its floor has a diameter of ten miles. Its bottom is largely covered with old alluvium. The mountainous scenery encircling this basin is beautiful beyond description. From Ewarton can be seen a band of white limestone, rising on the west side of the valley in a gentle arch, and extending for miles towards Moneague. This band has a steep face, and is crested by rugged points forming the plateau summit. The culmination of this arch is Mount Diablo, whose summit is 2,500 feet above the bottom of the basin. This valley is drained by about ten copious streams, which gather into a single arterial trunk, the Rio Cobre, by which they pass to the sea through the narrow gorge of Bog Walk Canyon. These streams have their sources in springs or caverns in lower portions of the limestone formation of the hilly perimeter near their contact with the impervious Blue Mountain Series. At one time in its history this valley had no direct outlet to the sea, but connection has been made by encroachment upon the divide by the former headwaters of the Rio Cobre, which was originally a simple marginal coastal stream, and its capture of the basin drainage.

The Clarendon Valley has been partially described in our remarks on the Clarendon Mountains. While this is of the same general type and origin as that of St. Thomas-in-the-Vale it differs from it in details of configuration, chief of which is the fact that the Clarendon Mountains rise from its centre so that the valley proper is confined to an annular area lying between these mountains and the surrounding white limestone escarpments. The Clarendon Valley is about 50 miles in length and 25 miles in width. Its longer direction corresponds with that of the axis of the plateau. The drainage, like that of St. Thomas-in-the-Vale, concentrates into an arterial trunk known as the Minho, through the canyon of which it outlets to the south coast.

The pouch-like basin of Hector River is almost connected with the northwest end of Clarendon Basin. At present the two are separated by a low drainage saddle which has no direct outlet to the sea. The stream from which the basin takes its name rises from springs at its west end, and sinks into the limestones to the east. Cave Valley in St. Ann Parish, is four miles in diameter, and is also almost connected with the Clarendon Valley, but is separated from it by a narrow limestone ridge less than a mile in width.

West of the Clarendon Basin similar circular depressions occur at short intervals, such as those at Oxford, on the boundary of the parishes of Manchester and St. Elizabeth; the great headwater amphitheatre of Black River, St. Elizabeth; the basins of Niagara River, the Mulgrave and Ipswich sinks; the Cambridge Basin; the basins at the head of Roaring River, and the King's Valley Basin near Jerusalem, the last two of which open into the Savanna-la-Mar (Plain by the Sea). Of these the Niagara, Mulgrave, and Ipswich basins have no drainage outlets.

The basins above described constitute a line of depressions along the central axis of the plateau. North of these in the high plateau region of the parishes of Trelawney and St. Ann, are many other basins. The most eastern of these, the Hampshire Valley, is about eight miles in length and averages less than two miles in width. The bottom of this basin barely reaches, if it does reach, the buried Blue Mountain structure, and has an elevation of about 400 feet. The surrounding hills rise 1,200 feet or more. To the west the Hampshire Valley is duplicated in miniature by the Basin Fontabelle. Then comes the Queen of Spain's Valley, a subcircular area five miles in diameter, whose bottom cuts down to within 370 feet of sea level. Only a low gap divides the latter from the great amphitheatre of Sunderland in St. James, which has been captured by the headwaters of the Montego River. South of this is the basin of Maroontown.

There are many other smaller and less important sinks in the western portion of the island, but those we have enumerated show the character of these widely distributed phenomena. From our descriptions it will be seen that many sinks have no outlet to the sea, although in their bottoms may be found limpid streams of water. The barriers of others, like those of Anchovy, Montpelier, Cambridge, and Chesterfield, lying along Great River, have been broken by capturing drainage, become connected with adjacent basins or coastal plains, and found outlets to the sea by the union of several streams. Others, like the Clarendon and St. Thomas valleys, were once entirely enclosed, but in later times have found narrow outlets through single gorges. Still others, like the basin of Westmoreland, have had their coastward barriers largely destroyed. In all, they are interesting features of the decay of the limestone plateau. The entire series of depressions we have described — the first incipient "hog-wallow"-like swales of the plateau, the acute cockpits, the small well shaped sinks of the Hampshire type, the great expanded basins of St. Thomas and Clarendon, and the old basins which have had their barriers partially broken away — are a series of connected phenomena, and illustrate the powerful effect of solution and erosion in producing the hilly topography of the White Limestone districts of Jamaica and the Tropics in general, and in degrading the plateau to the level of the sea. Should the island undergo no more uplift, the agency of solution alone would ultimately entirely remove the white limestones now veneering the older foundation of insoluble Blue Mountain rocks underlying them. Not only has the plateau region undergone vertical disintegration by erosion and solution, but, as will now be shown, its margins have been similarly affected.

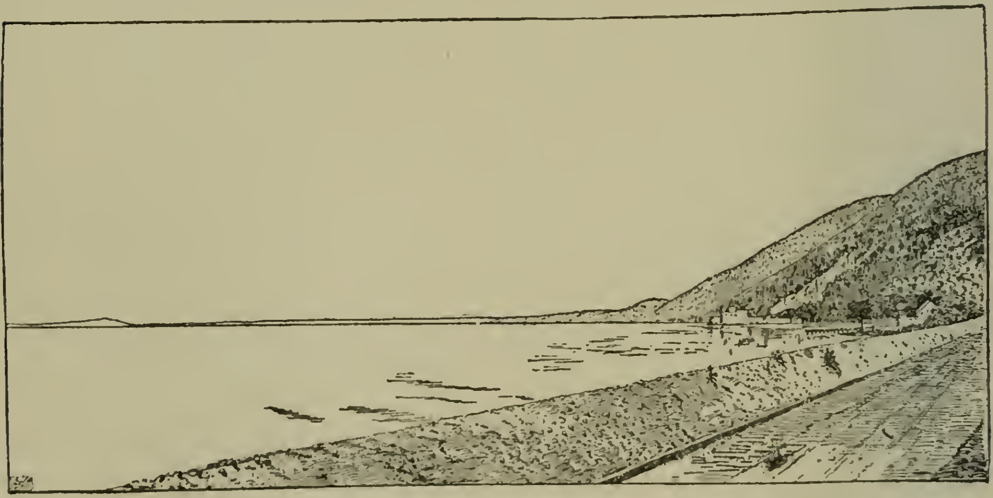


FIGURE 8. View of Back Coast Border from Rock Fort.

Topography of the Back Coast Border. — The former areal extent of Jamaica has been constricted by the horizontal planing away of its seaward margin, as shown by a further study of the back coast topography. This, as distinguished from the narrow strips of coastal plains at its foot, which will be next described, presents a steeply sloping mountainous sea front rising sharply above the sea except where cut through by transecting drainage, and its skyline has an average altitude of 1,200 feet along the north coast.

To the ordinary traveller this back coast topography is principally interesting from its scenic features. To the topographer it reveals a series of most interesting ancient terrace levels, which give important testimony concerning the history of the island. Some of these are beautifully shown on the east side of Montego Bay (see Plate XX.), where six distinct levels or benches separated by deep slopes rise above the sea in stair-like arrangement. At no other single locality are so many of these levels shown in such close juxtaposition but one or more of them can be individually distinguished at many localities entirely around the island, as well as some others as high as 2,000 feet. At a single glance these terraces in Jamaica do not present the perfection of the allied phenomena exhibited on the southeast coast of Cuba, but nevertheless, they record a similar geological history.

Naturally the integrity of these levels varies with their relative age and altitude. Those of higher altitudes are more fragmentary because degradational processes have been working upon them longer. Fragments of the lower benches are better preserved, although much broken by erosion, while none of them are as perfect in contour as the benches of the Coastal Plain. All have been cut across by rivers, etched and dissolved by rainfall, and undermined by encroachment of the waves, so that they are now often indistinct, but there are sufficient remnants in Jamaica to enable the student of geomorphology to recognize them.

Without an accurate topographic survey of the island, it is impossible to correlate correctly all the different benches or to do more than approximate their altitudes. The following general statements concerning them are based upon personal observations. The high sky line of the back coast border, as seen from the sea, in some cases represents the survival of the oldest summit topography of the plateau, and in others benches and terraces which have been successively cut out of it during intermittent periods of elevation. The highest of the old benches is John Crow Ridge, a long narrow shoulder which is seen in approaching the island from the Windward Passage; it projects seaward from the Blue Mountains and extends from back of Northeast Point near Port Antonio southeast to Holland Bay. It may be a remnant of the summit topography of the old plateau level. It is apparently a continuous horizontal plateau composed of several patches of level surface, ending to the southeast with the area known as the "Big Level." The interior or landward side of the John Crow Plateau is now separated from the Blue Mountain Ridge by the tremendous ravine of the Rio Grande. The higher summit of Yallahs Mountain on the south coast (see Plate

XIII. Fig. 2) is also apparently a remnant of the same level as the John Crow Bench, but the writer cannot positively establish this fact as he did not ascend to the summit of this hill. Probably Dolphin Head (alt. 1,800 feet) and other points of Hanover near the west end of the island are remnants of the John Crow level.

The next persistent level traceable in the back coast topography closely corresponds with the altitude of 1,500 feet. This is etched with great clearness upon the outline of the island, being noticeable as the long horizontal sky line of many of the so called mountains of which Long Mountain east of Kingston is a conspicuous type. On the south side of the island this is widely developed at many places, notably at Cambridge Hill (alt. 1,521 feet) west of the Yallahs River; Mount Salas (alt. 1,561 feet); Long Mountain, near Kingston (alt. 1,490 feet); and several localities along the coast of St. Elizabeth and Manchester, and the coast of Westmoreland at Hopeton. Another notable extent of this level is seen to the right of Porus along the railway towards Montego Bay. This general level is not visible in the north coast topography.

The next conspicuous bench has an altitude closely approximating 1,000 feet, the known altitudes ranging from 961 to 1,035 feet. This level is that of a greatly dissected plain, which dominates the summit topography of the back coast country of the north side of the island west of Port Antonio, and out of which all the lower terraces shown in the picture of Montego Bay (Plate XX.) have been cut. These summits called the "North Coast Ranges" are especially characteristic of a wide strip of country in Hanover, St. James, Trelawney, St. Ann, and St. Mary. On the south coast it is well marked, constituting the angular bench of the Yallahs Mountain profile, and a conspicuous ridge to the east towards Morant Bay as shown in Plate XIII. Fig. 2. These benches at the 2,100, 1,500, and 1,000 foot levels, are connected phenomena and represent a distinct stage of elevation in Antillean history.

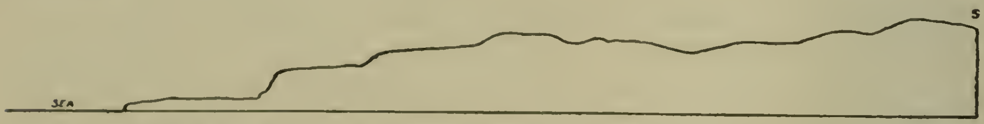


FIGURE 9. Profile, East Side of Montego Bay, showing Benches.

A lower group of bench levels occurs at altitudes of 650, 300, and 200 feet, becoming more distinct and persistent with decreasing altitude. The terraces of the Montego profile shown in Figure 9 mostly belong to the lower group of levels. On the south coast the 650 feet level may be seen in the Yallahs topography, the summit of Round Mountain, at Vere, and the Healthshire Hills west of Port Royal entrance. The 300 foot bench, or Bowden level, is very conspicuous around the east end of the island from Yallahs Mountain on the south to Port Antonio on the north, as well as on the west coast of the north side, at Cinnamon Hill and elsewhere in St. Ann, Trelawney, and St. James.

The back coast benches enumerated have all been cut out of the land by gradational processes (base levelling and marine erosion) and represent pausation stages in two long continued periods of elevation. Those between 700 and 2,000 feet were carved out of the white limestone matrix during the first period of emergence from the sea. The benches, from 100 to 700 feet in altitude are also cut out of the old limestone matrix, but were probably made during a second period of emergence and erosion following a period of subsidence as is explained later on.

This abrupt ending of the land, considered in connection with its accompanying terraces, the arch of the summit region, and the narrow submerged platform around the island, strongly suggests, as outlined in the geologic chapters of this paper, that the Limestone Plateau was once more extensive land, which, after its first elevation, underwent marginal erosion, drowning of its coastal plains by partial subsidence, and re-elevation into its present outline.

From the data given in the geologic portion of this paper, the time of these events was between the beginning of the Miocene (late Oligocene) and Pliocene time. There is much evidence that old gradational terraces of this type continue lower down upon the submerged slopes of the island, and that the phenomena of the Coastal Plain, next to be described, represent veneerings of organic, littoral, and terrigenous deposits upon old erosion planes of this character.

Benches of the Coast Plains. — A narrow strip of low land extends more or less interruptedly around the island, between the sea and the back coast border. In some places this is an old beach only a few feet wide; in others it has greater width and indents the back coast border for miles. This coastal strip is composite in character, being of three types of formations, such as elevated reef rock, marginal sea débris, and land derived alluvium. It presents distinct features of relief, including several benches of different height and origin, and a long and gentle slope known as the Liguanea Plain. The basements of these benches are old erosion levels which were submerged, covered with a veneering of constructional material, and re-elevated into land.

The highest of the benches composed of sea sediments are from 100 to 150 feet. These are well exposed around the east point of the island and along the north coast, where they occur in more or less disconnected patches. The bench at Manchioneal, shown on Plate XVII., is typical of this class. This is a well defined but narrow shoulder projecting from the higher back coast topography, with a vertical sea bluff. At Port Antonio this level is shown at the end of the long peninsula known as Folly Point, upon which the Boston Fruit Company's hotel is situated (Figure 11) as well as in the flat summit of Navy Island, lying a short

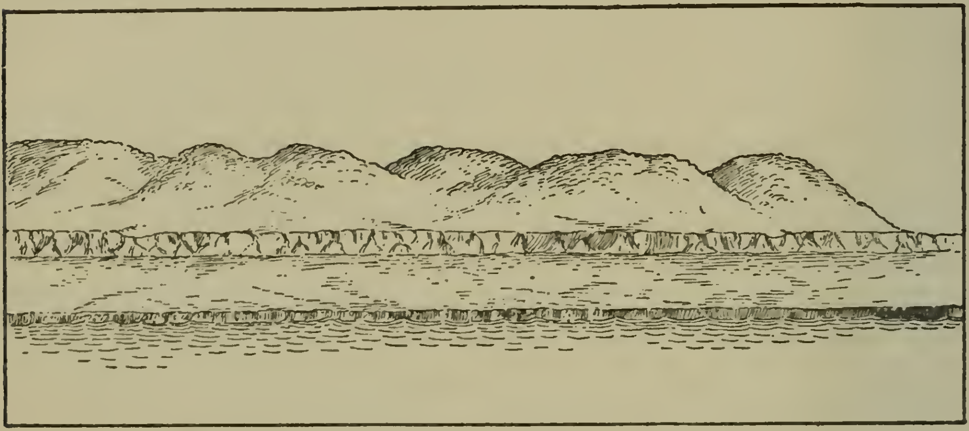


Figure 10. Benches of the Coastal Plain, St. James.

Figure 11. Folly Point, Port Antonio, showing Coast Benches.

distance to the west thereof. At Port Maria the same plain is visible both on the mainland and on Cabaretta Island, shown in Plate XIII. Fig. 1, which has been but lately severed from it. This level is largely, if not entirely, composed of the old Pliocene marginal sediments of the sea which have been raised to their present position by epeirogenic uplift.

Figure 12. Elevated Reefs, North Coast.

The Elevated Reef Levels. — These are more fully described in a later chapter.[1] They are three in number, approximating 15, 25, and 60 feet above the sea, respectively. Only the lowest of these has any considerable extent. These benches are usually composed of single strata, nowhere over 50 feet in thickness, made up of coral heads *in situ* and interstitial débris of the reefs, as they originally grew in the water, upon shallow submerged benches or marginal platforms, similar to those upon which they are now growing around the island, and which have since been brought into their present position by elevation of the island.

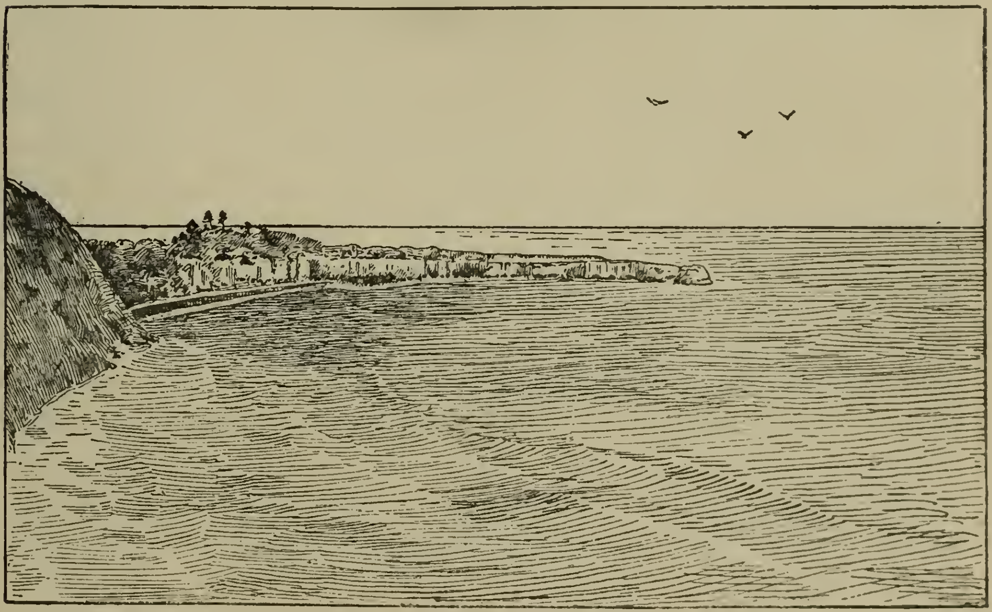


Figure 13. Elevated Reefs, Northeast Point.

[1] These are more fully discussed in the geologic portion of this paper.

The lowest reef constitutes a narrow rugose plain with a precipitous undermining bluff at its seaward margin, as shown in Figure 13, and occurs intermittently entirely around the island tipping the marginal points as seen upon the geological map. The surface is weathered into coarse, cavernous karrenfelder, the so called soborruco.

The lowest marginal plain next to the sea to which this reef belongs is a narrow strip of country seldom exceeding a half mile in width, and occurs nearly everywhere between the water's edge and the back coast bluffs. It is not everywhere composed of reef rock, however. In places it is calcareous sand and marl, which in some instances represent old littoral deposits and in others the débris which may have filled narrow lagoons between the fringing reefs and the coast, and which have been synchronously elevated with the reefs.

Coast Plains of the Liguanea Type. — The coastal plains and slopes covered with alluvium are of a peculiar type, and represent old plains of erosion; they include ancient bights eroded out of the plateau margin, and covered during long epochs of time by gravel and other aggradational land material. The deposits are composite in age, being contemporaneous in some stages of their history with the events of all three of the terrace-making epochs. All plains of this character are not horizontal, but have considerable slope from their interior margins towards the sea, and at least, in the case of Liguanea, much of the aggradational deposits were probably laid down as talus fans. These plains comprise extensive areas indenting the back coast topography, especially on the south side of the island, which is indented by them at eight places. In the eastern portion the plains, like those at the mouth of the Plantain Garden, the Negro, and the Yallahs Rivers, are more elongated and narrow than to the west, where as a rule they are much broader than they are long.

The most extensive of these phenomena is the Plain of Liguanea upon which Kingston is situated (see Figure 8). This is over twenty-five miles in length and averaging six miles in width. This is greatest near its western end in the district of Vere, Parish of Clarendon, where it is about fifteen miles. In all, it includes about 200 square miles. In general, the plain has the outline of a parallelogram, extending in an east and west direction from Hope River and Long Mountain through the parishes of St. Andrew and St. Catherine, to Clarendon Gully, some two miles west of Old Harbor. Its eastern and western thirds border the coast, but its central third, south of Spanish Town, is separated from the sea in two places; at one by the Portland Ridge of Clarendon, which constitutes the southern peninsula of the island, and at another by the extensive outliers of the Limestone Plateau known as the Healthshire and Port Henderson Hills, opposite the Naval Station of Port Royal. The latter are conspicuous features to the west as one enters Kingston Harbor. The Braziletto Hills of Clarendon extend into this plain, almost separating it into eastern and western divisions. The term Liguanea is restricted in local usage to that portion of the plain lying east of this prolongation. The interior margin of the plain terminates against the steep white limestone topography, except just north of Kingston, where it abuts against the Blue Mountain ridges proper. This interior margin is over 800 feet high near Constant Springs, whence it slopes rapidly to the sea at Kingston, six and a half miles distant.

In comparison with regions underlain by other formations, the physical aspect of this plain is arid and sterile. The flora, including thorny acacias and cactus, tends towards the chapparal type so characteristic of the Rio Grande Plain of Mexico and Texas, and presents a striking contrast to the deciduous tropical flora of the remainder of the island. To the west the next extensive plain of this character, known as the Pedro Plain in St. Elizabeth, indents the land to the east and north of Black River Bay. Its estimated area is over 100 square miles. This is analogous to the Plain of Liguanea, except that it contains much marshy ground, and the gravel formation is accompanied by marls. Back of Savanna-la-Mar there is another extensive plain of this type, which continues inward nearly one half the distance across the island. This is cut entirely out of the limestone hills, and, inasmuch as there is little gravel in the back country, the formation is of a marly nature. This plain is fully 100 square miles in area. On the west it is almost connected by a narrow arm with the marshes which border the western coast of the island. Plains of this character are singularly absent from the north side except at Montego Bay adjacent to the mouth of Montego River, where they are more feebly developed than on the south coast.

The history of the Liguanea type of Plains is a record of four distinct events: (1) the original cutting out of the topographic matrix during an antecedent period of base levelling; (2) the filling in of the débris which composes the present surface material of the plains; (3) the elevation of the plains into their present position above the sea; and (4) the cutting of the modern streamways across them. The surface formation of these plains is clearly deposited in pre-eroded valleys carved out of the White Limestone Plateau in preceding erosion epochs which took place during the rapid elevation of the island in Middle Tertiary time. It is evident that during subsequent epochs of subsidence these valleys were drowned and filled with alluvium from the bocas of the rivers which then debouched at their interior margins, and have cut lower streamways through them since the later periods of slight uplift which produced the reef levels.

The frequent occurrence of these plains on the south side and their scanty development on the north side of the island gives rise to a series of inquiries concerning the geographic extent of the island at the time of their formation. It might at first appear that a more extensive land area existed to the northward than at present, but on closer examination this hypothesis is untenable. The greater development of these old valleys on the south is due to the fact that the east and west axis of highest elevation lies nearer the north coast than the south, and the principal slope has long been in the latter direction. An intimate topographic relation exists between the aggradational plains of the coast and the large central basin valleys, and they present synchronous and parallel stages of development. In later times the two have been united in several places by headwater erosion, as shown in our discussion of the basins.

Drainage. — The drainage of Jamaica is peculiar, that of the Blue Mountain districts being frequent and constant in occurrence and copious in run-off, while in the region of the Limestone Plateau it is superficially somewhat deficient in streams which are largely of an underground nature. As a whole, the island presents two major types of streams, one of simple autogenous rivers flowing to either coast, and the other of the streams of the interior basins which have no outlet to the sea; a third and more complicated type of drainage, a combination of the two preceding, has been produced in certain instances by the capture of the second by the first type.

The rivers of the eastern third of the island divert to either ocean from the Blue Mountain Ridge. This drainage is mostly normal to the coast, with the exception of the Rio Grande of the north side, the Negro River of the south side, Plantain Garden River of the east coast, and Yallahs River; these are probably the most ancient members of the system, and flow for a large portion of their distances in directions subparallel to the main trend of the Blue Mountain axis, that is, in northwest and southeast directions. The streams of this region are marked by deep V-shaped canyons in their upper courses and great deposits of ancient alluvium in their lower parts. The run-off is constant, but variable in quantity owing to torrents. The wide alluvial filled valleys of the Liguanea type, through which the lower portions of the streams now cross to the sea, indicate the following episodes of history:— The bights occupied by the plains were once headwater amphitheatres from which the streams flowed out across a wider coastal border than the present. This extended margin was subsequently drowned by subsidence, so that the original headwater amphitheatres became estuaries indenting the coast into which the streams then debouched. Finally, elevation extended the headwaters of the streams, partially reclaimed the Coastal Plain, and revived the old lower channels or established newer courses across them to the sea.

The drainage of the White Limestone Plateau of the western two thirds of the island is both superficial and underground. The former includes the older and longer streams, such as the Cobre, Milk River, Black River (St. Elizabeth), Island River, and New Savanna River of the south coast; Orange River, Island River, Lucea River, Great River, Montego River, and Roaring River of the north coast, which in general present the same history as the streams of the Blue Mountain Ridge. These are ancient streams, which once brought down immense alluvial deposits now forming the material of the Coastal Plains, through which, since the slight elevation of the latter, they have cut newer direct channels to the sea. Others of this class consist of the short, simple, autogenous streams, probably of later origin, which drain from the bluffs of the back coast border, and are especially well shown along the north coast of St. Ann.

A third and entirely different type of streams, found only in the basins of the Limestone Plateau summit region, include the short local streams which rise from springs or caverns near the contact of the White Limestone and Blue Mountain Series. These flow for short distances, then disappear into the ground without having any visible outlet to the sea. Of this type of rivers are the Minho and Rio Hoe near Moneague; Great River in the southeast corner of St. Ann; Pedro River, which sinks at the corner of St. Ann, Clarendon, and St. Catherine; Yankee and Cave Rivers, which unite and disappear into a sink on the border of St. Ann and Clarendon (the latter river is ten miles long); Hector's River, forming the boundary of Manchester, Trelawney, (about as long as the last stream,) sinking at the northeast corner of St. Elizabeth; Hicks River in Trelawney; Pine and Dry Rivers in the northern part of St. Elizabeth; Niagara, Chester, and Tangle Rivers in the southern part of St. James; Cutting-Grass-Spots and Dean's Rivers, Westmoreland; and Content River in Hanover. It is supposed that the waters of these streams, after sinking into the ground, in some instances find underground connection along the contact of the Blue Mountain and White Limestone Series and into the coastal streams. In many cases the headwaters of the marginal streams have captured the drainage of the great interior basin valleys, especially the Minho, Cobre, Montego, Black River, and Great River. This is shown by the fact that the middle portion of these streams, where they cut the White Limestone Ridge between the plains and the central valleys, have newly formed V-shaped canyons containing no alluvial material such as occurs in the interior valleys which they drain and the lower Coastal Plains through which they flow. The topography of Bog Walk Canyon, shown on Plate X., illustrates the character of the more newly made, intermediate, connective portions of this compound type of streams.

Without details of the geologic structure, it is evident from this topographic review that the present land features of Jamaica are of complex origin, and record many past events of uplift and subsidence which have produced different phases of configuration and outline at different epochs of its history.

Summarized, this history involves: —

(1) Two periods of mountain making (including the elevation of the plateau in this category) accompanied by greater expansion of the island than its present area. The first of these has prevalent north of west trends; those of the second are east and west. The profiles of the former are angular, of the latter gently arched.

(2) Two great epochs of subsidence and contraction of the land, alternating with periods of elevation.

(3) Later uniform elevation which added the narrow modern coastal phenomena.

Finally, we may add that the configuration of Jamaica does not cease at sea level, but there is every evidence that the visible portion of the island is only the tip of a more extensive foundation below the level of the sea, which, especially to the south and east, presents terraced features somewhat similar to those of the exposed coast borders, and which indicate that once the island was slightly more extensive than at present.

PART II.

Geological Structure and Sequence.

The geologic formations of Jamaica belong to four great categories, as follows: —

1. A fundamental series of stratified shales and conglomerates (of terrigenous origin), tuffs and other débris of volcanic material (whose source is not apparent) and, rarely, marine limestones and marls, — all of which have suffered great displacement and deformation. This series characterizes the higher mountains and forms the nucleus of the island structure upon or around which all subsequent formations have accumulated.

2. A series of organically derived oceanic material — marls and limestones — which rest unconformably against and upon but do not completely overlap the more elevated outcrops of the first mentioned series. It constitutes piedmontal formations of great thickness around bases of the higher mountain summits.

3. Laccoliths, dikes, and sills of igneous rocks, which penetrate the first series and the lower portion of the second, and are, therefore, of later age than both.

4. Certain deposits of alluvium, oceanic marls, and coral reef rock, which are adjacent to the present coasts and represent fringing reefs and other accretions around the island's border after it had almost attained its present area and outline.

These four series of rocks are uncomformable to one another, and are the products of the greater events in the geologic history of the island. Together with the formations composing them, they are tabulated on the following page.

The Blue Mountain Series.

This series comprises the oldest rocks of the island. It consists of loose or slightly indurated beds of gravel, clay, boulders, and tuffs, with exceptional beds or bosses of hard indurated limestones and yellow clay. The rocks are usually of dark color (black, blue, or dull chocolate), in strong contrast to the glaringly light colors which characterize the succeeding formations of the Oceanic and Coastal Series. The material, with the exception of occasional limestone beds and a few outcrops of clay marls, can be traced to igneous rocks; it was first volcanic ejecta and subsequently and successively underwent various degrees of attrition

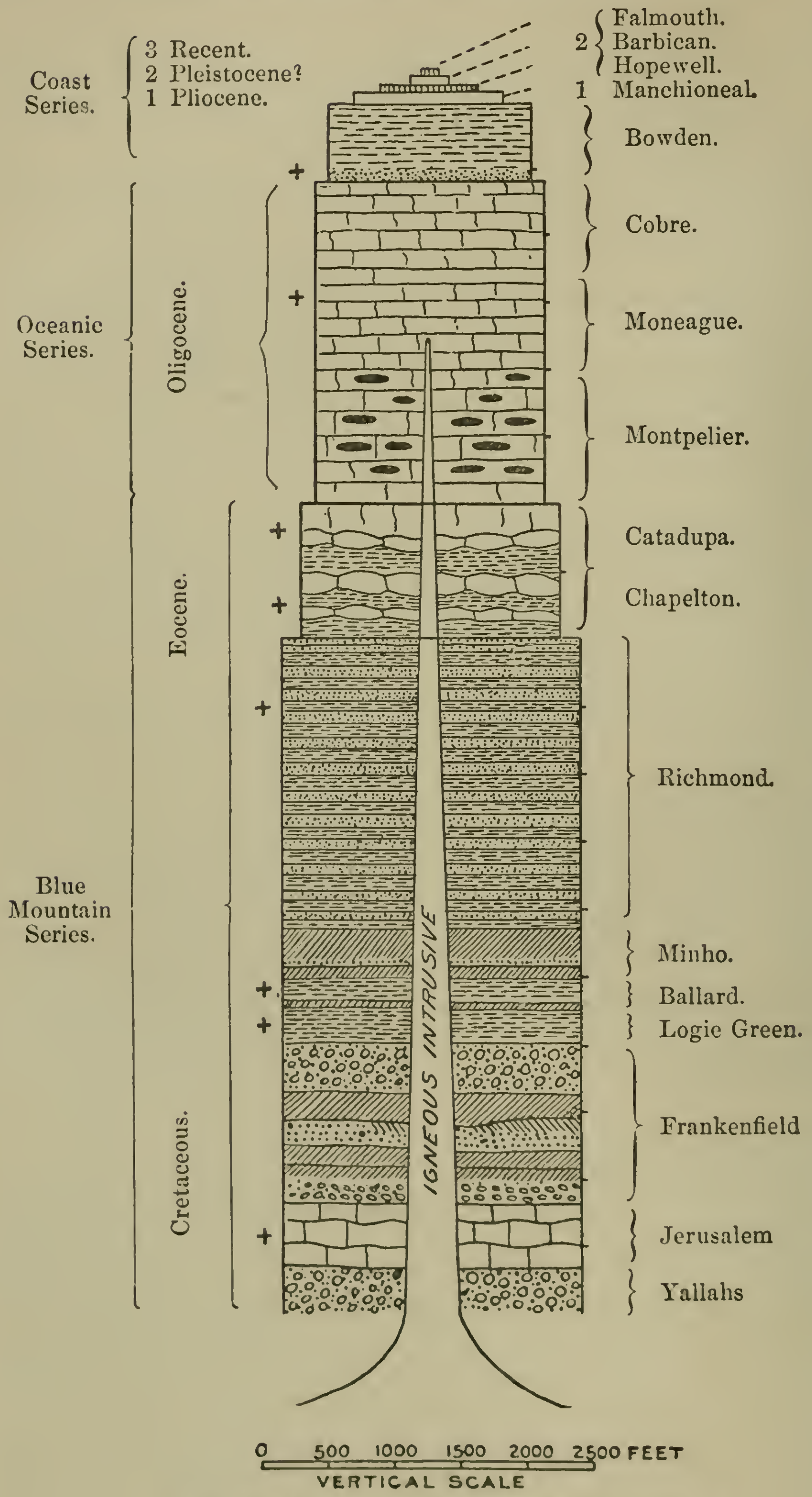


Figure 14. Sequence of Geological Formations.
+ + Fossiliferous Beds.

and sedimentation from coarse boulders and tuffs to finely triturated impure clay shale, — a process indicating extensive working over. These rocks are the material of the Central Mountains, composing the eminences above 3,000 feet, such as the Blue Mountain Ridge. They undoubtedly underlie the surface rocks of the rest of the island as occasionally revealed by erosion through the white limestone which veneers them, as seen in some of the central basin valleys, the canyons of the marginal streams, and certain bluffs of the back coast border along the northwest coast.

Nowhere on the island can all the beds of the series be seen in continuous exposure. As has been noted[1] concerning the rocks of the Blue Mountain district, "the strata are so excessively disturbed, so traversed and semi-metamorphosed by dikes of syenite and mixed up with porphyritic masses, that it is impossible to observe the intricacies of the stratification or to determine the sequence of the beds *inter se* without a lengthened and detailed investigation." Sufficient is known to state that it probably exceeds 5,000 feet.

Previous attempts to classify the rocks which are collectively arranged in this series have been confusing and unsatisfactory. De la Beche,[2] who first described them in 1828, referred them as follows: "Submedial or Transition Rocks" (Cambrian), "Submedial or Transition Limestone" (Cambrian), Medial or Carboniferous Rocks," and the "Supermedial or Secondary Rocks." The members of the later official survey showed that De la Beche's age determinations were erroneous, and the rocks were of Cretaceous and Eocene age. These writers gave no satisfactory statement of the subdivisions, which were described in a conflicting manner,[3] chiefly as the "Metamorphosed Series," "Black Shale,"

---

[1] Wall and Duncan, Quart. Jour. Geol. Soc. London, Vol. XXI., 1865.

[2] Mem. Trans. Geol. Soc. London, No. 36, 1826, pp. 151–169.

[3] The following names, many of them no doubt synonyms, are used in the Jamaican Report for beds included in our Blue Mountain Series: —

Lower Tertiary or Conglomerate Series; the Trappean Series; sandstone and gravel; upper sandstone clays and shales; black shale; Carbonaceous shales; sandstone formation; conglomerate.

Upper conglomerate; upper conglomerate series; lower conglomerate, etc.

Purple shale and conglomerate; purple shale and conglomerate formation.

Cretaceous group; Cretaceous limestone; Cretaceous series; Cretaceous and Hippurite limestone.

Metamorphosed Series; Metamorphosed or altered rocks; Metamorphosed Series and igneous dikes; Metamorphosed conglomerate; Altered stratified and igneous rocks; Altered Stratified Series.

Igneous formation; igneous rocks; porphyritic dikes, granite rocks, syenite, granite, and syenite of Tertiary age.

"Trappean Series," "Cretaceous Limestone," and "Yellow Limestone" (as used for the western parishes).

While it is still impossible completely to differentiate all the beds of the Blue Mountain Series, our observations have enabled us to make a more accurate classification of them than any hitherto presented, which may be stated as follows: —

Blue Mountain Series	Upper Division (Eocene)	Richmond Beds.	
	Lower Division (Upper Cretaceous)	Minho	Beds.
		Ballard	"
		Logie Green	"
		Frankenfield	"
		Jerusalem	"
		Yallahs	"

The Basement Beds. — The chief difficulty of classification is the complex folding and partial concealment which make it impossible to determine the exact base of the series. The Jamaican Reports present conflicting conclusions on this subject, inconsistently stating in different places that the base of the section is composed of igneous rocks, Cretaceous limestones, and a formation termed the "Metamorphosed Series."

From the tabulations, especially that given on the last page of the Reports, one infers that its authors believed the base of the Jamaican section was crystalline and overlain by the so called "Metamorphosed Series" beneath the limestones with Cretaceous fossils, but a careful perusal of the Reports does not justify this interpretation. In numerous places throughout the text of the work the intrusive nature of the igneous rocks into the beds of the Blue Mountain Series is noted, as further recorded in the portion of our report treating of the igneous rocks. Sawkins[1] expresses doubt as to the propriety of drawing a distinction between the Cretaceous and the so called "Metamorphosed Series," and clearly states that the latter "comprises strata of the Cretaceous and conglomerate formations which have experienced a change of structure due to the intrusion of igneous rocks."[2] In view of this fact, as verified by our own observations, the so called "Metamorphosed Series," as a structural formation, may be dismissed from consideration.

There may be doubt as to whether the oldest rocks are Cretaceous limestone, which Etheridge asserts[3] "is clearly at the base of the series,"

---

[1] Jamaican Reports, p. 55.

[2] Ibid., p. 47.

[3] Ibid., p. 308.

or "made up of conglomerates" as he states in another place.[1] Duncan and Wall,[2] whose opinions were based on the field observations of Wall, state that "It is difficult or impossible to determine the relation of the conglomerate and Cretaceous groups. This is especially the case in the highly mountainous eastern parts of Jamaica, where traces of almost obliterated Hippurites [Rudistes] and other fossils are detected in strata which from their confined position could not otherwise be classified stratigraphically." They state that in Clarendon, however, "the lowest members of the Cretaceous Series frequently consist of a thin bed of conglomerate formed of the harder material of the porphyries."

Barrett said[3] that it is "evident that the igneous rocks forming the base of this series, and interstratified with some of the shales and conglomerates, were erupted prior to the deposition of the Cretaceous limestone, and at intervals of time sufficient for the formation of aqueous interbedded strata."

The writer in his own investigations and in the literature of the island has found no proofs that the base of the section is limestone. The limestones of the Bath and Clarendon sections are clearly intercalations in vast beds of igneous débris. The limestones are certainly the oldest rocks paleontologically identifiable, but from the data to be given the writer believes the fossiliferous Cretaceous beds are local occurrences in the great and tangled series of tuffs and conglomerates, the latter of which constitute the visible base of the section. These are detrital formations of volcanic débris of unknown origin. The writer searched the exposures with particular care, but in vain, for evidence of some older or lower lying rocks beneath the classic formations of the Blue Mountain Series such as are reported in Cuba and Haiti, or a trace of ancient massifs or volcanic vents from which the detrital igneous rocks were derived.

The Clarendon Section. — The best partial section of the lower division of the series is in the parish of Clarendon, along the St. Thomas and Minho Rivers, where all the beds, not including the lowest and highest of the series, are exposed in a less disturbed condition than elsewhere. This parish was considered by Sawkins[4] and Wall and Duncan[5] to afford the most complete exposition of the relationship of the older

---

[1] Jamaican Reports, p. 307.

[2] Quart. Jour. Geol. Soc. London, 1865, Vol. XXI. p. 3.

[3] Quart. Jour. Geol. Soc. London, 1860, Vol. XVI. pp. 324–326.

[4] Jamaican Reports, p. 25.

[5] Quart. Jour. Geol. Soc. London, Vol. XXI. p. 4.

beds to be found in Jamaica. In order to verify these previous observations, the writer reviewed this section *de novo* and made the following record, which adds many new data. This section also shows the mode of occurrence of the fossiliferous Cretaceous rocks. Many of the Rudistes recently described by Whitfield came from this section.[1]

Clarendon Section, Rio Minho, Clarendon Parish.

14. Cambridge Beds, Chapelton Formation. — Yellow Marls and limestones (further described under the head of Cambridge beds) with Eocene fossils. Exposed between the town of Clarendon and St. Thomas River . . . . +500 ft.

13. Unconformity. Richmond Beds wanting.

12. Minho Beds. — Volcanic tuffs and breccias, composed of igneous pebble (hornblende-andesites) cemented by a fine-grained matrix. Groundmass ashen or dark green in color. Exposed in the banks of St. Thomas River west of the ford and the divide between the St. Thomas and Minho, and between Mile Posts 38 and 39. Estimated thickness . . . . +300 ft.

11. Impure granular semi-consolidated material of dark red color, with same pebble as above. This is largely an andesite tuff showing many particles of hornblende. This constitutes the faces of many fine bluffs between Mile Posts 39 and 40. Its base in contact with the foregoing is well shown at the crossing of the Minho. Estimated thickness . . . . +300 ft.

10. Stratified conglomerate of igneous pebble in red matrix becoming black downward.

9. Massive tuff or igneous rock . . . . 200 ft.

8. Chocolate-red colored breccia . . . . ± 50 ft.

7. Stratified (tuff?) conglomerate rounded black igneous pebble in indurated mass.

6. Ballard Clays. — Black, bituminous, laminated clays, sienna colored above, resembling in color the Richmond beds, with occasional yellow calcareous interbedded layers, containing small colonies of Rudistes. This is finely exposed between Mile Posts 40 and 41, the descent of Ballard Hill towards Ballard River, where over 150 feet are seen . . . . ±200 ft.

5. Tuffs.

---

[1] Bull. Am. Mus. Nat. Hist., Vol. IX., Article XII., New York, 1897, pp. 185–196.

4. Logie Green Beds. — Yellow clays, similar to those at Pennant's Great House on the St. Thomas, containing fossil Rudistes. Exposed at base of above section. Thickness of these clays indeterminate. They are exposed intermittently as far as Trout Hall, and Mile Post 44 . . . . +100 ft.

3. Frankenfield Beds. — Beds twenty feet in thickness of large igneous cobble stone of hornblende-andesite embedded in an ashen gray matrix of tuff, grading down into, or possibly unconformable upon, a great thickness of tuff without conspicuous pebbles. This formation is exposed in superb cuts on both sides of Frankenfield between Mile Posts 44–49. Towards Logie Green there are boulders of porphyry, becoming smaller above. These beds may be from 500 to 1,000 feet thick. Three hundred feet are exposed in the high hills back of Trout Hall . . . . +500 ft.

2. Limestone Beds. — Great masses of hard blue-white limestone over 20 feet thick, with gigantic Rudistes, Actæonella, and corals. Apparently bosses in the igneous conglomerate and tuffs.

1. Yallahs Formation. — Conglomerate of porphyritic boulders. Base concealed. This is the bottom of the section of the Blue Mountain Series, as seen in Clarendon Parish.

All the beds of the foregoing section have a very strong south dip of ±30° beneath the white limestones on the south of the Clarendon basin.

This section does not agree with that given by Duncan and Wall, as previously cited, in which the divide of the St. Thomas and Minho (Long Ridge) is represented as a hill of massive igneous rock protruding through and disturbing the sedimentaries. On the contrary, this hill is composed of stratified tuff.

The Clarendon section, although the best exposed on the island, does not represent the Blue Mountain Series in its entirety, nor are its facies everywhere uniform or continuous. Rocks similar to these compose the material of all the higher mountains of the eastern half of the island, but there they occur in such a disturbed condition that the members cannot be easily differentiated. A greater thickness of the lower conglomerates is exposed in the Blue Mountain districts. The hiatus in the Clarendon section between the top of the Minho beds and the Cambridge is elsewhere represented by the formation to be described as the Richmond beds as best seen on the north side of the island. Collectively the beds of the Clarendon section constitute the lower subdivision of the Blue Mountain Series, and with all its variations is quite different from the Richmond beds of the upper division.

In general, the Minho beds correspond in character with the "Trappean Series and Purple Shales and Conglomerate Formation" of the Jamaican Reports, occurring extensively from Clarendon eastward to Bath in St. Thomas, and notably near Gordontown, back of Kingston, in the ribbed salients (cuchillas) of Newcastle, and in Metcalfe. These beds are marked by great abundance of gravel and tuffs and purplish colors. They are placed in our section below the black shales and conglomerates of the Richmond beds, not above, as in the final tabulation of the Jamaican Reports.

The Fossiliferous Beds of the Lower Division of the Blue Mountain Series. — The massive limestones occur lower in the series in more or less isolated and widely separated outcrops, nowhere of great thickness, and characterized by the Rudistean fossils.

The Jamaican Reports treat of the fossiliferous Cretaceous beds included in the series as a single formation. It was described [1] as composed of two varieties of strata constituting an upper and lower part. The former was said to consist of marls and sands with corals and many Hippurites, the latter of compact massive limestones with many Radiolites and Barrettia. These statements are misleading. It is true that the oldest fossiliferous Cretaceous rocks exposed are limestones, and that the marly beds with Cretaceous fossils, of which there are several horizons instead of one, occur higher than the limestones; but these beds are merely incidents in the great series of volcanic tuffs and conglomerates with which they are interbedded, as is seen in the details of the Clarendon section. No. 2 of the Clarendon section with Cretaceous fossils is the lowest limestone. These are overlain by the Frankenfield tuffs. Above the latter appear fossiliferous beds of the Logie Green,[2] and Ballard clays which in turn are covered by the Minho tuffs.

The Cretaceous limestones are found in several other places on the island. Sometimes a limited mass occurs in a manner to create doubt as to whether it is a bed, a local lens, or a great transported boulder;

---

[1] Jamaican Reports, p. 26.

[2] Local beds of yellow marl and impure segregated limestone are also exposed near Trout Hall on the Minho, and at Pennant's Great House on the St. Thomas, and consist of a considerable thickness of the unctuous yellow clays and segregated limestone lumps with numerous specimens of smaller Rudistes (including many of the species described by Whitfield) and corals.

again, as in the canyon of Plantain Garden River in Portland, where the Cretaceous rocks of Jamaica were first noted by Barrett,[1] a single stratum of limestone is interbedded between overlying and underlying tuffs, conglomerates, and clays. Sawkins noted in southwest Portland "thin beds of Cretaceous limestone, interstratified with thick porphyritic breccias and conglomerates, enclosing contemporaneous trap rocks."[2]

The writer tried to visit all the localities mentioned, three of which, Clarendon, Jerusalem Mountain, Westmoreland Parish, and Bath, in St. Thomas, may be taken as typical. These are in the central, western, and eastern portion of the island respectively.[1]

Jerusalem Mountain Section. — In at least one locality Cretaceous limestones occur in extensive beds. This is near the extreme west end of the island at Jerusalem Mountain in the parish of Westmoreland. This was probably sufficiently remote from the centres of igneous activity to permit undisturbed oceanic conditions and continuous growth of life. Jerusalem Mountain is a low, isolated hill standing 570 feet above the sea and about 500 feet above the surrounding valley plains. It is composed entirely of Cretaceous limestones and dull yellow clays, except at its eastern base, where the Tertiary limestones rest unconformably against it, probably by faulting. The rocks dip slightly to the east. Here we made the following section: —

Later Formations at Foot of the Hill.

		Feet.
IV.	Yellow shale resembling Richmond beds, with beds of limestone; weathers into purple colors	25
III.	Minho Beds. Purple clays and blotched shales dipping east	60
II.	"White limestone" in bluish shale, fossils Tertiary?	50
I.	Level of valley plain of Mount Eagle. Alluvium	60

Section of the Hill.

VI. 14.	Summit of brown marls with Alectryonate oyster in thin limestone slabs, Pholadomya, etc.	25
V. 13.	Yellowish limestone with small fossils	15
12.	Red purple clay	10
11.	Dimension layers one foot thick, of impure limestone with Alectryonate oyster	10
10.	Yellow marl	22
9.	White fossiliferous limestone, Caprinella	20

---

[1] Quart. Jour. Geol. Soc. London, Vol. XVI. pp. 324–326.

[2] Jamaican Reports, p. 74.

		Feet.
8.	White limestone with Actæonella	40
7.	White limestone slightly yellowish	25
6.	Yellow marl alternating with limestone	50
5.	Purple shale in yellow limestone and marl	15
4.	Red "Trappean" conglomerate	6
3.	Yellow marls with limestone lumps and gigantic Caprinas	29
2.	Three feet layer of limestone with giant Caprinas	67
1.	Yellow clays and limestones	23

Nos. I., II., III., and IV. of the foregoing sections are undoubtedly of later age than V., and owe their present lower topographic position to faulting or later unconformable deposition. It is interesting to note that the gigantic species of Rudistes occurs at the base of this section in bed V. 2, — a low position apparently persistently maintained throughout the island.

It is unfortunate that here the relations of the fossiliferous formations to the other beds of the Blue Mountain Series are concealed.

It might be supposed that the yellow clays at the top of the Jerusalem section represent the horizon of similar material elsewhere widely separated from the lower limestones by vast beds of tuffs and igneous conglomerates. The paleontologic data do not demonstrate this conclusion, the fossils of the Jerusalem clay beds (Pholadomya and Ostræa) not being found at other localities, nor are some of the smaller species of Rudistes of probably higher horizons found here. Outcrops of "Cretaceous limestone" 500 feet thick in St. Thomas-in-the-Vale,[1] and 300 feet thick in Port Royal,[2] are also recorded, but the writer has not seen them.

It is barely possible that a locality in Portland, mentioned by Barrett,[3] may represent the upper clay horizon. This was described as "a sandstone conformable with a thick bed of clay containing Hamites, Baculites, Trigonia, and Pholadomya." This reference is the only mention of the first three fossils from Jamaica.

Near Bath, at the eastern end of the island, Cretaceous limestones are exposed in the elevated structure near the southern base of the mountains. This is the locality from which the Cretaceous of Jamaica was first described by Barrett, who published a figure of the section.[4] The principal formation of this vicinity is the Minho beds (Trappean of

---

[1] The Cretaceous of St. James, as described by Sawkins (Jamaican Reports, p. 245) is the Cambridge formation of this paper.

[2] Jamaican Reports, p. 138.

[3] Ibid., p. 92.

[4] Ibid., p. 77.

Sawkins), here composed of volcanic tuff with conchoidal fracture and weathering into rusty red clays, metamorphosed shale, and occasional pieces of contained impure limestone. About a mile up the Plantain Garden River the stream has a steep V-shaped canyon surrounded by hills. A new highway which is being constructed shows fine cuts of the prevalent Minho formation. In this we found exposures of hard strata of Cretaceous limestone, aggregating several feet in thickness, but the vegetation was so thick that the latter fact could not be determined positively.

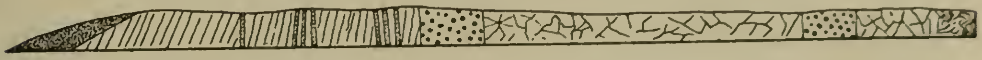


FIGURE 15. Barrett's Section, near Bath.

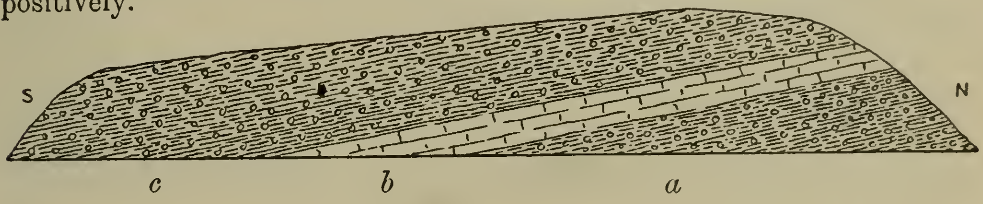


FIGURE 16. Plantain Garden River Section at Bath. *c.* Trappean Material above. *b.* Cretaceous Limestone. *a.* Trappean Material below *b.*

Below the limestone (*b*) are *altered shales* and decomposed volcanic conglomerates, some of which weather into dark colored chocolate or vermilion colors.

In nearly all the localities of the Jamaican Survey, with the exception of the Jerusalem exposure, the limestones have the appearance of localized beds in the midst of the general material of the Blue Mountain Series,[1] and not of widely extending or persistent strata.

These beds occupy no persistent horizon but occur at various intervals in the great aggregation of deposits. Our observations incline us to agree with Sawkins,[2] that "it would appear from the occurrence of the limestone in detached places that it originally formed isolated reefs."

The marls succeed the bedded limestones in ascending series, and vary from 50 feet to an inch in thickness as seen in the clays along the Minho, at Ballard's above Clarendon, at Pennant's Great House, and Trout Hall. In general, these clays contain fossils which represent intermittent life colonies which have found temporary habitation in periods of quiescence during the irregular deposition marking the formation of the earlier part of the Blue Mountain Series.

[1] Barrett, Quart. Jour. Geol. Soc. London, 1860, Vol. XVI. pp. 325, 326.

[2] The Metamorphosed Series, Trappean Series, Black Shale, and Conglomerate of Sawkins.

From the data presented, with the exception of the Jerusalem section, and the observations of other writers, it is evident that the limestones and marls containing the Cretaceous faunas occur interbedded with the conglomerates, tuffs, and shales of the lower portion of the Blue Mountain Series, and become less and less conspicuous in ascending sequence.

Sawkins[1] has spoken of the limestones as "being disposed in a zone around the higher elevations," and as "forming a zone around the great nucleus of upheaval of the island."[2] If this were correct, it might be possible that much of the Blue Mountain Series is antecedent to these beds. This statement is not accurate, however, for these limestones are found not only around but folded in the plexus of beds constituting the highest mountains, occurring on Blue Mountain Peak as high as Abbey Green, 4,200 feet above the sea. Even if true, the statement would be applicable only to the eastern end of the island, for all exposures of these beds west of the longitude of Spanish Town (except Jerusalem) are in the central basins where erosion has cut down to them through the overlying White Limestones and Blue Mountain Series. This is especially so at Clarendon, where the beds are covered by hundreds of feet of the same rocks which constitute the high summits of the east.

The tuffs, igneous pebble, and boulders of the lower subdivision are composed almost entirely of hornblendic material, — andesites and porphyries, — which shows that this was the chief eruptive material of Jamaica during this epoch, and of which the Minho beds apparently represent the débris of the last expiring extrusion. These indurated tuffs often have a superficial resemblance to altered clays and sandstones, and this aspect, in addition to undoubted occasional igneous metamorphism, was the reason why the beds were in places called the "Metamorphosed Series."

All beds of the lower subdivision, taken collectively, represent the product of disturbed conditions, such as active vulcanism accompanied by the piling up and contemporaneous degradation of vast quantities of igneous material much of which was deposited below sea level, alternating with short periods of quiescence, when shales and marls were permitted to accumulate and sparse faunas to gain temporary foothold. The alternations of shale and igneous material in the Blue Mountain Series indicate alternating conditions of sedimental placidity and volcanic extrusion, and a conflict between disturbed and quiescent conditions of deposition which finally culminated in the establishment of the latter in the succeeding Richmond epoch.

---

[1] Jamaican Reports, p. 105.

[2] Ibid., p. 22.

The Richmond Beds.

These beds constitute the upper subdivision of the Blue Mountain Series. Their arrangement and composition, consisting of shallow marine deposits of worked over and water assorted terrigenous material, indicate a succession of more quiet sedimental conditions than those which marked the preceding epoch.

The rocks are mostly black, bituminous, laminated clays, and ferruginous sandstones with occasional beds of loose conglomerate. They occur in uniform alternations of thin, regular, and evenly bedded strata, varying from an inch to a foot or more in thickness. They are dull blue-black on fresh exposure, but undergo excessive oxidation and hence are ordinarily of dark brown ferruginous colors. In general texture, arrangement, color, and stratification they resemble the Eo-Lignitic (Lower Eocene) beds of the southern United States. The clays contain many small flakes of carbonized vegetal matter, and silicified wood has been found in the gravel. The material is mostly derived from the antecedent beds of the lower division of the Blue Mountain Series. The so called "sandstones" are composed of cemented grains of water worn hornblende-andesite derived from the underlying igneous rocks, and the shales are the same material more finely triturated and mixed with vegetal matter. The conglomerates consist of rounded pebbles of various dimensions, and in places attain a thickness of 50 feet. They are almost entirely of the same material as those of the lower subdivision. Rounded fragments of the Rudistean limestone also occur in them. These have been noted first by Barrett,[1] then by Sawkins and others of the Jamaican Survey, in the parishes and districts of Portland, St. James,[2] St. George and Metcalfe, St. Mary, and St. Thomas-in-the-Vale. In addition to these rocks of the conglomerate, former observers have noted,[3] from the bluff at Port Maria, specimens of gneiss and crystalline slates, "rocks of which no trace either *in situ* or otherwise have hitherto been found in Jamaica; also a fine-grained granite to which nothing analogous has been noted on the island. . . . In this unique collection are many instances of rocks which have totally disappeared from the surface of Jamaica, but which must have existed during former epochs, either in the formations of this country or in adjacent lands that have been destroyed."

At the same locality, as also noted in the Jamaican Reports,[4] the

---

[1] Quart. Jour. Geol. Soc. London, 1860, Vol. XVI. pp. 324–326.

[2] Jamaican Reports, pp. 245, 246.

[3] Ibid., p. 130.

[4] Ibid., p. 130.

ordinary sandstone is rapidly transformed in its seaward extension into a promiscuous assemblage of large pebbles six or eight inches in diameter. This fact indicates that some of this material came from the area to the north, now occupied by the sea. In this same bed of conglomerate were found the Eocene corals described by Duncan, and a few species of mollusks. An excellent view of this exposure of conglomerate at Port Maria is given on Plate XXIII. The character of its beds as shown in Figure 17 is as follows: —

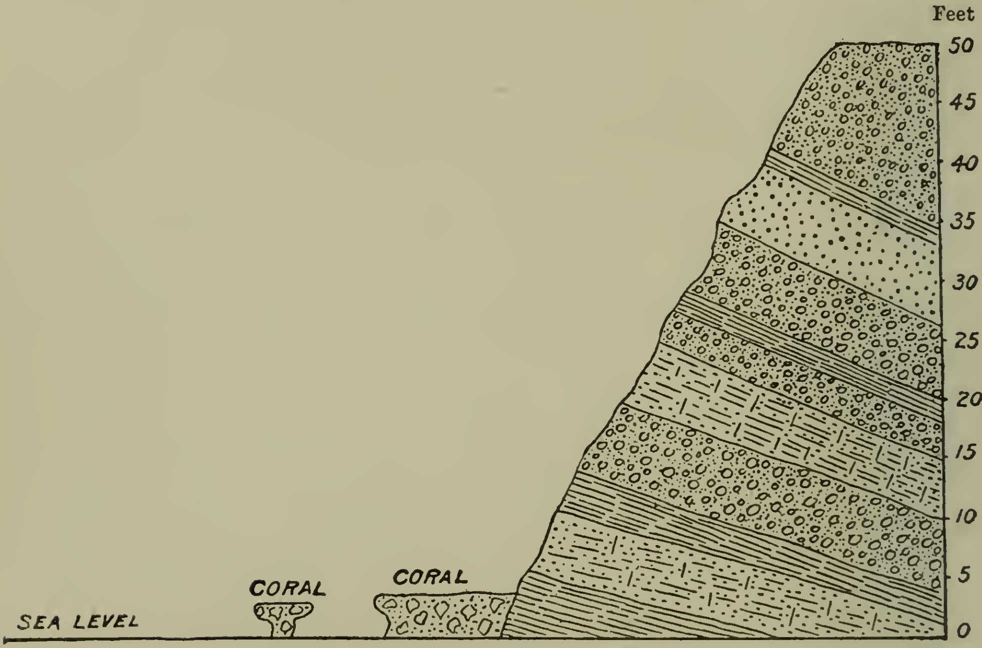


FIGURE 17. Section of Richmond Beds at Galinas Point. Section of Bluff West Side of Harbor at Port Maria.

	Feet.
Conglomerate	15
Shaly sandstone	3
Sandstone	10
Conglomerate	10
Shaly arenaceous clay	3
Conglomerate	5
Bluish rock, probably sandstone	10
Conglomerate	15
Shaly arenaceous clay	5
Bluish rock	11
Shale	+10
	+97

The Richmond formation is exposed in all parishes of the east adjacent to the Blue Mountain Ridge, but in a greatly disturbed condition. It is best seen in the north coast parishes of Portland, especially the districts of St. George and Metcalfe in St. Mary Parish; and in Hanover, in the bluffs and hills of the back coast country, east, west, and south of Lucea. Excellent and typical exposures are seen between Richmond, district of Metcalfe, St. Mary Parish, and Annatto Bay, the beds occurring in many short open anticlinal and synclinal folds. At Richmond a bluff in the banks of Flint River well shows the thin alternations of evenly bedded shales and sandstones overlying the conglomerates. (See Figure 18.)

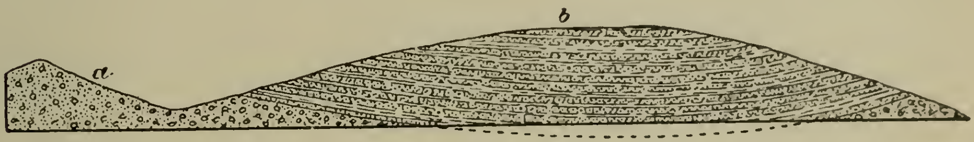


FIGURE 18. Section showing Richmond Beds at Richmond. *a*, Conglomerate grading into *b*, alternations of Conglomerates and Clays.

At Moral Cut, near Moral Station, thin flags of impure arenaceous limestone appear in alternation with the beds of shale (Fig. 19), and weather out in great quantities. This exposure is part of an openly folded anticline, over a mile in length, consisting of rusty brown gravel below, and shales, limestones, and sandstones above. In the west bank of Wag Water the Richmond beds are vertical. Many other excellent exposures occur in this portion of the parish of St. Mary, constituting the western terminus of a belt of the formation which extends thence in a south of east direction through Portland Parish. It is impossible to obtain continuous sections of these beds, owing to minute folding and concealment of contacts by vegetation and overlapping formations.

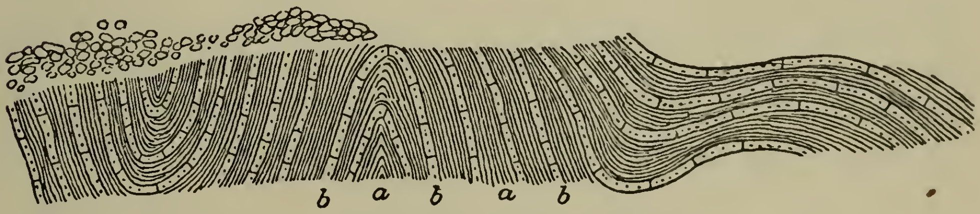


FIGURE 19. Folded Richmond Beds, St. Mary Parish. (From the Jamaican Reports.)

The Richmond beds of this district succeed without break the Minho formation (Purple Shale and Conglomerate Formation of Wall), which are described[1] as "great masses of green and red argillaceous strata and apparently belonging to a lower division of the group."

Wall[2] gives under the name of the "Black Shale" the following section of the Richmond beds in St. George and Metcalfe.

	Feet.
Red and light yellowish shale	± 100
Thin alternations of grayish sandstone and shale weathering brown	± 300
Brownish green shale, finely laminated, black color, containing alternations of thin sandstones, rubbly conglomerate, and pieces of Cretaceous limestone and fossil Hippurites and Caprinella much water worn	± 1,000
Purple shales finely laminated passing into metamorphosed conglomerate and shale (Minho beds).	

This section makes no mention of the upper beds containing limestones, which, in our opinion, represent a gradation into the overlying Cambridge formation.

In the northern part of Hanover Parish the Richmond beds have considerable development, and, so far as composition is concerned, present the same general facies previously mentioned. In this parish they are exposed in the back coast bluffs from the mouth of Great River westward, being capped above by the White limestones of the Oceanic Series, and in their seaward extension cut into many terraces, upon some of which are plastered old coral reefs like that shown near Barbican, in Figures 33 to 36. Superb exposures are seen around the interior end of Lucea Harbor and in the uplands to the south half way across the island along the road leading toward Savanna-la-Mar. In this region the beds are intensely folded, faulted, and overthrown, as shown in the view on Plate XXII. It is our opinion that nothing less than months of minute study of the complicated folds of this region would reveal the detailed sequence of the individual members of the beds in this parish. The following section may be inferred[3] from descriptions of Brown and Sawkins. The formation names are ours.

Richmond Beds.

	Feet.
Thin laminated beds of red, gray, and greenish shale	± 200
Beds of pebbly conglomerate, overlying beds of massive brownish and gray sandstone	300
Greenish brown laminated shale, interstratified with thin beds of fine-grained sandstone	+2000

[1] Jamaican Reports, p. 63.

[2] Ibid., pp. 121, 122.

[3] Ibid., pp. 252, 253 ("Black Shale").

Minho Beds.

Metamorphosed conglomerate "of subsequent date to that of the Cretaceous limestone," composed of "various crystalline rocks embedded firmly in a hard crystalline base; the whole is of a greenish color" (Tuff?).

The Richmond formation outcrops in many places a short distance back of the sea along the north coasts of the parishes of St. Ann and Trelawney. It is well exposed beneath the Cambridge beds south of Cambridge along the highway on the west side of Great River, as seen by the writer. It also occurs on the south side of the Blue Mountain Ridge in St. Andrews and St. Thomas. According to Sawkins,[1] in the latter parish at Blue Mountain Valley it consists of "alternate bands of red clay, yellow sandstone and light gray shales, 1,000 to 1,200 feet in thickness."

In general, this formation underlies nearly all the later rocks, and, in our opinion, prior to the Montpelier subsidence it occupied an area as large or larger than that of the island of to-day.

From data presented in the paleontological chapter of this work, the age of these beds is undoubtedly old Eocene, although it is impossible to draw an exact line between these beds and those of the lower division which we have termed Cretaceous, and they are no doubt stratigraphically continuous.

The uniform alternations of the Richmond beds indicate that they were rapidly deposited over a considerable shallow area of deposition; since much of this area was the present locus of the island, it is difficult to infer the situation of the near-by land from which the material was derived; some of it may have come from the old nucleus of Blue Mountain Ridge, but in our opinion this was not of sufficient size to afford all the material. These facts, together with the presence of foreign material, are at least strongly suggestive of the occurrence of land areas during this epoch, concerning the locality of which present knowledge is wholly wanting.

THE CAMBRIDGE FORMATION.

The beds are named after the typical locality of their occurrence at Cambridge, between Ipswich and Montpelier, in the parish of St. James, in the northwestern portion of the island, near the junction of the boundaries of St. James, Hanover, and Westmoreland.

---

[1] Jamaican Reports, p. 105.

In places the Richmond beds grade up into irregular alternations of impure clay, marls, and yellow limestones, which, in general, occupy a transitional position between the obviously land derived beds of the Blue Mountain Series and the ocean derived limestones of the Oceanic Series. Argillaceous calcareous marls appear in the upper part of the Richmond beds, become successively more and more frequent, and finally dominate. These are accompanied by thin beds of impure blue limestone of a segregational character, oxidizing yellow on weathering and alternating with the marls which gradually increase in thickness and relative proportion until they preponderate. Finally, these yellow limestones become more purely calcareous in ascending series as the sediments become clearer and freer from land derived material, until they finally pass into the purer White limestones.

This formation has limited exposures at many places in the island, notably around the lower margins of the interior basins in Trelawney, Westmoreland, and Clarendon, and in the eastern parishes, as mentioned later. We shall first describe their occurrence in two typical localities at Catadupa near Cambridge, and at Chapelton, Clarendon Parish, respectively. Owing to certain differences which at present do not permit of perfect correlation, these will be respectively termed the Catadupa and Chapelton beds of the Cambridge Formation.

The Catadupa Beds.

They are well exposed on the east margin of Great River valley, in the new cuttings along the Montego Bay Railroad between Ipswich and Montpelier stations, and especially between points two or three miles south of Catadupa and one mile north of Cambridge. Here the railway cuttings reveal splendid exposures, and afford good places for collecting fossils and studying the stratigraphy. These beds occur in a series of short open folds, as shown in Figure 20.

These folds are all less than two hundred yards in length, but the continuity of the beds is so broken that their exact sequence and thickness can be made out only with difficulty. Here the beds consist of alternations of massive and friable strata of yellow blue limestone, one to three feet in thickness, separated by thin bands of blue-black shale containing oysters, large Cerithii, Lucina, Rudistes, Carolia, Triloculina, etc.

A general geological section of the east slope of the valley of Great River, between Cambridge and Catadupa, showing the relations of the formation, is as follows.

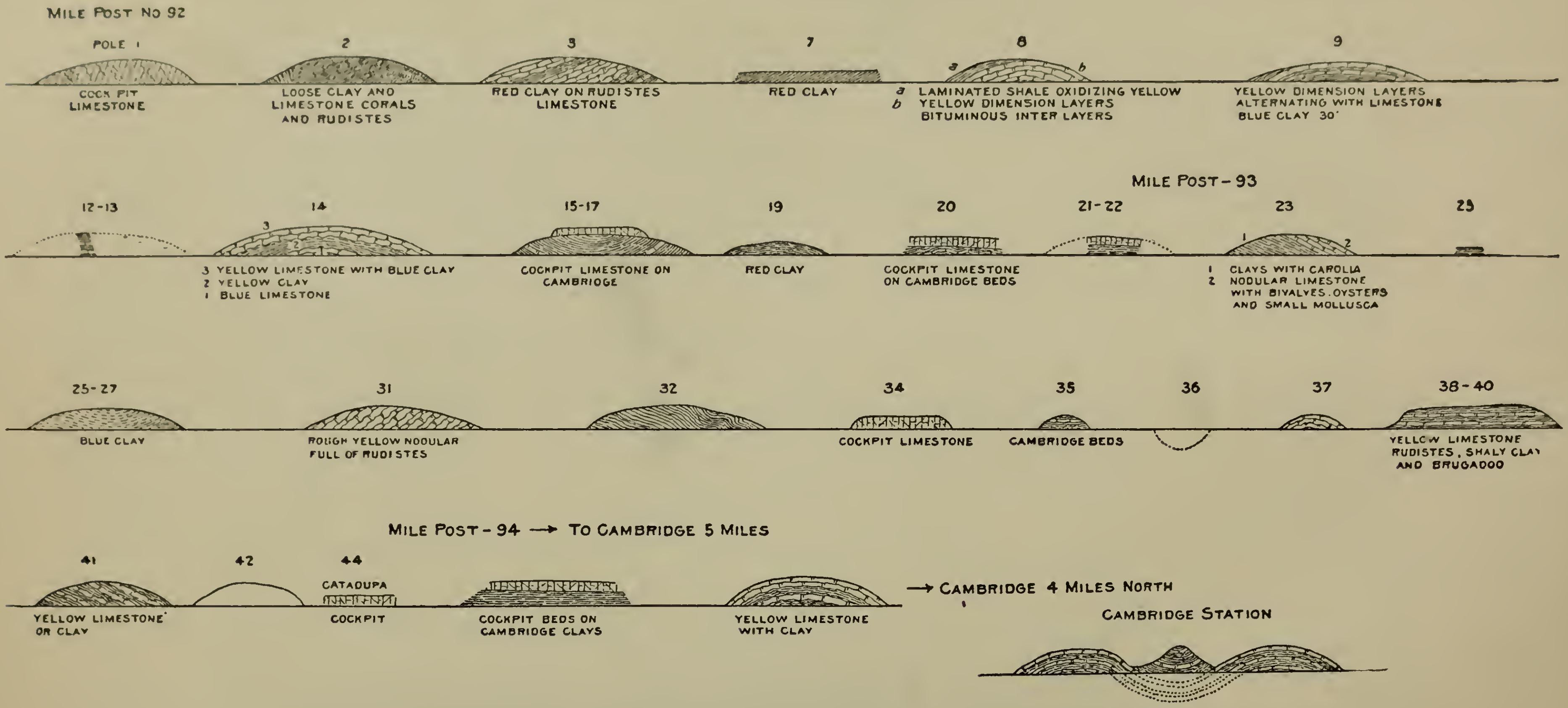


FIGURE 20. Exposure of Cambridge Formation near Catadupa and Cambridge.

	Feet.
Montpelier Beds.	
Homogeneous textured white chalky limestone with flints, resting unconformably upon the Cambridge beds	+500
Cambridge Beds.	
Yellow colored granular limestones (blue before oxidation) alternating with clays, with many fossils	±100
Blue, black, and purple clays grading into above	±100
Richmond Beds.	
Blue and black clays without calcareous beds grading down into thin alternating beds of clay and sandstone	±25
Purple colored clays, without regular lamination	±25
Slightly calcareous beds in above	±25
Purple and blue-black arenaceous clays, extending down to bed of Great River	+200

The clays and marls are black and unctuous in some places; in others they are yellow, excessively calcareous, and full of minute Foraminifera (Miliolidæ), and grade from black into blue and gray colors upon drying, and into yellow on oxidation. The Foraminifera are so abundant that they give an oölitic look to some of the rocks, but on oxidation they crumble into small specks of pulverulent lime. This lime, after solution and redeposition, largely makes the segregations of limestone. Sometimes the clay seams are so bituminous they have the appearance of thin lignitic beds.

The limestones occur in layers of various thickness up to two feet; they are nodular and irregular both in thickness and texture. At some places they are firmly indurated, at others they are friable and shaly. They are clearly chemical and clastic segregations in the great mass of clays, and gradually increase in proportion as we ascend in the series, while the clays similarly decrease. In freshly exposed portions the limestones are also blue-black in color. On weathering they become bright yellow, as a result of the oxidation of small amounts of iron which accompany the fossil colonies.

Many fossils — Echinoderms, Corals, Rudistes, and other Mollusca — which are listed in another chapter of this report, occur in the calcareous portions of these beds, both as free shells in the clays or making the greater mass of the limestones. Some of the latter in the cuts south of Catadupa are almost entirely composed of Rudistes, which also occur more sparingly in the beds at Cambridge. Oysters and

Mollusca are most abundant in the "Bruggadoo," as the black clays at the railway cut where so much slipping has occurred are called.

Chapelton Beds.

In Clarendon Parish, at Chapelton, and in the slopes of the Minho River east of that town, beds allied to the Cambridge formation are exposed. These present two subdivisions, the upper of which consists of more or less massive beds of yellow foraminiferal (Orbitoidal) marl alternating with bedded yellow limestones and grading up into the white Montpelier limestones; the other is mostly composed of creeping blue, black, and red clays known in Jamaica as "Bruggadoo," resembling similar material of the Catadupa section, and in which occasional fossiliferous calcareous layers only an inch in thickness and a few yards in length are exposed.

The higher subdivision has its typical occurrence along the main street of the village of Chapelton, between Chapelton Hill and the River St. Thomas. The second is exposed along the "lower" road which parallels the foregoing street but follows a lower contour in the valley of the Minho. The following local section of this subdivision was observed at Chapelton, between the hill in Chapelton upon which the residence of the Inspector of Constabulary is situated, and the bed of St. Thomas River two miles north. This section is the upward continuation of the general Clarendon section given on page 46. The thicknesses given are approximated: —

	Feet.
3. Bed of yellow marl and thin limestone alternating, containing Orbitoides and small Ostrea, estimated thickness	185
2. Blue and purple clay	115
1. Yellow marl, clay, and limestone	75

At Mr. Craig's estate in the river valley a considerable mass of yellow limestone (No. 1) is exposed, but it was impossible to find determinable fossils therein, or to decide the exact position of this mass relative to the clays. It was our impression that it occurred about midway in the general section. Down the valley slope, on the so called lower Chapelton road, which follows the river and cuts into beds lower than those of the above section, many isolated cuts are exposed, composed entirely of the blue and purple clays, with an occasional thin local layer of yellow clay containing crumbling fossil oysters, Carolia, and Foraminifera. From reasons given in the paleontologic discussion, these lower beds are supposed to be equivalent to those of the Catadupa section, and the upper are a higher extension of the same.

In addition to the particular localities of the Cambridge beds mentioned, there are many others throughout the island. Near Mooretown, Mt. Pleasant, and Shrewsbury, Portland Parish, are beds described by Barrett,[1] which correspond closely with them in position, arrangement, and fossiliferous remains.

On the north side of the east end in St. Mary's and Portland parishes the Cambridge beds are much more calcareous than elsewhere, as seen in an exposure at the foot of the bluffs west of Port Antonio, where its characteristic fauna is found in beds of pure white limestone and calcareous marl much resembling the overlying white limestones of the Montpelier formation, into which it here grades without perceptible break. A considerable mass of the white marl at this locality is composed of large granular Foraminifera very like those found in the black shale of the Catadupa locality. This white foraminiferal marl is probably the same as that from near Carron Hall, St. Mary,[2] in which parish, near Guy's Hill, the typical Cambridge fauna is found just below the flint beds of the Montpelier. At this locality the beds have their characteristic variations of color. Near Preston Falls, in the same parish, the lime beds of the formation grade down into the Richmond beds. In this parish Wall estimates the thickness of beds which we place in this formation described by him, together with a part of the overlying white limestones, under the name of the "Calcareous Marl,"[3] to be between 500 and 600 feet.

In the district of St. Thomas-in-the-Vale, parish of St. Catherine, the Cambridge formation, with the typical Chapelton fossils, consists of yellow marl and red and blue colored clays with impure lignite, and is about 300 feet thick. It is well displayed in the hilly district southwest of Guy's Hill.[4] Near Spring Vale, in the same parish (St. Catherine), south of Linstead, at the southern angle of the St. Thomas basin, the Cambridge beds are composed of yellow clays and sand extremely rich in Ostrea and Foraminifera. In the parish of Manchester, the Cambridge beds occur at many places, notably at Spice Grove, Amby, Lower Mayfield, Oxford, Cowie Park, along Hector River and at Christiana. A good description of the beds at these localities is given under the head of "Yellow Limestone" by Brown.[5] The following section of these beds on Hector River is by him: —

---

[1] Jamaican Reports, p. 84.

[2] Ibid., p. 129.

[3] Ibid., pp. 129, 130.

[4] Ibid., p. 130. Described under name of "Calcareous Marl."

[5] Ibid., pp. 169–171.

	Feet.
Hard compact yellow limestone, very crystalline; thickness about	10
Soft yellowish shaly limestone	5
Soft shaly yellowish limestone, showing peculiar strained concretionary nodules in one part of the bed	2½
Yellowish limestone, hard and coarse	2
Yellow marl	
	+19½

It is an interesting fact that Brown considered the yellow limestone beds of Christiana, from which Mr. F. C. Nichols later collected several of the Rudistes recently described by Professor Whitfield,[1] to be of Eocene age. This strongly suggests that future study of the locality may reveal a mixture of Cretaceous and Eocene genera like that occurring at Catadupa.

The Cambridge beds, with their characteristic fossils, especially the oyster and large Cerithium, outcrop at many places in St. Ann, notably at Cave Valley, Boroughbridge, Yankee River, Pedro estate, and in the beds of Negro and St. Ann Rivers. They have also been noted in Trelawney at several places, and beds of Orbitoidal limestone with other fossils are well exposed near Freeman's. The outcrops of the Cambridge in Westmoreland and Hanover parishes are all in the same general district as those of Catadupa and Cambridge in St. James, — the three parishes meeting in this vicinity. The thickness is from 40 to 300 feet.

The identity of this formation is involved in Jamaican literature. In places it is clearly defined and in others its identity is entirely lost. In De la Beche's chapter on the "White Limestone" of Jamaica,[2] many descriptions of these beds and their fauna can be recognized. It is also the "Nodular Limestone" of Barrett's posthumous section published by Woodward,[3] and mentioned in our introductory chapter.

In the Jamaican Reports it is the "Yellow Limestone" of Sawkins's general section on page 24, and of the western parishes of St. Elizabeth, St. James, Hanover, and Westmoreland, as described by Brown, who considered the formation to be Eocene. In the descriptions of the remaining parishes it has been so confused under many names with other beds of different age and position that its identification is somewhat difficult, although by careful study of the reports uncorrelated descriptions

---

[1] Bull. Am. Mus. Nat. Hist., New York, 1897, Vol. IX. pp. 185–196.

[2] Jamaican Reports, pp. 169–182.

[3] The Geological Magazine of 1864.

of its parts are occasionally recognized. In reports on the other parishes it has been termed "White Limestone," and "Calcareous Marl" of St. Thomas-in-the-Vale, Metcalfe, and St. Mary, and referred to the Cretaceous, Eocene, and Miocene ages.

The term "Yellow Limestone" is peculiarly applicable to these beds, but unfortunately this name was also applied, through the erroneous correlation of Wall,[1] Etheridge,[2] and others, to the beds of Oligocene age at Bowden, as shown in the Introduction of this report. In view of these facts, it is unwise to continue further the term "Yellow Limestone" as a formation name for any of the Jamaican beds.

The highest point at which the Cambridge beds are known to occur is 3,000 feet, near Luidas Vale, St. Catherine Parish.

There are several paleontologic and stratigraphic features of the Cambridge beds which are peculiar, and will require more extensive field work for final explanation. We have reason to believe that the beds are not connected, but occur in broken patches, which, at least in their lower portion, like the Cretaceous beds, represent sporadic colonies of lime making organisms, which found temporary foothold at intervals during a period of turbulent deposition generally unfavorable to a large development of marginal life. These deductions are based upon the fact that in no two localities are the sequence of sediments or association of species identical, while in others the beds do not appear between the Richmond and Montpelier. Furthermore, the fossiliferous horizons of the Lower Cambridge are so like some of the Cretaceous that the one has been frequently mistaken for the other. The mixture of Cretaceous Rudistes and Eocene corals and mollusca at Catadupa, as seen by us, and of Orbitoides and Rudistes in Portland, as noted by Barrett,[3] indicates a transgression of Cretaceous life into the Eocene, and further denotes the anomalous nature of this formation.

These beds, while showing sedimentary relations to the Richmond, undoubtedly represent a transitional step in the deepening which later produced the Montpelier formation. In some places it seems perfectly conformable beneath the latter, while again, as shown by Brown and seen in several places by us, they are unconformable. These apparently irreconcilable conditions can probably be explained upon the hypothesis that the island was undergoing subsidence during the Cambridge epoch, although parts of it were then dry land, which was still further covered

---

[1] Quart. Jour. Geol. Soc. London, Vol. XXI. p. 56.

[2] Jamaican Reports, p. 311.

[3] Quart. Jour. Geol. Soc. London, 1860, Vol. XVI. pp. 324–326.

by the Montpelier beds during the succeeding epoch. As shown in another chapter, the age of these beds, although containing a remarkable mixture of Cretaceous and Tertiary fossils, is undoubtedly Eocene, and with the Richmond beds they constitute the Eocene system in Jamaica.

THE WHITE LIMESTONES. (OCEANIC AND COAST SERIES.)

Introductory Statement. — The transitional Cambridge beds grade up into rocks of organic oceanic origin. These are the White Limestone formation of the official Jamaican Reports. They have no genetic relationship with the rocks of the Blue Mountain Series, and differ from them in every physical and chemical aspect.

The interpretation of the white limestones has been one of the greatest problems of Jamaican geology. There have been so many diverse opinions concerning their age and sequence that it is almost impossible to obtain from current literature any approximation of their true relations and significance. The difficulties can be readily seen by any one who reads the conflicting and apparently involved conclusions in the Jamaican Reports. The fragmentary descriptions of their local occurrence are frequently well written, but through lack of correlation and erroneous deduction they fail to clear up the sequence and age of the beds.

All the white limestones have been usually discussed by field observers under one general head, and treated and tabulated as a single formation in the discussion by European geologists who wrote the Appendix, and one would infer that they are not stratigraphically subdivisible. There are numerous references, however, in the body of the Jamaican Reports,[1] from which it is obvious that some such distinctions were at least observed, although the geologists failed to differentiate, name, or correlate them, as we shall endeavor to do in the following pages.

De la Beche[2] included all the rocks from our Cambridge beds to the recent inclusive in his White Limestone, but recognized differences of age therein and correctly referred the basal portion to the Eocene.

Of the field geologists upon the Jamaican Survey, Sawkins held concerning the White Limestone that "Uncertainty has prevailed respecting its precise geological position, but paleontological evidence seems to determine a Mid-Tertiary or Miocene period as the epoch of deposi-

---

[1] See Jamaican Reports, pp. 45, 53, 121, 214, 230, 231, 241, 250, 257.

[2] Mem. Trans. Geol. Soc. London, 1829, pp. 169–171.

tion."[1] Lennox held that the "White Limestone of Jamaica appears to have been deposited slowly and steadily in the bed of a tranquil sea, during the period known to geologists as the Miocene."[2] Wall,[3] through his unfortunate error of mistaking the overlying Bowden yellow marls for the underlying Cambridge yellow limestone, placed the whole of the White Limestone above the Bowden beds now known to be of late Oligocene (Miocene) age. Etheridge, Woodward, Jukes-Browne, Harrison, Duncan, and others, misled by Wall's stratigraphic error, accepted this conclusion. Etheridge stated that the White Limestones were of Pliocene[4] or Post-Pliocene[5] age. Gabb,[6] upon the ground that all the Jamaican white limestones were synchronous with the Post-Pliocene coast limestone of San Domingo, wrongly correlated them as follows: "The Coast formation of Santo Domingo is extensively represented in most if not all the West Indian Islands. In Jamaica, as the White Limestone, it covers more than three fourths of the island and may be computed at 2,000 feet in thickness."[7] Sawkins first considered it as Miocene, but in the end of the book it is put down as Post-Pliocene. Jukes-Browne and Harrison[8] state: "With respect to the age of the [Jamaican] White Limestone the reports of the surveyors are inconsistent with one another; in some[9] it is spoken of as Miocene, in others[10] as Pliocene, and in the Tabular View at the end of the volume it is labelled 'Post-Pliocene.' Mr. Barrington Brown, however, to whom we wrote on the subject, informs us that this last reference was a mistake; that during the course of the Survey and before the fossils were examined there was naturally much uncertainty with respect to its age, but it was finally intended to class it as Pliocene, because it was found to rest on a fossiliferous yellow limestone which was considered by Mr. R. Etheridge to be of Miocene age, and probably late Miocene." The same writers (Jukes-Browne and Harrison), after presenting much evidence to show that these "Yellow Limestones" of Wall and Etheridge — the Bowden beds — were of late Miocene age, and accepting the erroneous deduction that the latter lay beneath instead of upon the

---

[1] Jamaican Reports, p. 23.

[2] Ibid., pp. 23 and 149.

[3] Quart. Jour. Geol. Soc., Vol. XXI. p. 67.

[4] Jamaican Reports, pp. 307 and 342.

[5] Ibid., Tabular View at end of volume.

[6] Geology of San Domingo, p. 110.

[7] Jamaican Reports, p. 307.

[8] Quart. Jour. Geol. Soc. London, 1892, Vol. XLVIII. pp. 219, 220.

[9] As on pp. 23 and 149, Jamaican Reports.

[10] Ibid., pp. 129–301.

great White Limestone Series, concluded that, "this being so, it is clear that the overlying White Limestone Series cannot be older than early Pliocene."[1]

The truth is, the white limestones of the Jamaican sequence represent several distinct formations and ages, from Vicksburg to recent inclusive, but that the greater portion of it, as I shall show, is of old Oligocene age. There are even some white limestones in the Cretaceous in Clarendon which are almost lithologically indistinguishable from those of the Tertiary. In recent years English geologists have observed the discrepancies of previous interpretations of the white limestone, and suggested, from specimens of the material sent them, that at least an upper and lower division might be distinguished.[2] Our investigations will show that not two but several subdivisions can be made, and that the rocks hitherto classified under this general head really belong to several distinct formations of two great series, the Oceanic and the Coastal, the former constituting most of the rocks of this character and occupying large areas of the interior upland, while the latter are confined to a narrow belt along the coast.

The older white limestone formations, constituting the greater mass of these rocks, are found in the upland area of the island, and are all of Tertiary age. More exactly speaking, they are of the Vicksburg stage, which is placed in the Eocene by some writers and in the Oligocene by others. The later white limestone formations — including the Coast Limestone of the Jamaican Reports, which we shall describe as the Falmouth Formation, and the Hospital Point Limestone of Montego Bay — are of Pliocene, Pleistocene, and recent age.

There has also been much vagueness concerning the origin of these rocks, accompanied by an opinion on the part of many that they are of coral reef origin. They have been described[3] as "great coral structures, from the débris of which the enormous calcareous development of the White limestone has been derived," and as the "great coralline structure which covers the greater part of the island."[4] Opinions of this nature have caused some writers to believe that all the white limestones were of coral reef origin, and led to the rather careless assertion that reef rocks of great thickness occur in the Antilles at heights exceeding 2,000 feet, when in fact such rocks nowhere except in Barbados exceed 100 feet in altitude or thickness. On the other hand, even the local descriptions of the Jamaican Reports controvert the conclusion that

---

[1] Quart. Jour. Geol. Soc. London, 1892, Vol. XLVIII. p. 220.

[2] Ibid., p. 219.

[3] Jamaican Reports, p. 24.

[4] Ibid., p. 189.

they are as a whole of coralline or coral reef origin, as has also been shown by a few hand specimens collected without reference to horizon and sent to England, studied by specialists, who recognized them as being of foraminiferal composition.

Not the least important result of our researches will be a demonstration that the larger thicknesses of these limestones are neither of molluscan, coralline, or reef rock origin, but are foraminiferal oceanic deposits and other offshore calcareous oceanic muds composed of organic detritus laid down at depths below that at which reef rocks were formed and in periods of geologic time prior to the appearance of the modern reef building species in the sequence.

The white limestones of Jamaica, both of the Oceanic and Coastal Series, are various manifestations of the vast agency in past times of animal life as extractors of carbonate of lime from sea water, similar to what is now going on throughout the warm regions where the oceanic waters are comparatively free from land sediment. That white limestones, entirely distinct from true reef rock, are now being formed throughout the tropics is a matter of common observation. Wherever calcareous organisms abound around the margins of shores uncontaminated by land débris, the beach wash of calcareous material is rapidly cemented by its own solutions into white limestone rock of various textures; shells into coquina; shell débris and corals into "oölite," which, when wave washed and sea sprayed, like surfaces of the elevated reefs, indurate into hard partially crystallized surfaces. In addition to the near shore deposits, as shown by A. Agassiz and others, calcareous muds of foraminiferal origin are being formed to depths of 5,000 feet or more. When elevated into land these form white limestones.

It is also apparent that white limestones may be partially coralline, as attested by well preserved coral remains, and yet not necessarily of coral reef origin, or in any manner connected with reef making phenomena. All stony corals are not reef builders, and many solitary forms, such as are found in some of the White limestones, inhabit oceanic water to a depth of 1,000 fathoms below the zone of 100 fathoms, below which true reef building corals do not live. Yet it has been customary to call any limestone with sparse traces of these solitary corals "coralline," and from this it was easily transposed into coral reef rock.

In general the tropical white limestones may originate in several ways, as shown in the following table.

Origin of White Limestones.

I. Organic Extractions from Sea Water.	Remnantal Bottom Accumulæ. Ascending organic growth.	Chalk, Shell, Mud, etc. Reef Rock.
II. Chemical Precipitates.	*a.* Original Oceanic? *b.* Subsequent alteration.	Chalk Crystalloids. Crystallized.
	Interstitial alteration.	Sinter Deposits. Cavernous or Honeycomb Rock.
	Superficial.	Tufa. Sinter.
III. Mechanical Accumulations.	Submarine.	Coral Mud. Lagoon Rock. Coquina. Cantera.
	Littoral.	Beach Wash: Cantera. Cay oölite. Caleche. Coquina.
	Terrestrial.	Æolian (Bahama Rock).

In the foregoing processes we have not considered the possibility of the chemical inorganic agencies. Walther has advocated that ammonium carbonate derived from decaying animals may precipitate calcium carbonate from sea water, but this is not the opinion of modern chemists. Reinhard Braun[1] summarizes the various processes producing oceanic lime, and says that most, if not all, massive limestones and chalks are of organic origin.

The Oceanic Series.

The upland white limestones or Oceanic Series, as we shall call the Tertiary formations under discussion to distinguish them from the later deposits of the Coastal Series, consist of white limestones of varying texture and hardness, and probably aggregate 2,000 feet in thickness. These present a perplexing series of surface and interstitial changes under the influences of solution and oxidation, as explained in their detailed descriptions, which render their study a difficult task. They consist of deeper water organic deposits and are free from coral reef rock, littoral shell agglomerates (such as coquina, cantera, and caleche), beach wash, æolian débris or other clastic formations which characterize

---

[1] Chemische Mineralogie, Leipsic, 1896, pp. 376–379.

the rocks of the Coastal Series. They contain few macroscopic fossils by which their age can be independently determined, but this is fixed by their microscopic fossils and their position between including fossiliferous horizons, — the underlying Cambridge beds and the overlying Bowden gravels and marls.

In general, the Oceanic Series occupies most of the Plateau region, which practically includes all the island under 3,000 feet in altitude outside of the Blue Mountain district, except its immediate coastal borders. In the mountainous region of eastern Jamaica these rocks occur as a high piedmontal peripheral border around that end of the island. In the western half of the island the beds of the Oceanic Series completely cover the old Blue Mountain Series and occupies the higher summits of that portion of the island.

Owing to the elevation of the Plateau region which took place after the deposition of these beds, and the subsequent contraction of its oceanic borders by erosion and subsidence, the coastward extension of the rocks is truncated and partially embedded near the littoral by the still later formations of the Coastal Series, which are deposited unconformably against them.

The Montpelier Beds. — The Cambridge beds north of Cambridge are succeeded by stratified white limestones and marls containing nodules of flint. The limestones are of non-crystalline (chalky) texture, and usually break with dull, earthy, conchoidal fracture. The texture, fracture, and presence of flints distinguish this formation from others of the great series of white limestones of many ages, which, above the Cambridge beds, dominate in the rock structure of Jamaica.

Concerning the grosser lithology of the Montpelier beds, little can be added to the excellent description of them in Hanover and Westmoreland, given by Charles B. Brown as a portion of the "White limestone," as follows:[1] —

"It consists of thin beds of white limestone interbedded with a soft white chalky marl, the limestone beds invariably containing nodules of flint. The limestones are chiefly soft, but seldom compact or crystalline; they form thin beds, which vary from a few inches to four feet in thickness, and are much disturbed, so as to dip in almost every direction over small areas. The marl beds being interstratified with these of course show the same disturbance and dips, and are similar to them in thickness. The flints and chert contained in the limestone beds lie usually in flattened nodular masses in lines of stratification, and are

---

[1] Jamaican Reports, pp. 250, 251.

rarely in beds themselves. They are not connected continuously, but are in long hollow flat masses, and have all the appearances of having been deposited around or in the substance of some organic form which was embedded in the limestone. These flints are chiefly of a brownish pink, brown, and gray colors. At Knockalva and other places in the vicinity the limestone contains small veins of silica, and also has become so thoroughly impregnated with that substance as to be completely changed into a siliceous limestone."[1]

Microscopic examinations show that the calcareous beds consist of organic oceanic material, and are composed of the shells of Foraminifera, occasional sponge spicules, and fine crystals and amorphous particles of carbonate of lime, like those usually found in all chalky oceanic deposits. No terrigenous material whatever has been found in any specimens examined. The Montpelier beds are singularly free from molluscan or other visible fossils, except a large species of Orbitoides in its lower beds. Nummulinæ have also been found.

William Hill[2] has studied microscopically a specimen of white limestone, Hanover County, which undoubtedly came from the Montpelier beds. This, according to Jukes-Browne and Harrison,[3] is an oceanic deposit in which "Thick-shelled Globigerinæ, similar to those of the Barbados rocks, are conspicuously abundant, and one or two Radiolarians can be seen in outline."

Some of the flints are also black or gray in color and flattened, oblong in shape, like those of the Upper Cretaceous of England and Lower Cretaceous of Texas; others are round and opalescent. The whitened exterior surfaces of many specimens are masses of silicified Foraminifera, — Orbitoides, Nummulinæ, and Miliolidæ, — and these can be made out in the interior of some of the specimens collected from Montpelier Hill. Similar occurrences of Foraminifera coating the flints have been noted from St Mary. In places they occur in great abundance as requently described in the Jamaican Reports, and are found in no other formation so far as we have observed. Occasionally there are also hard siliceous lumps in the limestone, which suggest that secondary alteration into flints may have been possible. In general, these seem to be silicified lumps of organic skeletal remains. Several specimens of

---

[1] The description above given refers to Brown's lower division of the white limestone (our Montpelier beds); the upper beds (our Brownstown beds) are more compact and massive, and contain fewer interstratified marls.

[2] Quart. Jour. Geol. Soc. London, 1891, Vol. XLVII. pp. 248, 249.

[3] Ibid., 1892, Vol. XLVIII. p. 180.

the Orbitoidal flints from St. Mary collected by Wall have been studied by T. Rupert Jones, and published in the Geological Magazine,[1] as further commented upon in the paleontologic portion of our paper. Our studies enable us to show the exact geological position of these specimens, which has been hitherto unknown. The Orbitoides are quite large, and can be collected usually in close proximity to the flints sometimes attached to them. They closely resemble the forms so abundant in the yellow marls of the Chapelton formation and may be specifically identical.

Under the microscope the entire mass of most of the chalks collected by us consists of Globigerinæ, which at present form great deposits on the ocean's bottom between 1,500 and 2,900 fathoms. The specimens collected from Montpelier Hill, the foothills north of Savanna-la-Mar, Dover, between Annatto Bay and Buff Bay, St. Margaret, and near Buff Bay, — widely separated localities, — were entirely made up of Globigerinæ.

The Montpelier beds are best exposed in the hills of the north side of the island in the bluffs of the back coast country along the north coast road, notably near St. Ann, Falmouth, and Montego Bay; from Port Antonio westward into Hanover Parish; and typically along the line of the Jamaican railway between Montpelier to Montego Bay, and at many other places around the island. They are exposed almost continuously across the island in the parishes of Westmoreland and Hanover, between Anglesea near the coast, five miles east of Savanna-la-Mar, and Montego Bay via Montpelier, where they have been well described by Charles B. Brown under the name of "White Limestone," as previously mentioned. Here they constitute most of the uplands or hills of the back coast country, except where eroded through in the processes attending the making of the sinkhole and cockpit countries. In the valley in which Montpelier is situated, and also that near the heads of Thicket and Morgan Rivers, many peculiar isolated buttes standing upon a floor of Cambridge and Richmond beds are made up of the Montpelier limestones; also the railway cuts between Montego Bay and Montpelier are composed of them.

They are repeatedly exposed in great thickness along the front of the back coast hills along the coast road from Montego Bay to St. Margaret Bay east of Port Antonio. At Cinnamon Hill (St. James) the beds are almost vertical, inclining to the north coast. Here the limestone of homogenous texture is in thin evenly bedded layers at the base, suc-

---

[1] Quart. Jour. Geol. Soc. London, 1864, Vol. XIV., foot-note page 104.

ceeded by thicker beds, both of which contain flints and large Orbitoides. The exposure is very near the base of the formation, the Richmond beds outcropping at no great distance. Between Falmouth (Trelawney) and St. Ann Bay (St. Ann Parish) the whole north front of the back coast country is made up of these beds, as described on the upland road from Runaway Bay to Falmouth via Brownstown. Near Landovary about five miles west of St. Ann Bay, the back coast bluff consists of the basal portion of the Montpelier beds with flints in contact with the Richmond gravel, as shown in the accompanying Figure 21. At St. Ann Bay, the base of the Montpelier beds is also seen in the bluffs. The rocks at Landovary have a strong south dip. In St. Mary Parish the road from Runaway Bay to the summit of the hills of the back coast country (altitude 1,450 ft.) *en route* to Brownstown, passes over at least 1,500 feet of white limestone, the lower 500 feet of which are composed of the Montpelier beds with flints, grading upward into the Moneague beds. From Retreat (St. Mary) to Falmouth in Trelawney, the Montpelier beds are occasionally well exposed along the upland interior road, especially in the bordering slopes of Hampshire Valley, notably near the Blanksford and Highgate estates. From the summit of the divide between the Hampshire Valley and the sea, 920 feet of the flint bearing beds are exposed between that point and Falmouth. On the highway from Moneague to St. Ann, in going from the high-

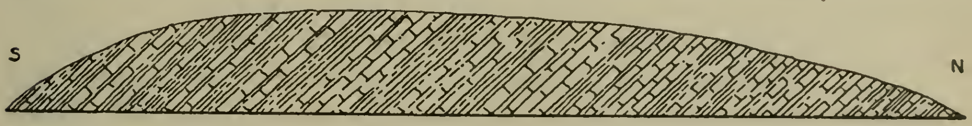


FIGURE 21. Montpelier Formation at St. Ann Bay.

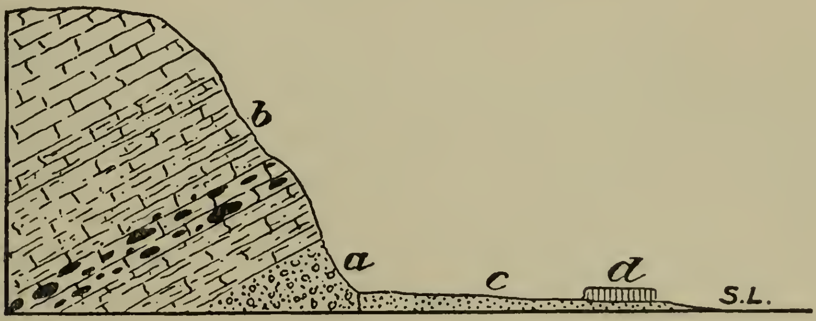


FIGURE 22. Section at Landovary. *a*, Richmond Beds; *b*, Montpelier Formation; *c*, Coast Plain; *d*, Elevated Reef, Sea Level.

lands to the coast, the Montpelier beds are magnificently displayed in the road cuttings. Here the road descends through a thousand feet of the white limestone, the lower half of which consists of the Montpelier beds.

The hill country back of Port Maria is largely made up of the Montpelier beds, which are also well exposed near Dover, where Globigerinæ chalks with flints make up the beds.

At the bluffs from one to two miles east of Buff Bay, which are more fully described under the head of the Bowden beds (see Figure 23 and Plate XXVII.), the Montpelier flint beds are seen beneath the Buff Bay formation. They are here exposed at and just east of the tunnel. This section shows gradation upward into chalks without flints, and reveals clearly that the Montpelier beds are stratigraphically below the Bowden Oligocene. Three miles east of St. Margaret Bay, at a high bluff, there is a good exposure of the Montpelier flint beds. The collections of the chalky limestone in which these flints were embedded consist of Globigerinæ. The beds here have a strong south dip. From the locality above mentioned to near Port Antonio, the flint bearing beds frequently outcrop in the bluffs and are capped by the Bowden beds.

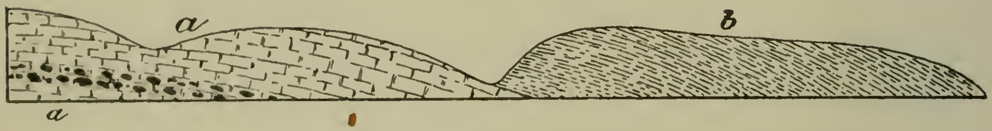


FIGURE 23. Section of Bluff East of Buff Bay. *a*, Montpelier Beds, with Flints; *b*, Bowden Marls.

The high bluffs backing the bay about one mile west of Port Antonio afford a good exposure of beds which apparently represent a phase of the Cambridge beds grading up into the Montpelier. Here the bluff is made up entirely of white limestones of varying texture and greatly disturbed. The lowest rock exposed is very hard limestone, subcrystalline in texture in some places, and in others showing thin lamellæ of blue-black clays suggestive of the Cambridge beds. From the lower and harder limestones casts of several of the molluscan species of the Cambridge beds were collected, including a gigantic Nerinæa and a Lucina. These fossils, together with the impurities of clay shale, suggest that this portion of the beds belongs to the Cambridge formation. Just above the foregoing strata there is a soft pulverulent bed of granular texture which is composed entirely of Cambridge Miliolidæ. The still higher strata of the bluff are apparently the Montpelier beds with flints. East of Port Antonio there are several other outcrops which belong to the Montpelier beds; from the literature we infer that they constitute the summit formation of the John Crow Ridge.

On the south side of the eastern portion of the island beds corresponding to the Montpelier have been noted in a locality mentioned by Sawkins,[1] near Orange Park, in St. David, where their relations to adjacent formations can be seen, and in Long Mountain back of Kingston. In our reconnoissances of this portion of the island, beds apparently belonging to this formation were seen between Bath and Bowden.

No exposure of the Montpelier beds on the south slope in the region between Long Mountain east of Kingston and St. Elizabeth is known. In fact the formation seems to be missing in the Bog Walk and Clarendon sections, though it may be represented there by a hiatus between the Cambridge and Brownstown formations. In St. Elizabeth the beds are again well exposed apparently unconformably below the Brownstown at Springfield and thence to Pisgah. From the details above given it is apparent that before its dismemberment during later erosion this formation completely girdled the island and entirely buried the old Blue Mountain Series in the western two thirds of its area.

The thickness of the Montpelier formation is difficult to determine, owing to lack of continuous exposures. Our observations have led to the conclusion that they do not exceed 1,000 feet. Everywhere these beds show great disturbance, but not to the degree of the Blue Mountain Series, usually consisting of more open folds.

The Montpelier beds are the deepest sediments preserved in the geological structure of Jamaica, and represent the culmination of the great subsidence initiated in the Cambridge epoch. Judging from the rapid transition between the littoral Cambridge formations and the chalks of the Montpelier formation, this subsidence must have been rapid in geologic time.

The age of the Montpelier beds most probably corresponds to that of the late Eocene (old classification) now called the early Oligocene, agreeing approximately with the position of the Vicksburg stage of our American Tertiary. This inference is based upon the position of the beds above the undoubted Lower Eocene of the Cambridge formation, and below the undoubted late Oligocene of the Bowden formation, together with the occurrence of Orbitoides mantelli.

---

[1] Jamaican Reports, p. 53.

The Moneague Formation. — The Montpelier beds grade up into more massive limestones, white in color, firmer in texture, often semi-crystalline, sometimes containing casts of fossil mollusks and solitary corals, and occurring in well defined bands of stratification from one to five feet in thickness. More massive texture and regular bedding especially distinguishes this formation from the other white limestones of the island, such as the chalky rocks of the underlying Montpelier and the irregular lumpy texture of the overlying Cobre formations. These rocks contain many cavernous moulds of Mollusca and single corals, indicating that a considerable amount of shell débris may have accompanied their original deposition. The fossils obtained near Ewarton, Retreat, and Cinnamon Hill, in a firm limestone matrix, were mostly poorly preserved moulds of corals and mollusks, which the paleontologists could not determine.

These rocks become very cavernous through interstitial solution and the surface is usually indurated and karrenfeldate. Sometimes the limestone is in small angular fragments or lumps with sharp edges, as if it had been shattered by some great stress, — a condition which may in part be due to shearing, but is also largely produced by irregular consolidation and solution. This angular aspect is well shown on the right hand side of Plate XXVI.

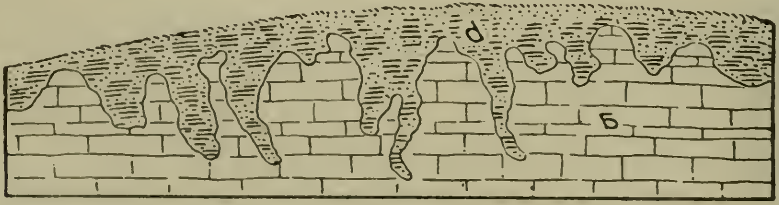


FIGURE 24. — Residual Clays in Limestone Sinks at Frankenfield.

In places the Moneague formation weathers into a yellow ferruginous clay subsoil, constituting a thick surface coating. This is the residual clay and iron which remains after the transportation of the soluble lime by water. Exposures along the railway between Porus and Ipswich show some beautiful subaerial alteration. Deep natural wells or pits are seen in the limestone. These are filled with the residual clay, similar to the occurrence previously shown in my report on Cuba. Where the soils of these limestones have been cultivated the ruinate is

---

[1] Notes on the Geology of Cuba. — Bull. Mus. Comp. Zoöl. at Harvard College, Vol. XVI. No. 15, 1875, Plate I. Fig. 7.

usually grass-covered and not retaken by shrubs and trees, as in the case of the abandoned soils of other formations.

William Hill has made microscopic examinations[1] of a rock from Mile Gully near Kendall in the centre of the island, 1,100 feet above the sea, which apparently belongs to the Brownstown formation. The nature of this material, as described by him, is as follows: "Mile Gully, specimen 1. Angular fragments set in a matrix of what was in all probability fine mud, but now granular calcite. The structure of the fragments and mud is obliterated by general crystallization. Mile Gully No. 2. Made up originally of large fragments set in matrix of fine mud. Structure of fragments mostly lost, outline shown by patches of crystalline calcite. Fragments of Lithothamnion and fragments of probably Amphistegina. Contains also ossicles of a recent starfish. Mile Gully No. 3. Patches of clear crystalline calcite in a matrix of granular calcite. One or two fragments can be seen to be Echinoid plates or ossicles."

Jukes-Browne and Harrison state that these specimens from Manchester and St. Elizabeth were found to resemble coral limestones,[2] and Hill also compares them[3] to rocks of this origin, but from these descriptions we do not see the resemblance, — especially to rocks of reef origin or reef débris.

From their usual association with and occurrence above the Montpelier beds, there is little doubt that they were continuously deposited with the latter, and possibly may represent shallowing but nevertheless deep water beds after the culmination of the Montpelier subsidence. Our knowledge of the upper contact of these beds is very deficient. In Clarendon and St. Elizabeth they clearly occur below the Cobre and Porus (Bowden) formations.

These beds occur at many places in the western half of the island, especially in the vicinity of Brownstown and Retreat, St. Ann Parish. At these localities, as in Trelawney, St. James, Hanover, and Westmoreland, they occupy the highlands of the interior, constituting the surface formation out of which the cockpit country is largely eroded. Beds of allied lithologic character are exposed at Moneague in the excellent cuttings along the Montego Bay between Ipswich and Catadupa; at Retreat, Trelawney Parish; at Cinnamon Hill, St. James Parish; on the north coast road, and in the bluffs at the railway station at Ewarton.

---

[1] Quart. Jour. Geol. Soc. London, 1891, Vol. XLII. pp. 248, 249.

[2] Ibid., Vol. XLVIII. p. 219.

[3] Ibid., Vol. XLVII. p. 248.

With the probable exception of the Mile Gully ridge, nearly the whole surface of the northern half of Manchester Parish, as crossed in a northwest and southeast direction by the Jamaican Railway line, between Porus and Phœnix Park, is composed of the stratified beds of the Moneague formation similar to the exposures at Ipswich, and consists of alternations of hard compact limestone, dull gray-white in color, semicrystalline in texture, with alternations of white calcareous chalky marls. The beds are quite cherty in places, which, with their stratigraphic proximity, suggest the nearer relationship of these beds to the Montpelier than to the Bowden formation. Casts of fossil Mollusca and small single stems of branch coral like those found at Retreat also occur. These beds are especially well displayed in the cuttings of the river near Williamsfield.

At Ewarton the railway terminal is quarried out of the beds which occur in massive uniform layers several feet thick. A few molluscan fossils weather out upon the surface of the rocks, but they are too indistinct for identification. From Ewarton to Moneague the beds can be seen from the highway, arching over the western border of the St. Thomas basin. At Moneague they have wide surface development, especially to the westward via Brownstown, Stuart Town, and Retreat. At Ipswich and thence on towards Catadupa the regular bedding is beautifully seen in the deep railway cuttings, as shown in Plates XXV. and XXVI.

We are not prepared to state positively that the beds of these different localities are identical, for paleontologic material is very rare, but from their resemblance we incline to think that future research will show them all to be parts of the same formation.

The Cobre Formation. — Between the town of Bog Walk,[1] on the south side of the interior basin valley of St. Thomas-in-the-Vale, and Spanishtown, on the Liguanea Coastal Plain, the Rio Cobre cuts a canyon through a white limestone plateau separating the two localities. This canyon, known as Bog Walk, is one of the great scenic features of Jamaica, and terminates at the Liguanea Plain as a true boca,[2] from which it took its original name, Boca del Agua.

The canyon of the Cobre is about 200 to 300 feet deep, with sloping sides, a fine view of which is shown in Plate X.; it is cut entirely out of certain problematic beds of white limestone, which will be described

---

[1] English corruption of Boca del Agua.

[2] Among other uses Boca is applied to the mouth of a canyon debouching upon a plain.

as the Cobre formation. The slopes are usually covered with dense vegetation, good rock exposures not being plentiful except in the immediate streamway. Even then they are encrusted with tufaceous material, so that their structure and arrangement are largely concealed. The following extract from the notes of our traverse of this canyon will give an idea of the composition and structure of these beds. Miles read north from Spanishtown.

0–4¼ miles.[1] — The river flows in a V-shaped alluvial plain indenting the canyon to this point.

4¼ miles. — A road metal quarry reveals the texture of the white limestone, which is here composed almost entirely of small angular lumps of firm limestone, chalky white in color, associated with a matrix of very fine pulverulent chalky sinter, free from clay, but commonly termed "White Marl," as are all other soft formations. There are also a few small lumps of compact gray or dove colored limestone (dolomite?). This formation is of cavernous or "honeycombed" texture and weathers into irregularly crystalline limestone, constituting ragged karrenfelder on horizontal surfaces. Furthermore, the faces of the bluffs are in places coated with self-derived tufa, and are so indurated that these outcrops have a massive non-stratified appearance. This limestone differs from that of the Cambridge and Montpelier beds in the entire absence of lamination or traceable lines of bedding.

4½–8½ miles. — The limestone is continuously exposed in the vertical bluffs through which the river cuts its way. No trace of bedding can anywhere be made out, and the surfaces of the cliffs are everywhere very indurated.

8 miles. — The inclination of the beds, hitherto indeterminate, shows a strong south dip.

8½–9 miles. — The vertical cliffs show dips to south of 30° (estimated), the angle increasing in steepness as we go north. While these exposures are more massive looking than those before noted, quarries reveal the same texture as that noted at Mile Post 4½.

9–11 miles. *Bog Walk Village.* — Here the canyon ceases, and the country opens out into the interior valley of St. Thomas-in-the-Vale. Superb exposures of the Cobre limestone and its basal conditions are shown in the bluffs at the upper end of the canyon, as illustrated in Figure 25.

The pebble and buff-colored marls grade into the limestone, and represent its initiatory littoral. A few poor and indeterminate casts of fossil

---

[1] From Spanishtown.

Mollusca occur in these beds. The lumps in the marl are largely fossils; three specimens are Echinoids, and one is a large Conus, two inches long. Casts of Natica and Cypræa were also recognized, as well as two species of coral, — one a simple form, the other a compound form, but both so poorly preserved as to be indeterminate. None of these forms suggest the Bowden fauna except the simple coral, and probably they represent a slightly earlier and preceding horizon.

From Bog Walk Station to a point where the highway to Linstead crosses the railway track, one and a half miles due north, following the south margin of the basin valley, the surface exposures consist of later alluvium. At the last mentioned point the railway cuts through an inlier of white limestone of the Cobre type. This exposure contains an abundant molluscan fauna, but all the specimens are poor casts, among which the genera Bulla, Arca, Cardium, and Lucina are evident. No corals or Echinoids were found. A few miles farther, at Linstead, the Moneague beds appear, apparently beneath this section. The aggregate thickness of the limestone of the Cobre section cannot be less than 1,000 feet, and is probably much more.

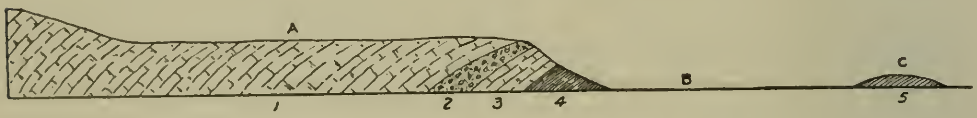


FIGURE 25. Section of Northern End of Bog Walk Canyon.

1. White stratified Cobre Limestone with Marl Pit.
2. Conglomerate of small Igneous Pebble.
3. Buff colored Limestone, banded.
4. Buff, granular, laminated Marl, with little Conglomerate, oxidizing Red.
5. An Outlier to North of this Locality, which will be described later.

The extent of the Cobre formation is not completely determined. We have personally seen the formation only on the south side of the central portion of the island. Good exposures of it are seen in Clarendon along the highway from May Pen Station, on the Montego Bay Railway, and Chapelton. Here the limestone has the same general character as that of the Bog Walk section, and constitutes the summits of the Minho Mountains. Between the Minho River and Retreat,[2] the limestone is underlain by more massive bedded layers resembling the Moneague for-

---

[1] Echinolampas or B. thiiopygus.

[2] Not to be confused with Retreat in Trelawney, previously mentioned in discussing the Brownstown formation.

mation. In this region the Cobre formation is very much honeycombed, and weathers into blood-red soils. At one place where laborers were blasting unusually large masses of the limestone, specimens from its interior were secured, which clearly showed the red iron blotches in the interstitial cavities.

There are a number of isolated outliers of this formation standing in the midst of the Liguanea and other plains composed of later alluvium in the parishes of St. Catherine and Clarendon, as shown in Figure 26.

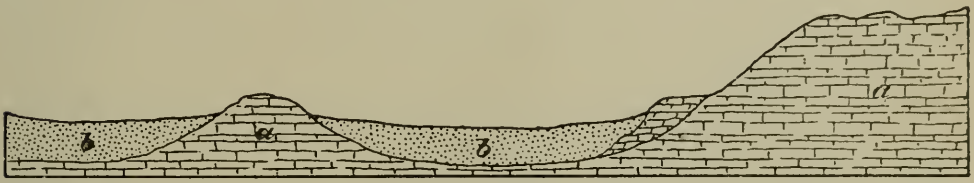


Figure 26. Outlier of Limestone in Liguanea Plain, near Spanishtown. *a a*, Cobre Limestone. *b b*, Kingston Formation.

These are of the type known in America as monadnocks. Two of these may be conveniently seen on the Kingston road a mile or two east of Spanishtown.[1] These consist of the same limestone as that seen in the Bog Walk section (see Fig. 25).

At the convict quarry back of Rock Fort, about four miles east of Kingston, where Long Mountain bluffs against the seacoast, a superb exposure of limestone has been made by quarrying. It is so lumpy that it is worked by the pick and used for road metal. Under the microscope it is composed of numerous undetermined species of Foraminifera, entirely different from those of the Montpelier and Cambridge beds. In the western group of parishes, forming the county of Cornwall, it may constitute the summit formation and pointed hills of the cockpit country. This idea is suggested by the lithologic aspects of the rocks comprising these hills, and from outcrops in Manchester along the highlands bordering the Montego Bay Railway. Close research has not been made to determine this. A prominent feature of the Cobre formation is the blood-red residual subsoils which everywhere result from its surface decay.

From the Bog Walk section it is evident that the Cobre formation lies stratigraphically above the supposed Moneague beds at Ewarton

---

[1] Lennox (Jamaican Reports, pp. 149–151) described the formation of these hills under the name of the "Port Henderson Limestone."

and below the May Pen formation. Its relations with the Bowden beds of our section are not established. It apparently occupies an intermediate position between the Moneague and the Bowden.

THE COASTAL SERIES.

Older Portion. — The Bowden and Allied Formations.[1]

This series includes a class of formations which represent the products of events more recent in the history of the Jamaican sequence than those hitherto enumerated. Its members occur around the coastal perimeter of the island, principally along the margins of the sea at altitudes nowhere exceeding 250 feet, and deposited unconformably against the sides of an older mainland. Here and there on the south coast they fill previously formed erosion plains. They were all made during epochs subsequent to an epoch of elevation whereby the white limestones of the Oceanic Series and all preceding formations had been elevated into land, had undergone tremendous denudation, and had again suffered partial marginal subsidence.

They are of four types of formations, to wit: beds of impure marine limestone, gravel, and marl; alluvium of the Kingston type; elevated coral reefs as illustrated in the Barbican and Hopewell formations; and littoral deposits of calcareous mud, with embedded fossils of contemporaneous origin with the elevated reef formation. The four types in their general lithologic characters are analogous to the marine littoral, alluvial, and coral reef formations now being made around the margins of Jamaica.

The Bowden Beds.[2] — The Bowden and allied formations of later Tertiary age constitute the older beds of the Coastal Series and are all marginal to the main upland mass of the island. They apparently represent a series of fringing formations extending around the older Plateau region. These in turn are bordered by still later and lower lying formations.

Along the south coast of the east end of the island, between Morant Bay and Port Morant, there is an extensive occurrence of gravel beds less than 50 feet in thickness, containing rolled specimens of nearly every species of volcanic rock found in the island, which grades upwards into an impure stratified brown and buff colored marl, the latter

---

[1] The "Yellow Limestone" of Etheridge, Wall, Jones, Woodward, and others; not the "Yellow Limestone" of Sawkins and Brown.

[2] This name is adapted from Dall.

having a thickness of 200 feet as measured in the bluff upon which Captain Baker's house at Port Morant stands. The loose gravels at the base of this section have a very recent appearance, a deception which is further aided by the fact that they occur at beach level, and contain perfectly preserved fossils resembling modern shells. The fossils heretofore reported from Bowden are found in the gravel bed, and, less abundantly, in a few feet of the lower part of the overlying marls, at the foot of the hill, at the beginning of the road leading up the hill to Captain Baker's, and in such abundance that as many as 400 species of Mollusks have been determined by Dr. Dall from two barrels of material collected by Messrs. J. B. Henderson, Jr., and C. T. Simpson and the writer. A few specimens occur higher up the hill, while near the summit there is a body of firm crystalline secondary limestone containing moulds of the characteristic fauna. The physical characters of this formation can be traced from Bowden to Morant Bay and beyond nearly to Yallahs Island, but there it loses its identity. On the road from Bath to Bowden its position above the Cambridge beds is fairly well revealed.

The stratigraphy of the formation has not hitherto been presented correctly, although in the Jamaican Reports under the name of the "Yellow Limestone" it was partially confused with the entirely different beds herein described as the Cambridge formation, and the gravel beds were mapped with the Pleistocene and recent formations.[1] Hence its identity as a formation did not appear in these Reports.[2]

It is only on the south coast of the east end of the island that the Bowden beds have the characters mentioned. It is evident that the formation with modified lithologic features occurs elsewhere on the island, for the Bowden fossils have been found on the opposite side by us, and reported from round the district of Vere near the coast of Clarendon by other writers, in formations of quite a modified lithologic

---

[1] Careful search of Barrett's writings show that he made two brief references to these beds. In one place (Jamaican Reports, page 44) he merely mentions "beds of marl, sand and conglomerate of the Bowden series," and alludes to sections and further descriptions to be given, but which were never published. Upon another page (Ibid., pages 45, 46), under the head of "gravels, clay, and yellow marl," he gives the following account of what we now know as the typical Bowden locality: "On the northeastern portion of the Port at Bowden we find the upper beds both thicker and more inclined (10° S. E.) than on the west, and are also more fossiliferous. Below the Pteropod marl are beds of the most perfect Tertiary shells yet known on the island."

[2] The fossils of the Jamaica Survey from Bowden in the Museum at Kingston are also labelled the "Yellow Limestone."

nature. Probably the Buff Bay, May Pen, and Porus formations, next to be described, are allied and synchronous deposits.

The Buff Bay Beds. — A formation closely allied to the Bowden beds is exposed in the superb coast bluff one mile east of Buff Bay on the north side. A good view of this is given in Plate XXVII. and the stratigraphical relations shown in Figure 23. This exposure consists of over 100 feet of bluish white, earthy, semi-indurated marl, containing very finely worn pebbles of igneous rock scarcely as large as peas, sparsely disseminated through it. It is in evenly bedded strata sometimes separated by thin laminæ of bluish calcareous clay. The beds contain many fossils, most of which crumble into calcareous powder on exposure to air, but some are sufficiently preserved to enable Vaughan to identify the corals. These beds at Buff Bay rest directly upon a pure white chalky marl, which in its lower part grades down into the Montpelier beds seen at the railway tunnel.

The beds of this locality are slightly more calcareous, but nevertheless are texturally related to the marl exposed at Bowden; they likewise contain gravel in very finely rolled particles, possibly indicating that the beds are a slightly deeper water stage than those exposed at Bowden. Probably the Bowden exposures represent the littoral of the formation, while those of Buff Bay are of slightly deeper water origin. The identity of the two localities is proved by the fact that one of the typical and peculiar fossil corals of Bowden occurs in the Buff Bay material as determined by Vaughan.

At Navy Island, a detached portion of the mainland lying off Port Antonio, there are impure yellowish clay marls and thinly bedded limestones. These are also seen on the point of mainland at Port Antonio on which the hotel of the Boston Fruit Company is situated. The beds at Navy Island have also been correlated with the Bowden beds by Duncan and Wall.[1]

The May Pen Beds. — At May Pen Parish of Clarendon, on the Montego Bay Railway, and extending from there westward to Clarendon Park and eastward to near Old Harbor, along an east and west line corresponding with the width of the parish of Clarendon, there outcrops a peculiar formation corresponding in general position to the Bowden beds of the east end. This material consists of a loosely consolidated mixture of yellow colored limestone lumps and clay marl, and contains many casts of Mollusca. The only good exposures we have seen are in the railway cuttings. The beds at May Pen clearly rest

---

[1] Quart. Jour. Geol. Soc., Vol. XXI. p. 14.

against the southern margin of the Cobre formation, as seen immediately back of the station in May Pen village; it apparently occurs along interior margins of the plain between Old Harbor and Clarendon Park, known east and west of the Minho as Harris Savanna and Lime Savanna respectively, and is thus apparently deposited along a former coastal margin which once here attinged against the low back coast uplands through which the Bog Walk Canyon is cut, and previously shown to be composed of the Cobre formation.

Stratigraphically the May Pen beds occupy a position immediately preceding that of the ancient alluvial deposits elsewhere described as the Kingston. Fossils are numerous at May Pen, consisting entirely, so far as we observed, of indeterminate casts of Mollusca, being free from corals, especially of the reef building species. Further study of this locality is very desirable.

The Porus Formation. — From the crossing of the Cobre to beyond Porus there are in the railway cuts many fine exposures of a formation resembling that at May Pen, consisting of loose, coarse textured yellow clay marls accompanied by irregular lumps of limestone and containing poor casts of fossils. Sufficient material was not obtained from it to determine with exactness its stratigraphic position, although it is, in general, to the coastward of the Bog Walk limestone, and apparently above it. The fossils which we have seen from it have facies more resembling those of the Bowden beds than of the later formations presently to be described.

There is also evidence that beds analogous to those of Bowden occur on the south coast of Clarendon Parish at the foot of Round Mountain near Bath, which, according to Sawkins,[1] contain fossils of the same genera as those found at Bowden (Port Morant). A coral from this locality described by Duncan, and an Orbitulina by Jones, indicate further identity of the horizons. Unfortunately, the writer has not visited this locality.

Of the beds described, only the Buff Bay and Bowden localities can be correlated with positiveness at present. The inclined position of the former shows that they participated in some of the later orogenic movements of the island.

The final key to the Jamaican sequence depends upon the determination of the upper relations of the Bowden and allied beds. That they clearly overlie the greater mass of the white limestones I am most positive, and are not at the base of all the white limestones, as asserted

---

[1] Jamaican Reports, p. 162.

without presentation of proof by previous writers, whose conclusions, as stated in the Introduction to this work, are known to have been based on the erroneous correlation of these beds with the Cambridge Yellow limestones which we know underlie the white limestones as a whole. That they lie entirely above the vast thicknesses of white limestone included in the Montpelier, Moneague, and Cobre formations is certain, and we have no reason to believe that any great mass of white limestones succeed them, the white limestones of the later formations being relatively trivial in comparative thickness.

The Coastal Series. — Later Portion.

The Manchioneal Formation. — On the abrupt east coast of the island, notably at Mulatto Bay and Manchioneal, and at various localities between those points, there is a marine formation composed of alternations of loose yellow marl and lumpy white limestone slightly resembling the May Pen beds, but differing in that it possesses in places well defined bedding planes and sometimes alternations of evenly bedded marl and impure limestones.

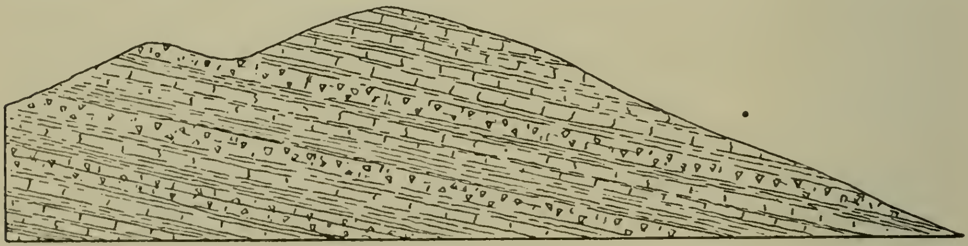


Figure 27. Exposure of Pliocene at Mulatto River with Coral Heads.

East of Pellew Bay are exposed 200 feet of a formation consisting of rotten and honeycombed white lime boulders, embedded in white marl which weathers exteriorly into yellow clay. Against the eroded sides of this is an unconformable deposit of elevated reef rock.

At Mulatto River the road cuts through superb exposures, showing 200 feet of beds similar to the foregoing, except that the limestone and marl are in persistent uniform alternations dipping strongly to the north. In these beds may be seen occasional heads of reef coral. About the middle of the section there is a ten foot stratum almost made up of the latter, which clearly represents old reef rock, the oldest thus far encountered in the ascending series of the Jamaican section. The accompanying figure will give an idea of these beds.

From Priestman's River to Manchioneal this formation makes a bluff 150 feet high, located slightly back of the shore line until within one mile of Manchioneal, when it approaches the edge of the sea. In the bluffs encountered just north of Manchioneal along the coast road are exposures of the formation 100 feet or more thick. Careful search for fossils in this bluff revealed only a few undetermined casts, — a few mollusks, a single species of reef building coral, as determined by Vaughan, many specimens of a Terebratula which Charles Schuchert has kindly studied as elsewhere reported, and a single pteropod.

The Manchioneal formation continues south of Manchioneal as far as Priestman's River at the east end of the island, where our traverse left the seacoast and turned inland via Bath, reaching it again at Bowden. The beds may also be exposed along the intervening strip of coast between Priestman's River and Bowden.

Barrett has reported from various localities at the east end of the island between Port Antonio and Morant Bay, at Old Harbor, Manchioneal, and capping the hill at Bowden, a formation to which he gave the name of the Pteropod Marls.[1] His lithologic and stratigraphic descriptions of this formation are so meagre that it is difficult to identify the beds to which he intended the name should be applied. Even why it was called Pteropod Marl is not apparent, as only three species of pteropods were reported from it. Others alleged that it was composed largely of Foraminifera, thirteen species of which, as determined by T. Rupert Jones, are enumerated on page 314 of the Jamaican Reports. Our reconnoissance of the east end of the island was largely made to study this formation, but we were unable to recognize any beds corresponding to it as a unit. We found marls with pteropods both at Manchioneal and at Bowden, each of which localities was specifically mentioned by Barrett, but inasmuch as these two places represent outcrops of distinct formations, the same name can hardly be applied to them, although there is but little doubt that they succeed each other stratigraphically.

Marine Pliocene formations analogous to the Manchioneal beds of the east are but sparsely represented in the western part of the island. At only one locality have we seen anything analogous to it. From eight to nine miles southwest of Montego Bay on the coast road at and near Round Hill, there are extensive beds of yellow marl, resting upon a foundation of the Montpelier white limestone, which occupy the stratigraphic and topographic position of the Manchioneal beds of the

---

[1] Jamaican Reports, p. 82.

east coast and closely resemble them in composition and texture. This formation is apparently the oldest of the Coastal Series of this vicinity occurring by later and unconformable deposition in a pre-eroded plain back of Montego Bay, which in former times was evidently a bight into the present back coast hills.

It is our opinion that the position of the Manchioneal beds along the south coast west of Yallahs Mountain is largely occupied by the older part of the Kingston formation next to be described.

Nowhere have we seen the Manchioneal beds occur at a higher altitude than 300 feet, if that high. Barrett[1] mentions them as occurring at a height of 140 feet at Blue Hole, and 300 feet near Port Antonio.[2]

From the low position of the Manchioneal formation adjacent to the coast and unconformably against the older and more disturbed white limestones, it is evident that it was a marginal fringing deposit. Its stratigraphic position above the Bowden formation and below the undoubted elevated reef rock to be described later, as well as the paleontologic evidence of its pteropods and Brachiopoda, indicate the Pliocene age of this formation. The contained corals, here poorly developed and occurring in increasing proportions in the succeeding beds, mark the first definite appearance of the marine reef building species in the Jamaican sequence.

The Kingston Formation.[3] — The extensive gravel covered plains of the south side of the island of which that known as the Liguanea is a type, have been fully described in the chapter "Geography and Physiography," Part I. of this Report.

These plains are composed of formations consisting mostly if not entirely of aggradational material derived from the adjacent uplands of the mountains and plateau. This material varies in composition, being mostly detritus of the Blue Mountain Series to the east of

---

[1] Jamaican Reports, p. 66. From his submarine explorations of the adjacent seas he estimates that similar deposits are now forming at 150 fathoms (900 feet), and that the sea bottom has been elevated this amount plus the present altitude of the formations (300 feet), or a total of 1,200 feet since they were made.

[2] Ibid., p. 82.

[3] The material of the Kingston and allied formations are well described under the general head of "Alluvium," in the portions of the Jamaican Reports dealing with the parishes of St. Andrew, St. Dorothy, Vere (now a district of Clarendon Parish), and St. Catherine. See Jamaican Reports, pages 101, 102, 142, 149, 161, and 186. They are also discussed under the head of "Plains" on page 100 of the same Report.

the Rio Cobre and largely white limestone débris to the west of that stream.

It has been successively accumulated through several geologic epochs, and may ultimately be classified into several distinct terraines. For the present, however, we shall recognize but two principal stages, — an older one, to which the name of Kingston will be applied, and a newer one, which will be called the Montego.

The Kingston formation is the oldest of the formations of old gravel and other alluvium occurring upon the plains of the Liguanea type. This is the formation upon which the city of Kingston and suburbs are built, including the strip of land known as the Palisades, and the plain extending back of Kingston to the foot of the mountains (see Plates VI. and XIX.). The material consists of boulders, gravel, and pebble of varying sizes, usually very angular, and representing every known material of the Blue Mountain Series. These are embedded in a matrix of dull red arenaceous clay, producing a chocolate soil and derived from the Minho beds so conspicuously exposed *in situ* in the mountains north of Kingston.

The thickness of this formation is unknown, but over 200 feet are exposed in the thalweg of Hope River, and probably fully this thickness is concealed. It is even likely that it may be nearly a thousand feet in places.

To the west in St. Catherine the material is similar in composition to all the rocks of the mother region drained by the Cobre. Sometimes it grades into a true marine marl, including some white limestone débris.

Concerning the origin of this material in St. Andrew, there is no doubt but it has been deposited by Hope River, as it debouched from the mountains. While most of the material was originally estuarine, some of its upper layers were made by talus fan deposits similar to those now seen in the arid region of North America where the mountain streams debouch upon the desert plains.

As a whole, it represents excessive deposition, first as estuarine or littoral material during an epoch when the coasts were submerged, and later talus deposits of subsequent epochs, when the land was rapidly rising and stream erosion was very active, as discussed more fully in Part I., p. 39, of this paper. The alluvial deposits in the bottom of the larger interior basins are also closely synchronous with the Kingston formation, and it is probable that these basins are products of the same great erosion epoch which preceded the Kingston deposition.

Fossils[1] are generally missing from the Kingston formation; speculation concerning its age must be founded entirely upon stratigraphical relations. In our opinion it is clearly older than the elevated reefs of the Barbican and Hopewell formations of presumable Pleistocene age, and younger than the Bowden formation, being nearly allied by position to the age of the Manchioneal which we consider Pliocene.

The present beds of both the Hope and the Cobre Rivers deeply indent the Kingston formation, cutting far below the surface of the plain. The alluvium of these stream valleys and their general level constitute distinct deposits which are later described under the head of the Montego formation.

The Elevated Reefs. — The coast of Jamaica, like many of the other West Indian Islands, is in places bordered by a peculiar formation composed of rocks which were once growing coral reefs similar to those now bordering the island, and which have been raised above sea level by general regional elevation in late geologic time. These formations are found in small, limited, interrupted areas in Jamaica immediately adjacent to the coasts, and at altitudes of less than seventy-five feet. They do not have the wide areal development which is seen on the north coast of Cuba, nor do they veneer the higher summits as in Barbados.

The elevated reef rocks usually constitute horizontal beds of strata from ten to forty feet in thickness. These have a more or less massive exterior, due to surface induration, but when cut into, as they frequently are by the undermining of the sea or in the construction of highways, their interior structure is seen to consist of porous limestone material of varying texture, always more or less minutely honeycombed, and of irregular hardness, with red oxidized spots or yellow patches here and there. They show all degrees of induration, from that of the practically unchanged reef material to firm semi-crystalline white limestones.

These rocks are composed of coral heads of various sizes embedded in a matrix of marl, — the latter being sometimes indurated into limestone. The heads usually have the erect position which they maintained when they were growing organisms. Some of these are of great size, one specimen, which can be distinguished in the illustration on Plate XXIX., was six feet in height. The marl represents the reef débris which is found between the growing or dead coral heads of living reefs, and is

---

[1] Brown, in the Jamaican Reports, page 166, describes a formation similar to that of the Kingston in the parish of St. Elizabeth along the coast from Alligator Pond Bay to Green Bay, in which remains of land shells are found.

often accompanied by shells of Mollusks, Echini, etc. In greatly altered reef rock the coral heads and marls become consolidated into firm semi-crystalline white limestones, marked by irregularity of texture and numerous minute cavities representing the original interspaces of the coral skeleton, or sometimes representing places from which the coral structure has been dissolved away. These cavities are frequently filled with red clay or sinter.

This reef rock not only in Jamaica, but in Barbados, Cuba, Panama, Haiti, Guadaloupe, and elsewhere, has an individuality whereby it can usually be distinguished from white limestones of other than reef rock origin. Even when greatly altered by interstital change, true reef rock shows by the traces of reef coral structure and by its rough, cavernous, crystalline, and altogether unhomogenous texture its original nature. Hand specimens showing no coral structure can be selected from a mass of reef rock, for mud, coral débris, molluscan shells, and even shallow water Foraminifera often fill considerable spaces between the coral heads. Such specimens are exceptional occurrences, however, and do not warrant the frequent generalization that great masses of limestone, which show no signs of coralline texture, may often be of coral reef origin. It may be considered reasonably certain that a rock mass in which remains of reef corals are not visible is not coral reef rock.[1]

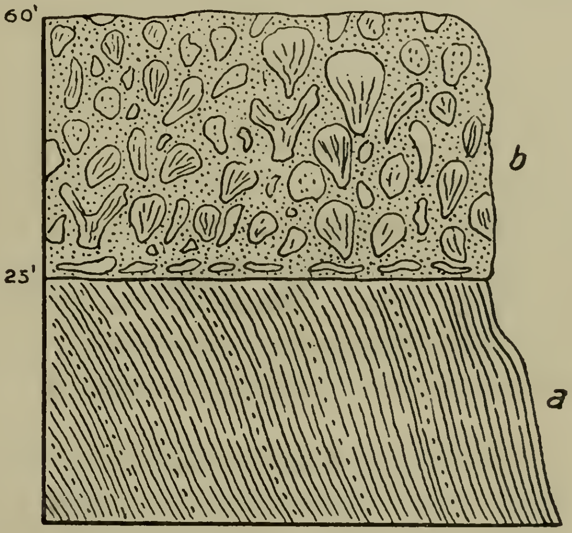


Figure 28. Showing Composition of Old Reef, 18 Mile Post, near Hopewell.

---

[1] "Coral reef rock is of very varying composition; the coral grows in hummocks separated by more or less narrow spaces which are filled up by coral sand, broken

Generally the Soboruco or old reef rock occurs immediately at the water line, forming an abrupt undermining bluff from five to ten feet high (See Plate XXVIII). In addition to the low level formation, two distinctly higher reefs are sometimes discernible, often a hundred yards or more back of the present beach line, at altitudes of 25 and 70 feet respectively, and constituting distinct formations. Owing to the fact that the old reefs of these three levels are conspicuous bench marks whereby the succession of other formations can be determined, we shall discuss them, where separable, under the names of the Coast Soboruco, Barbican, and Hopewell formations, respectively. Where not separable, or where their exact equivalence is indeterminate, the general term Soboruco will be used. Furthermore, while we believe the sequence of all the formations of the Coast Series is as given in the general table, page 42, for the purpose of discussing the reef made formations together, that order will be temporarily departed from and the latter will now be described.

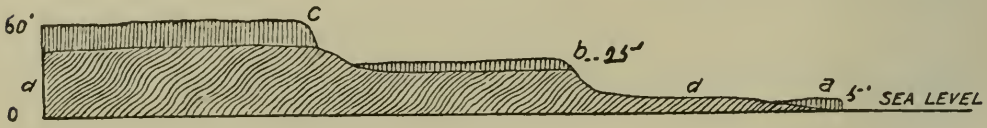


FIGURE 29. Relations of Elevated Reefs near Hopewell.

The best exposures[1] of the Soboruco observed by us were along the road following the coast of the east end of the north side of the island between Port Antonio and Northeast Point, but the sequence of the suc-

---

shells, Foraminifera, etc. Microscopic examinations of fragments of limestone broken from coral reefs sometimes show no traces of coral structure. Coral, moreover, is more readily decomposed than shell, sand, or foraminiferal limestones." — Nat. Sci., November, 1897, p. 290.

"*Coral-reef Rock.* — The rock forming the coral platform and other parts of the solid reef is a white limestone, made out of corals and shells. In some parts it contains embedded corals; in others, it is as compact as any Silurian limestone and without a fossil of any kind, unless an occasional shell. The compact non-fossiliferous kinds are formed in the lagoons or sheltered channels; the kinds made of broken corals, on the seashore side, in the face of the waves; those made of corals standing as they grew, in sheltered waters, where the sea has free access. Large portions are a coral and shell conglomerate." — Manual of Geology, by James D. Dana, Fourth Edition, New Haven, Conn., 1895, p. 146.

[1] The distribution of the Soboruco in Jamaica is well shown on the Geological Map accompanying the Jamaican Reports, and in the text it is discussed under the head of the Coast Limestone. The text of the Reports gives only passing attention to these rocks, and does not differentiate them into distinct formations.

cessive reefs is best shown on the west end of the north coast between Montego Bay and Lucea in the parish of Hanover.

Extensive patches of Soboruco border the coast two miles east of Port Antonio. This is made up entirely of large coral heads[1] and superficially consolidated into rough jagged surfaces. It forms a low bluff about ten feet high, which is being undermined by wave action. It extends back from the water only a short distance, and numerous indentations have been cut into it by the sea. There are similar exposures on both sides of Williamsfield Harbor, making the coast line for two or three miles. The horizontal surface of these constitutes a bench against the line of back coast hills, here composed of yellow Pliocene marl. In places in this vicinity the Soboruco is backed by swamps lying between it and the hills. These swamps may have once been lagoons attending the landward side of the Soboruco when it was a reef in the sea. On Plate XXVIII. is an illustration of the Soboruco bench in this vicinity, which shows in the foreground the jagged indurated surfaces of the rock, and in the middle ground and distance the undermining bluff and wave indented incisions. Plate XXIX. shows the composition and structure of the Soboruco, here made up of large individuals of reef making corals. The Soboruco of the east end of the island is unconformable upon the Montpelier white limestones, the Bowden, and the Manchioneal formations.

The straight east coast of the island which extends to Point Morant is reached after passing Northeast Point. At the mouth of Priestman's River a cross section exposing the entire thickness of an elevated reef is seen on both sides of the river for a considerable distance back from the sea, where it forms a vertical scarp some 25 feet in thickness. It overlies the yellow Manchioneal marls in which the present streamway is situated. This exposure of Soboruco is made up of gigantic reef coral heads and its surface constitutes a wide flat bench extending from the sea to the back coast mountains. The top of this old reef is about 70 feet above the sea, an altitude equal to the level of the Hopewell old reef formation on the west side of the north coast, and the greatest height at which any undoubted reef rock is known to occur on the island.

The Priestman's River terrace extends a considerable distance towards Black River. South of the latter as far as Holland Bay its level is continued by a baselevelled plain underlain by the older limestones,

---

[1] The species of corals from the localities mentioned are all given in the paleontologic portion of this paper.

probably the Cambridge and Manchioneal formations. Below this level the low coast Soboruco occasionally occurs in spots, as seen between Manchioneal and Hector's River where it stands about 20 feet above the sea and tips nearly all the little points of land projecting into it.

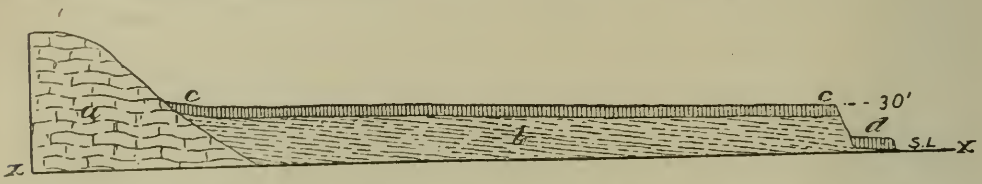


FIGURE 30. Section of Elevated Reef Rock at Mouth of Priestman River.
xx. Streamway of Priestman's River.
d. Later Terrace of Elevated Reef Rock.
c. Older Terrace of Elevated Reef Rock.
b. Manchioneal Beds.
a. Back Coast Mountains of White Limestone.

The east end of the south coast line, between the mouth of Hector's River and Bowden, was not examined, and we cannot from personal knowledge say whether or not the Soboruco exists there. None was seen on the south coast from Bowden to old Port Royal west of Kingston.

Our traverses between Annatto Bay and Falmouth on the north side were mostly through the back coast country, and did not immediately approach the sea except at Port Maria, St. Ann Bay, and between St. Ann Bay and Runaway Bay, but the Jamaican Reports, in the discussions of the parishes of Metcalfe, St. Mary, and St. Ann, under the head of "Coast Limestone," give good descriptions of the Soboruco at many points along this stretch.

One mile west of Port Maria a very small patch of Soboruco abuts against the foot of the great bluff of Richmond beds shown on Plate XXIII. This old reef stands about ten feet above the sea, and is cut by waves into detached islets, specimens of which are shown on Plates XXX. and XXXI. The material consists of coral heads, of which some were over three feet in length and had to be blasted away by the road builders.

Between St. Ann Bay and Runaway Bay, nine miles to the west of Port Maria, there is a narrow ribbon of coast plain abutting against a background of the flint-bearing Montpelier beds. The lowest Soboruco outcrops at several places along this road, and is apparently synchronous with the Falmouth formation described on a later page, which here sometimes replaces or grades into the reef rock. Patches of Soboruco tip the points of land to the east and west of Runaway Bay (not noted on the official geologic map), and nowhere does it stand over ten feet above the sea or extend back from it over a few yards.

Near Orange Bay east of Port Maria the railway cuts through a mass of old Soboruco some 25 feet in thickness, which is very much consolidated and crystallized, and resembles more nearly the true white limestones than any other exposure of old reef rock seen on the island. It is made up almost entirely of coral heads. Three miles west of St. Margaret Bay there is a bluff of very old looking Soboruco, standing 35 feet above the sea. Between St. Ann Bay and a point within four miles of Montego Bay, the coast plain for the most part consists of the beds of white marl elsewhere described as the Falmouth formation, although occasional patches of Soboruco are seen immediately bordering the sea, standing about five feet above mean tide level.

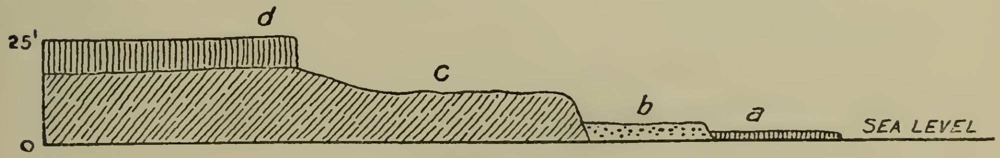


Figure 31. Elevated Reefs, Mile Post 97, Coast Road, East of Montego Bay.
a. Coast Reef.
b. Grand Plain.
c. Bench of Vertical Richmond Shales.
d. Old Reef.

About four miles east of Montego Bay there is a fine exposure showing two distinct terraces of Soboruco. The older of these is 25 feet high and corresponds to the Barbican terrace. This is a considerable distance from the shore bluffs toward the sea; the newer reef merely tips the coast at the sea margin, and is only five feet above it. There are several patches of the lowest Soboruco at the town of Montego Bay and on the western portion of the bay before reaching Round Hill Point in the vicinity of the mouth of Great River. Round Hill Point is an abrupt escarpment about 100 feet high. The background is composed of Montpelier white limestone. Against this, at a lower level are other beds possibly equivalent to the Manchioneal formation, while at the foot of the bluff is a small patch of Soboruco as shown in Figure 32.

In Hanover Parish, between the mouth of Flint River, twelve miles west of Montego Bay, and Lucea Harbor, are the best and most instructive exposures of Soboruco to be seen around the island. These consist of three distinct formations occurring at 70, 25, and 5 feet above sea level. The highest and oldest of these is well exposed at the 18 Mile Post from Montego Bay, near Hopewell (see Figure 28) along the stretch of coast between Mosquito Cove and the east point of Lucea Harbor. Here the highway is located upon a narrow strip of low coast plain, following an inland bluff whose base, to a height of 30 feet, is composed of the black shales of the Richmond beds, which stand almost vertically. Above these is a firm scarp rock of old Soboruco 30 feet thick. This Soboruco is made up of gigantic coral heads of many species, as shown on Plate XXIX. The heads are embedded in a matrix of dirty white and yellow marl, and have been so altered by induration and crystallization that they could be broken by the hammer only with great difficulty. The summit of this reef constitutes a level which is visible for several miles. It corresponds in altitude, thickness, and lithologic character with that elsewhere noted at the mouth of Priestman River near Northeast Point in Portland. This Soboruco is the oldest not only by occurrence, but also in appearance; the coral heads are more consolidated and crystallized, and the embedding material is of a yellow color indicative of long oxidation. The unconformable contact of this old reef with the almost vertical Richmond beds is clearly shown in a bluff over 100 yards in length.

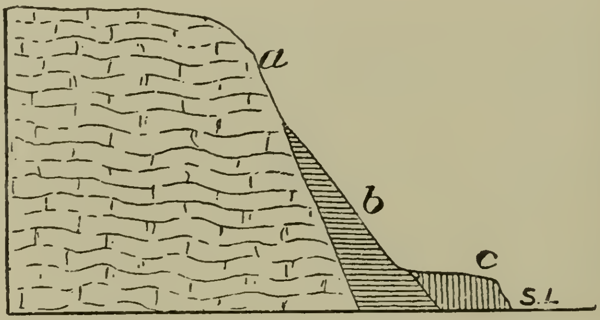


Figure 32. Bluff, West Bank of Mouth of Great River, near Round Hill Point, Montego Bay.

a. Back coast country of old White Limestone.
b. Yellow Marls allied to Manchioneal Formation.
c. Soboruco near sea level.

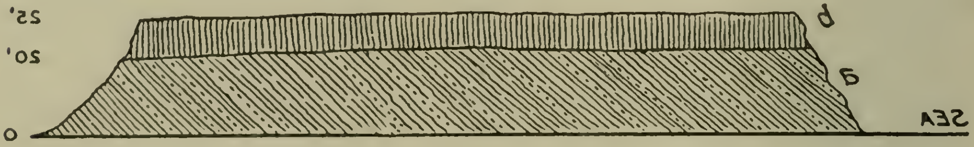


Figure 33. Old Reef unconformable on Old Eocene Clays near Barbican.

a. Subvertical Richmond Formation.
b. Reef Rock.

Another type of old reef rock is seen near Barbican, some three miles east of the foregoing locality, in an excellent exposure. This is similarly situated relative to the road and sea as the Hopewell Reef, and likewise occurs unconformably upon the black Richmond shales, here having a dip of 45 degrees. This old reef, which we term the Barbican formation, is only three feet in thickness, and is largely composed of a species of coral having an elongated cylindrical or club-like form, and a concentric arrangement of its layers. Figures 34, 35, and 36 show the occurrence of the Barbican reef and its relations to the adjacent topography.

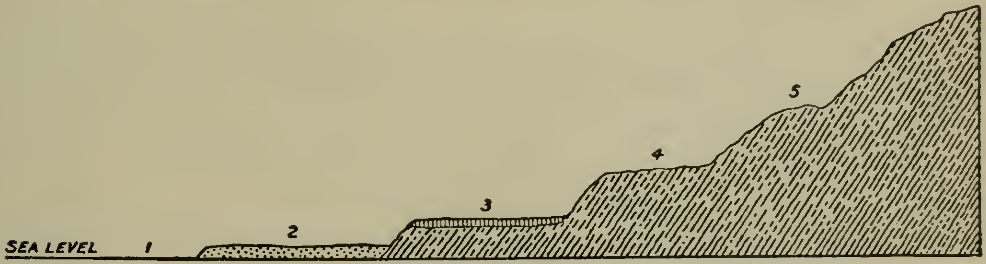


FIGURE 34. Elevated Reef and Profile near Barbican.

1. Caribbean Sea.
2. Low coast plain five feet above sea, and 200 yards wide.
3. The Barbican Reef.
4. A bench 70 feet above sea, occupying the level of the Hopewell Reef.
5. Back coast country, largely composed of the vertically tilted Richmond Beds of the Blue Mountain Series.

The juxtaposition of the Hopewell and Barbican reefs and the lowest coast terrace relative to each other are well shown in the topography adjacent to Mile Post 19, displaying three distinct benches or terraces against the mountainous back coast country.

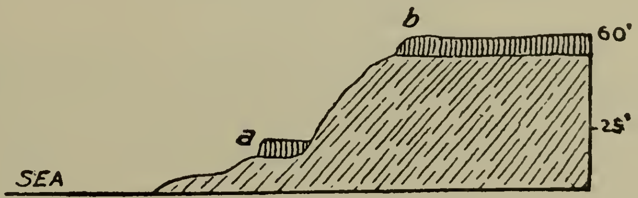


FIGURE 35. Relation of Barbican and Older Reef near Mosquito Cove.

Immediately at Barbican the Barbican terrace, or twenty-five foot level, approaches close to the sea and overlies a fossiliferous sinter or marl which is exposed at the foot of the escarpment, and which is full of molluscan fossils resembling those of the Falmouth formation.

This marl, in turn, is tipped at the sea by the lower Soboruco. A general section of the Barbican and lower rocks at this point is as follows.[1]

	Feet.
5. Coast Soboruco, made up of coral heads largely Meandrina, occurring at and four feet above sea level . .	4
(Unconformity).	
4. Coarse marl with shells and corals, irregularly indurated and cemented. Forms base of bluff . . .	6
(Unconformity.)	
3. Barbican formation. Soboruco of coral heads, firmly cemented, resting unconformably upon 1	8
2. Marly bed with many broken branch corals (reef débris) which generally underlies the above in this region .	4
(Unconformity.)	
1. Richmond beds, forming the fundamental rocks upon which all of the above are deposited. Only partially exposed.	

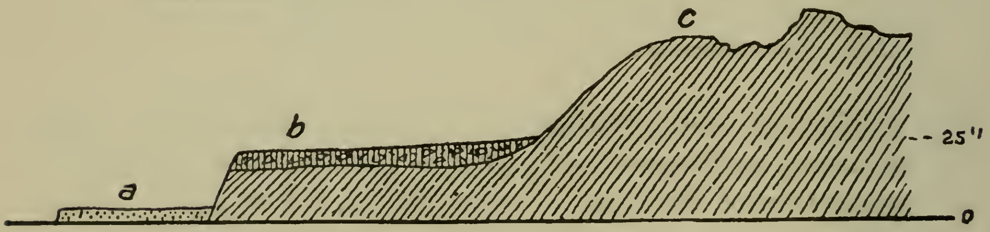


FIGURE 36. The Barbican Reef at Barbican.
a. Coast Marl.
b. Barbican Reef.
c. Richmond Beds.

From Mile Post 19 to Mile Post 21½ the coast topography shows only two of the benches, the immediate coast plain and the Barbican or twenty-five foot terrace, which projects out from the back coast hills. At twenty-one and a half miles from Port Antonio the seventy foot or Hopewell reef terrace again appears as a prominent feature in the coast topography.

Lucea Harbor has the shape of an elongated mule shoe and is a bight cut out of the land mass, here principally made up of the Richmond shales. The points of the harbor adjacent to the sea are tipped with the low coast Soboruco.

---

[1] In lithologic characters this agrees in the main with that given of the locality by Brown on page 248 of the Jamaican Reports.

The foregoing descriptions of the Soboruco practically include all localities studied by us, except the coast adjacent to Savanna-la-Mar. The observations include points around the entire perimeter of the island except the extreme west coast and the south coast west of Kingston.

FIGURE 37. Cross Section, West Side of Lucea Harbor.

a. Soboruco.
b. Elevated Reef.
c. Folded Richmond Beds.

Those portions of the coast not seen by us have been sufficiently described and mapped by the official surveyors to show that the Soboruco occurs at many points in them. From Brown's description of Westmoreland[1] it is evident that the ten foot or coast Soboruco, and the twenty-five foot or Barbican Soboruco, are each represented there at a different locality, the former between Scott Cove and White Hill Point, and east of Homer Cove, and the latter at South Negril Cliff. The same author[2] describes, in a general way, the Soboruco in St. Elizabeth, where it forms low cliffs 15 or 20 feet high and rests upon the "White Limestone." He ascribes it to a Post-Pliocene age. No definite mention is made of this formation along the coasts of Manchester or Clarendon (Vere) by the Jamaican geologists, although it is placed upon the map by them.

CONCLUSIONS CONCERNING THE ELEVATED REEFS AND THE HISTORY OF REEF BUILDING CORALS IN THE JAMAICAN SEQUENCE.

The old reefs grew upon marginal benches or terraces, which previous to their submergence were probably wave-cut constructional or gradational plains like those now seen upon the land configuration. As they successively rose during subsequent elevation to within 20 fathoms or less, the zone of coral growth, they were occupied by the polyps which constructed the reef which has since been elevated into land.

That Jamaica was once a more extensive land than now, with benched and terraced margins which were submerged by subsidence, is shown not only by the adjacent submarine configuration but by the elevated reefs

---

[1] Jamaican Reports, p. 228.

[2] *Op cit.*, pp. 208, 209.

themselves, such as that at Barbican, which can be seen to be clearly deposited upon a surface horizontally eroded across the vertical structure of the old Blue Mountain Series. Similar submerged plains are now occupied by the growing reefs around the island. That these elevated reefs were formed on former land surfaces which had been submerged and were in the process of emerging, is attested by every topographic feature. The streams have cut continuously downward through steadily rising old reefs, leaving no evidence of alternating periods of drowning between them, such as veneerings of later sea deposits across them.

Our studies of the Oceanic Series have shown that true reef building corals do not occur in the great mass of white limestone composing the structure of the back coast country of Jamaica, or at altitudes greater than 70 feet. Our paleontologic discussion also shows that the true modern reef building coral species first appear doubtfully in the Bowden beds, then sparingly in the Manchioneal formation, along the coast between Mulatto Bay and Manchioneal and near Round Point, Hanover. These and all succeeding beds containing reef coral occur only immediately adjacent to the present seacoast and unconformably against the pre-eroded perimeter of the main area of the island.

These reefs are laid down on various formations from the Richmond shale to the Manchioneal beds, respectively. On the north coast of the island they are seen in contact with the Richmond, Montpelier, Moneague, and Manchioneal formations, while upon the south side they lie upon the Cobre, Bowden, and Montpelier.

In general, the old reef rock of Jamaica consists of three distinct formations occurring at three levels, 70, 25, and 10 feet (or less) respectively. From the persistency of these three levels on the north, east, and southwest end of the island, it is evident that their present position above the water is due to continuous epeirogenic elevation after the present outlines of the island had been chiefly defined.

Miscellaneous Coastal Formations contemporaneous in Origin with the Elevated Reefs.

The present land margin is not continuously fringed by growing reefs, but they occur in interrupted patches, alternating here and there with strips of different kinds of bottom, such as alluvial deposits opposite the mouths of rivers, shell sand, or lagoon mud. Similar conditions prevailed during the time of the creation of the old reefs, and hence we find with them many diverse formations of contemporaneous origin, some of which will now be described.

The Falmouth Formation.

On the coast of Trelawney, Hanover, and Westmoreland, immediately adjacent to the sea and seldom rising more than 15 feet above it, there is a formation of white chalky marl, usually friable but frequently indurated. In this are preserved numerous mollusks and fragments of reef building corals. The fossils retain all the nacre and other characteristics of living species, and have been pronounced by Dall to be of Post-Pliocene age. This formation indurates in places into a close textured chalky white limestone, superficially indistinguishable from many beds of the Oceanic Series, but on close examination it can always be distinguished by the numerous fossils, as well as by its entirely different microscopic structure, which shows it to be old beach marl. Among the numerous fossils are many species still living in the adjacent waters, including Strombidæ and a small Bulla, the latter being the same which is common in the limestone of Yucatan, the island of Barbuda, and other localities in the West Indies. This formation is important, because it has wide occurrence throughout Tropical America, and, when properly studied, will assist in general correlation.

An outcrop of white limestone, similar to the Falmouth formation, occurs at Hospital Point, north of Montego Bay. This contains the remains of large Strombidæ, and other well known species living in the present sea. Fragments of coral heads of the reef building species are quite common in this material. Good collections of the fossils of the Falmouth formation were also made near Landovary about seven miles west of St. Ann. These consisted of many molluscan species associated with single heads of reef coral. The formation here is so indurated that it might well be termed white limestone, and easily confused with the white limestones of the Oceanic Series. In St. George and Metcalfe the formation consists of almost horizontal beds of white marl with the mangrove oyster, between Canewood and Spanish River, and from Low Layton to Retreat and Savanna Point.

The Falmouth formation was nowhere seen to be more than half a mile wide on the north coast, but on the southern coast of Westmoreland, back of Savanna-la-Mar, it indents the country for a considerable distance. Its occurrence at this locality has been well described by Brown under the name of "White Marl"[1] and "Bulla Limestone."[2] Here it consists chiefly of a soft white lime marl, usually bedded, and having some layers more eroded than others. Back from the coast the

---

[1] Jamaican Reports, pp. 229, 230.

[2] Ibid., pp. 228, 229.

fossil remains are few, but adjacent to it they abound and are well preserved. Owing to the fact that the formation here lies comformably upon the Montpelier beds, and that they have strong lithologic resemblance to it, it is difficult always to distinguish them. At Little Bay the fossils especially abound, and include numerous teeth of sharks. Thanks to Professor Duerden, of the Institute of Jamaica, we have Brown's collections from these localities in Washington, and they correspond perfectly with those made west of Falmouth on the north coast.

The marls and limestones of the Falmouth formation are consolidated sea mud, consisting of material exactly similar to the so called shell and coral sand which frequently makes the present sea border around Jamaica. It is entirely distinct from true reef rock, for it is not original reef material at all, although much of it may have been derived from reef débris. It is littoral organic oceanic débris which has been deposited around the perimeter of the island, along borders free from land sediment or in lagoons between the reefs and the land.

In age the Falmouth formation is newer than the older or highest elevated reefs, and probably synchronous with the middle and lower Soboruco; hence it must be assigned, like them, to the Pleistocene or a later epoch.

Miscellaneous Pleistocene and Recent Formations. — In addition to the old Kingston formation and kindred deposits in the interior valleys, there are many aggradational formations of more recent origin, around the margin of the island, occurring as alluvial streamway deposits disgorged along the coast, or gravel beds resulting from the undermining of the Richmond formation where it approaches the sea. The gravel of this material is mostly of the Blue Mountain Series, but it also contains pieces of various other formations.

The Montego Formation.

At numerous places around Jamaica are patches of swamp or morass adjacent to the sea and almost level with it. These are usually composed of alluvium brought down by the rivers, and are more recent than the Kingston formation previously described. They are well shown along the immediate coast at the mouth of Montego and Retirement Rivers south of Montego Bay town and thence around the coast, proceeding eastward, as follows: near Montego Bay town and Umbrella Point, St. James Parish; Half-Moon Bay, Trelawney Parish; Palmetto Point, district of St. George in Portland Parish; between Plantain

Garden River and the coast south of Morant Point; the Salt Ponds near Yallahs Point; bordering Hunt Bay between Cobre River and Apostle's Battery on the west side of Kingston Harbor; from Cabiretto Point to West Harbor on the east coast of the district of Vere, Clarendon Parish; along the south coast of Vere and Manchester from Portland Ridge to Cut River; between Star Cut Bay and Scott Cove extending inland adjacent to Black River on the southwest coast of St. Elizabeth Parish; from Bluefields Bay to St. John Point in Savanna-la-Mar; along the truncated west coast of the island between South Negril Point in Westmoreland Parish to Orange Bay in Hanover Parish, and around Green Island harbor, Hanover Parish.

Where these morasses extend a few miles inland up the rivers they occupy eroded indentations cut out of the lower Soboruco or Liguanea levels, as is especially well shown at Montego Bay, Long Bay, and the mouth of Black, Milk, Cobre, Plantain Garden, and Green Island Rivers. In one or two places, as along the north coast between Palmetto Bay and Buff Bay, the Salt Ponds, and elsewhere their configuration strongly suggests that they were originally lagoons on the interior side of barrier reefs.

These morasses are most extensive at the mouth of Black River, St. Elizabeth, and at Long Bay, west end; and near Morant Point, east end, where they extend back from the sea for two or more miles. Elsewhere they are elongated narrow strips less than a half mile in width and occur between the sea and the back coast border.

These formations occur relatively to the Manchioneal, Hopewell, and Barbican formations of the Coastal Series, in the same manner that the Coastal Series, as a whole, occurs relative to the rest of Jamaica, i. e. they are deposited in eroded bights and on eroded plains cut out of the preceding formations.

The Bogue Island Formation.

The last to be described, but by no means the least interesting formation of the Jamaican sequence, is that which composes a number of atoll-like islands in Montego Bay about one mile west of the city. These lie just off shore in the greatest indentation of the bay. Looked down upon from the elevated back coast hills, as seen in the illustration (Plate XX.), these islands appear to be a group of typical coral atolls, consisting of small circular belts of land enclosing interior lagoons. When visited and closely inspected they are found not to be of this character.

There are eight of these islands, none of which exceeds a few acres in area, and most of them are perfectly circular in outline. Five of the circular islands and one of quadrangular outline enclose interior lagoons. Until one puts foot upon them they appear to stand eight or ten feet above the sea, owing to the dense growth of mangrove trees which rise to that height. Then it is seen that several of them show no land whatever above the water, but consist of circular patches of mangrove trees growing out of the sea. Others visited by us consist of a low ring of wind-blown shell and coral sand, nowhere rising over three feet above the sea. A shallow living reef underlies the whole area of the sea where these pseudo-atolls occur, and constitutes the platform from which they rise. A typical island presents the following cross section, Figure 38.

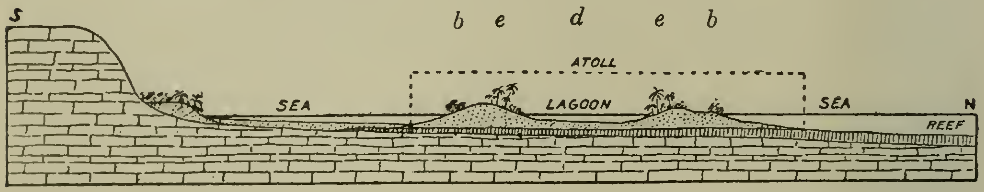


Figure 38. Cross Section of the Pseudo Atolls at Montego Bay.

d. Interior Lagoon of brown colored brackish swamp water.
e. Land composed of coral sand and shell, covered by palms and cocoanut trees.
b. A ring of mangrove bushes growing from the water around the island.
s. The floor of the sea is a living coral reef, with many Algæ, Echinoderms, Mollusks, etc. The top of this reef is about two feet below the surface.

We can offer only one hypothesis to explain these islets, and that is as follows. As described by A. Agassiz[1] in the instance of the Florida keys, "young mangrove plants drift in immense quantities upon the submerged flats which reach nearly to the surface of the sea or become awash." These grow up in clumps like some of the small islands now seen. By wind and wave action the reef débris is accumulated around the roots of these trees, gradually embedding them and ultimately rising above the water as land. The circlet of land thus made cuts off the older mangroves from the sea water. The older and original mangroves, now sand clogged, become the interior of the islet, and decay and die for want of access to salt water. Rain charged with carbonic gas from the decaying vegetation then compacts and dissolves the shell sand, and converts the central portion into lagoons around which newer land continues to be made by wave and wind. Meanwhile the new growth flourishes adjacent to the salt water.

---

[1] Three Cruises of the Blake, Vol. I. pp. 52, 53.

In addition to the true islets there is a circular head projecting from the land as a peninsula, the narrow neck of which, if severed, would leave an islet of the kind we have described. This and the land immediately back of the island is a mangrove covered morass of the type we have just described as the Montego formation.

Nowhere can so grand a combination of erosive and constructional processes or the successive formations of the Coastal Series, as a whole, and their relations to the older formations of the island, be seen in a single view as at Montego Bay. This is a great indentation into the coast, the back country of which is composed of beautiful hills covered with tropical upland vegetation, rising in a series of grand terraces to a height of 1,000 feet or more, as shown in Figure 6 and on Plate XX. This plain is composed of the following formations of the Coastal Series: the Manchioneal beds, the twenty-five foot level or middle old reef, the low level Soboruco, and the Montego formation, while the Bogue Island formation barely appears above the waters of the bay. In the shallow bay fringing reefs are growing, and Mollusks, Echinoderms, and other sea shells are dying and contributing shell débris, which near the shore is mingling with the aggradational alluvium brought down by the rivers. Elsewhere it forms great deposits of purest calcareous sand.

The Montpelier formation, with its contorted beds of chalk and flints, forms the back coast hills in which this scene is set, and against which the various other formations lie in unconformable contact. Fragments of the yellow marls allied to the Manchioneal formation can be seen against this on the west point of the harbor between the mouth of Great River and Round Hill Point. The old Soboruco, now converted into a white limestone rising fifty feet or more, constitutes the opposing northeast point of the bay. The railway station back of the town is upon a low level plain made up of shell bearing marls equivalent to the Falmouth formation, while the low coast Soboruco borders the sea at the city and Round Hill Point. The Montego formation occupies a still lower plain, almost or at sea level, cut out of the low Soboruco and Falmouth formation, as seen in the morasses south of the city. The indentation comprising the bay and coastal plain was cut by the combined forces of erosion baselevelling the land, and wave action indenting the shore, probably in late Pliocene time; afterwards this plain was submerged, veneered by deposited sediment from the land, and inhabited by growing reefs. Later elevation brought the interior margin of the bay above the water, constituting the present low land extending between the sea line and the back coast hills, while coral reefs continued to grow upon the shallow portion which remained submerged. These processes are more fully discussed in the chapter dealing with the geological history of the island.

THE IGNEOUS ROCKS OF JAMAICA.

The following discussion of the igneous rocks of Jamaica is based upon our field observations, including a study of the principal localities enumerated in the Jamaican Reports and many new exposures opened to view by the construction of the Port Antonio Railway; the microscopic studies of specimens collected by us, and of those collections of the Jamaican Survey which were loaned us by the Museum of the Institute of Jamaica, are by Whitman Cross. No microscopic studies of Jamaican igneous rocks have hitherto been made, so far as we are aware, nor has any systematic discussion of the rocks been attempted, although details of occurrence are given in the Jamaican Reports.

Barrett, speaking of the porphyry in St. Thomas,[1] said in an early paper that it is "evident that the igneous rocks (porphyries) forming the base of this series, and interstratified with some of the shales and conglomerates, were erupted prior to the deposition of the Cretaceous limestones, and at intervals of time sufficient for the formation of interbedded aqueous strata." This assertion may have led the geologists in England who wrote the Appendix of the Jamaican Reports to believe these rocks fundamental, but Barrett himself, as well as Sawkins, in their later reports on the eastern parishes of Jamaica, clearly show that the rocks are intrusive and not fundamental. (See description of Blue Mountain Series on pp. 51–53, also pp. 111, 112, of this work.)

Sir Roderick Murchison has said that the igneous rocks "are for the most part either of the Miocene age, or posterior to that era; some of them, as is well known, having been indeed recently erupted."[2] One would also infer a pre-existing foundation of igneous rocks beneath the sedimentary section of Jamaica from the columnar section on page 341 of the Jamaican Reports, and the unqualified statement by Etheridge, page 306 of the same Reports, that "the conglomerate and Cretaceous series rest upon Granitic and Porphyritic rocks," and from numerous references to granites throughout the body of the Report. Careful study of the individual reports upon the different parishes re-

---

[1] Quart. Jour. Geol. Soc. London, 1860, Vol. XVI. p. 326.

[2] Jamaican Reports, Introduction, p. iv.

veals the fact that the rocks alluded to are clearly intrusive into the overlying sedimentary section. Our personal observations enable us to say positively that, while the oldest known rocks of the island are undoubtedly rolled eruptive volcanic débris, no fundamental massifs of plutonic crystalline rocks, granite or other kind, are known to occur as a previously formed basement or axis to the sedimentary section of Jamaica. On the other hand, these rocks, by occurrence, are all eruptive and intrusive, and in age are contemporaneous in origin with the sedimentary rocks.

The igneous rocks can be classified by age, occurrence, and mineralogic composition into three distinct categories, as follows: —

I. The andesitic (mostly hornblende) boulders, pebbles, and tuffs of the Blue Mountain Series, of eruptive origin from unknown vents, contemporaneously deposited with the Cretaceous sediments of the lower beds and occurring as rolled and worked over material in the Richmond beds of the upper part of that series.

II. The hornblende diorite and granitoid porphyries of the five eastern parishes of the island, constituting dikes and masses, or laccoliths, intruded through the rocks of the Blue Mountain Series and into the Montpelier formation of the Oceanic Series. These rocks are of Mid-Tertiary age.

III. Eruptive amygdaloidal basalts of the Low Layton stock or volcanic neck in the north coast of Portland. Mid-Tertiary.

I. *The Boulder Material of the Blue Mountain Series.* — In the general description of the Blue Mountain Series we have noted the predominance of conglomerates, boulders, pebbles, and tuffs, composed of rolled volcanic rock, and the fact that the accompanying shales and sandstones are made up almost, if not entirely, of this material, which has undergone aqueous trituration. This boulder material is the oldest formation exposed on the island, and it has survived by rolling and redeposition through all succeeding epochs, being especially conspicuous in the Richmond, Bowden, Kingston, and modern aggradational deposits.

Particular attention was paid by us to the study of the composition and origin of this material. Specimens from what are apparently the oldest formation of the island, — the Frankenfield conglomerates of the Rio Minho section of Clarendon, — as determined petrographically by Cross, show that the material is almost exclusively composed of hornblende-andesites and hornblende-andesite tuffs.

Original masses *in situ* from which this boulder material could have derived, are nowhere known to be exposed on the island, and hence its exact mode of origin is questionable. From its vast quantities, — probably aggregating 3,000 feet in thickness, — its eruptive nature, its size and freedom from foreign material, and the occasional colonies of Cretaceous species which found temporary foothold during its deposition, there can be no doubt but it represents the piled up débris of a great volcanic vent or vents which rose from the waters of the Caribbean Sea in Cretaceous time, approximately where the island of Jamaica now stands, and constituted a nucleal land around which all subsequent terrigenous formations now entering into the structure of the island, and largely made up of its worked over materials, were derived. This fact is one of the most apparent in Jamaican history.

There is some reason to believe that the eruption of the hornblende-andesites continued throughout the epoch recorded in the deposition of the lower part of the Blue Mountain Series up to the time of the commencement of the Richmond formation. The thick beds of tuff alternating with beds of black shale in the Minho beds of the Clarendon section are the last of the undoubtedly volcanic formations in the series.

The more regular stratification and composition of the Richmond beds, although containing vast amounts of water worn volcanic pebbles, indicates that the sedimentary conditions had become more stable and were free from the disturbing effects of volcanic outbreaks. The pebble and conglomerate beds in the Richmond Series are much water worn and distinctly stratified, and occur interbedded with the shales and sandstones, or, when traced out, pass continuously into the latter, which is largely made up of water-rolled grains of igneous rock. These conglomerates are mostly composed of the hornblende-andesite with rolled fragments of Cretaceous limestone. Wall has noted from the Port Maria bluff (see Plate XIII.), from which he collected the Eocene corals described by Duncan, a singular admixture of pebbles composed of "gneiss and crystalline slates, rocks of which no trace either *in situ* or otherwise had hitherto been noticed in the island."[1]

In addition to the hornblende-andesites in the Richmond gravel at Port Maria, Cross found one which may be a dacite. He describes this as follows: —

"No. 52 *a*. — Port Maria. (Pebble in Richmond formation.) A probable surface volcanic rock. It contains many fresh plagioclase crystals with glass inclusions, a few augite prisms, and very little magnetite. The predominant groundmass is cryptocrystalline and may contain a

---

[1] Jamaican Reports, p. 130.

large amount of silica. The rock is to be generally classed with the andesites rich in silica and poor in iron, and thus may be a *dacite*."

Whether these are exotic or have been derived from more ancient rocks composing the structure of the island and now concealed by later formations, are speculative questions. For the present it is only safe to say that, together with all the other pebbles of the Richmond beds, they are detritus derived from rocks which were originally made in previous geologic epochs, and that there are no indications of contemporaneous volcanic activity during the Richmond epoch.

II. *The Hornblende-diorites, Porphyries, and Granitoid Rocks.* — These rocks are found *in situ* only in the third of the island lying east of a north and south line between Spanishtown and Port Maria in the parishes of St. Andrew, St. Mary, Portland, and St. Thomas, and barely extending into the northeast corner of St. Catherine.

They occur as dikes cutting through the Blue Mountain Series into the Oceanic Series, and as deep-seated interior masses from which such dikes extend upward. These are the "granites," "syenites," "diorites," and "porphyries," in part, of the Jamaican Reports, which contain many excellent detailed descriptions of their occurrence,[1] but nowhere satisfactorily discuss or fully describe them as a whole.

The terms granite, syenite, and porphyry are used interchangeably in the Jamaican Reports for what is practically the same rock or differentiation of the same magma, which being true, most of the rocks under discussion can be reduced to two classes, the first of which is the above mentioned gneiss of porphyritic granitoid rocks, the second, hornblende-diorites. According to Cross, the latter are "all simple normal granular rocks, with much more plagioclase than orthoclase, common green hornblende, and some altered biotite. The quantity of orthoclase and quartz varies in different specimens." In occurrence these rocks cannot well be separated from one another, or at least have not yet been separated. In St. Thomas-in-the-Vale [2] the syenitic, dioritic, and feldspathic porphyries seem to succeed one another to the westward.

While certain rocks are called granites throughout the Jamaican Reports,[3] Sawkins in speaking of these has clearly noted that they differ from the true granites by the absence, abundance, or replacement of one of the constituent minerals. "It must, therefore, be understood

---

[1] They have also been described by De la Beche, but in both cases without microscopic aid.

[2] Jamaican Reports, p. 139.

[3] Ibid., p. 106.

that the composition of this rock throughout Jamaica is not always that of quartz, mica, and feldspar, which are the constituents of true granite, but more frequently feldspar, hornblende, and quartz, . . . and throughout the whole series feldspar and hornblende occur more abundantly than quartz."

According to the microscopic studies of Cross, the exact nature of these so called "granites," "syenites," and "porphyries" is as follows: —

"Specimen No. 95. — On road to Blue Mountain Peak. A very distinct porphyry of the structural type common in the laccolithic masses and intrusive sheets of probable early Tertiary age in Colorado, and adjacent territory. The rock is near the line between granite-porphyry and quartz-diorite-porphyry, its feldspar crystals are so much decomposed that their character cannot always be made out. Some are plagioclase, some may be orthoclase. I think the rock had hornblende crystals in its fresh state. Now the ferro-magnesian constituents are so far decomposed that they cannot be identified. They were never abundant. The groundmass consists largely of quartz and orthoclase in a fine earthy granular structure."

"Specimen No. 146. — Feldspar Porphyry. District of Port Royal. Salt River. Shelf 6, Institute of Jamaica. Labelled Metamorphic Series. A much altered porphyry with small phenocrysts of orthoclase and plagioclase and a dark silicate now indicated by calcite and chlorite. The outlines of this latter constituent are not sufficiently clear to permit inferences as to whether it was augite or hornblende. Groundmass has some quartz but is mainly orthoclase feldspar."

"Specimen No. 207. — Copper in syenite. District of Metcalfe, Parish of St. Mary. Shelf 7, Institute of Jamaica, 'Granitic Series.' A granite porphyry with much quartz in its irregularly granular groundmass. Pink orthoclase feldspar is the principal component, in irregular large grains seldom of good crystal form, and in the groundmass with quartz. Chlorite replaces a former dark constituent, — probably biotite.

"This granitoid group of rocks, exposed by erosion at many places in the Blue Mountain region, is best developed in a limited area embraced in the district of Port Royal (St. Andrew Parish, St. George, Portland, Metcalfe, St. Mary), and immediately adjacent to the corner of the parishes of St. Andrew, St. Mary, and St. Catherine. All these localities are in a small district of the island near the western half of the Blue Mountain range, occurring in some places over considerable areas. Sometimes these apparently occur beneath all the sedimentary rocks, but usually they can be clearly seen as dikes, stringers, or masses protruding into the overlying rocks, which clearly show their subsequent origin."

Splendid exposures of hornblende diorites are seen along the highway and railroad as they follow the valley of the Rio Doro for five miles, between Williamsfield, St. Catherine, and Newport, St. Mary. Usually these are very weathered and so decomposed that they break down into friable rotten yellow and ferruginous débris, which is cut away with spades by the road makers, but maintains a porphyritic structure to the last. Just north of the new iron bridge the railway cuttings exhibit for the first time exposures of the material in a fresh and comparatively unaltered state, specimens of which are the basis of Cross's description. This material everywhere has a vertical arrangement, as if it had been thrust up from below. On the south side of the area in St. Catherine it is overlain by the Cambridge formation, while to the north near Richmond, St. Mary, it is covered by the Richmond beds.

The intrusive nature of these rocks, both dioritic and granitoid, is seen everywhere throughout the districts mentioned. The dioritic dikes abound in the same localities east of Clarendon, traversing the whole of the Blue Mountain Series.[1] In fact, wherever the rocks of this series occur east of Clarendon, the intrusions can be seen pushed through the strata and altering the adjacent rocks. But few of these dikes are of narrow even sided proportions, but are mostly broad and ragged, and often 300 feet or more thick.

In Metcalfe the granitoids underlie and protrude into the conglomerates of the Minho beds. In the Plantain Garden region according to Barrett,[2] these are immediately below the Hippurite bearing Cretaceous limestone; in Portland, *vide* Barrett,[3] south of Port Antonio, they underlie the same limestone, which has been highly altered and metamorphosed along the line of contact. Between Guava Ridge and Content they have pushed up into the shale beds of the Blue Mountain Series,[4] as seen by us; in St. Andrew they clearly protrude through the various rocks of the Blue Mountain Series.[5] South of Port Antonio they have apparently elevated all the rocks of the Blue Mountain Series and the Montpelier beds of the Oceanic Series;[6] in St. Catherine they occur between the top of the Blue Mountain conglomerates and the base of the white limestones, and abut against and metamorphose the latter in the northeast corner

---

[1] Jamaican Reports, pp. 65, 71, 93, 95, 112, 122, 144, 188.

[2] Ibid., p. 308.

[3] Ibid., p. 75.

[4] Ibid., p. 97.

[5] Ibid., p. 105.

[6] Ibid., p. 86.

of the parish;[1] according to Lennox,[2] "the granite in the adjacent regions of St. Thomas-in-the-Vale is certainly posterior in date to the White Limestone."

The numerous observations of the Jamaican geologists, verified by our own, justify the opinion expressed by most of them that these so called granites are of Tertiary age,[3] and we think at least of a date later than the Montpelier epoch, — a conclusion borne out not only by the facts presented but also by the absence of the débris of these rocks in the conglomerates so abundant in the preceding formations.

From the fact that the composition of these rocks shows them all to be of deep seated origin, and from their occurrence as masses beneath various formations into which they send dikes and sills, and owing to the fact that no evidence exists that they were ever protruded to the surface, we believe they represent the various phenomena of a great laccolith which in Tertiary (Middle Oligocene) time was protruded upward into the then existing formations of the Jamaican sequence. Furthermore, it is our opinion that the intrusion of these rocks was associated with the elevation of the island, and the progressive shallowing so evident in the ascending sequence of the White Limestones, whereby they changed from the deep sea foraminiferal deposits of the Montpelier beds into more shallow limestones, and, finally, into the land areas which existed at the time of the peripheral deposition of the Bowden Oligocene.

III. *The Low Layton Eruptives.* — At only one locality on the island is there supposed evidence of the occurrence of true eruptive rocks *in situ*, or of igneous rocks of later age than those already described. This is at the Black Hill near Low Layton, adjacent to Savanna Point, on the north coast, between Bluff Bay and Hope Bay, in the parish of Portland. This is a ridge extending from the seacoast near Retreat to near Low Layton, accompanied by one or two outliers and reaching an altitude of 700 feet. Here it has been asserted there is a neck or stock, or possibly the remains of old lava flows of what was once apparently a true volcano protruding through the Pliocene limestones. This hill has undergone great denudation.

---

[1] Jamaican Reports, p. 146.

[2] Ibid., p. 147.

[3] Barrett (in the Jamaican Reports, p. 81) states: "The porphyry has altered the Cretaceous and Eocene rocks, and it is contemporaneous with the lower part of the White limestone series, so that it was erupted after the deposition of the Eocene (Black Shale) series, but before the formation of the Pliocene (White limestone ?) strata; its geological age is therefore Miocene" (Oligocene). See also pages 146, 182, of same report for like opinions of other writers.

This material and the accompanying phenomena of the outcrop have been described by Brown,[1] as follows: —

"The kinds of rock of which it is composed are amygdaloid and a pasty-looking brown agglomerate. The amygdaloid is composed of a hard blackish base or matrix containing kernels of carbonate of lime, and the agglomerate is made up of blocks of this amygdaloid embedded in a reddish iron stained material, which is extremely siliceous. Down the slope from the top of the volcanic ridge to the valley the bare patches of brownish lava, with blocks of amygdaloid sticking in them, evidently indicate the direction of the old lava flows. Masses of rock jut out from the face of the hill, which have all the appearance of huge rubble walls cemented with lime; on examination they are found to consist of large blocks of lava intermingled with white limestone. In these the limestone has become cherty."

Two hand specimens of this rock petrographically studied by Cross were determined by him as follows: —

No. 143. — District of St. George. Low Layton. Basalt. (Plagioclastic.) Fresh typical basalt, holocrystalline, vesicles filled with crystalline calcite. No Globigerina.

No. 141. — Low Layton. Dense reddish groundmass obscured by ferritic material and containing olivine (altered), plagioclase, and augite. Vesicles partly filled with very distinct Globigerina.

Since the date of Brown's observations, the Jamaican Railway has tunnelled through the base of the hill, but the only new data it contributes is the fact that the igneous rocks are encountered 700 feet below the summit of the hill, and shows the latter to be of the nature of a volcanic neck rather than an entirely superficial lava flow.

It is also probably older than the Post-Pliocene to which Brown assigned it. Our reasons for the latter conclusions are as follows. The fact that the débris of the basalt is intermingled with the flint bearing white limestone of Vicksburg age (supposed to be Miocene or later by the Jamaican Geological Survey) does not necessarily prove the Post-Eocene age of the basalt. On the contrary, the presence of the characteristic fossils and chalk of the Montpelier limestone in the scoriaceous cavities of the basalt clearly shows that this limestone was deposited contemporaneously with or after the basalt. The yellow calcareous marls described as lying almost horizontally upon portions of the volcano were tentatively considered at the time of our examination to be the Buff

---

[1] Jamaican Reports, p. 120. These rocks were also mentioned by De la Beche, *op. cit.*, pp 185–187.

Bay (Bowden) formation of late Oligocene age. If this hypothesis is true, then the Low Layton rocks were made before or during the Montpelier epoch and previous to the Bowden Oligocene. Further research is necessary to determine this question finally. In any event, the Low Layton "volcano" represents the latest of the igneous rocks in Jamaican history, and nowhere are there evidences of further vulcanism.

Metamorphic Influences of the Tertiary Intrusives. — The intrusion of these granitoid and dioritic rocks into the strata of the Blue Mountain Series and lower part of the Oceanic Series has locally produced extensive metamorphism of the adjacent rocks, baking the shales into hard friable slates, and indurating the Cretaceous limestones. According to Sawkins,[1] even the white limestone in St. Catherine "is so completely metamorphosed as to be entirely different from the ordinary type." The Jamaican geologists have also asserted that in places the shales have been converted into porphyries[2] and the limestones into serpentines. We are not prepared to affirm or deny these assertions.[3]

In localities where the metamorphism and alteration of the Blue Mountain Series has been extensive, the Jamaican geologists have referred to the rocks under the formation name of the "Metamorphosed Series," which they have distinctly defined[4] as "conglomerates, shales, sands, and limestones, that have undergone various changes by the intrusion of igneous dikes." It is evident from their descriptions, as previously noted, that they did not intend to give these rocks a definite place in the Jamaican section otherwise than contemporaneous with the conglomerates, shales, and Cretaceous limestones of the Blue Mountain Series in general; but the editors of the final table in the Reports,[5] and of the general geologic map and sections, have given this series a definite position in the geologic section below the "Hippurite limestone" and above the "granite and syenite," thereby creating the erroneous impression that the metamorphosed beds constitute a distinct formation.

---

[1] Jamaican Reports, p. 147.

[2] Ibid., pp. 62, 188.

[3] Ibid., p. 62.

[4] Ibid., p. 41. See also p. 105 for a similar definition.

[5] Ibid., p. 341.

PART III.

Paleontology of the Jamaican Sequence.

The entire Jamaican section contains many unfossiliferous horizons. In other words, while there are a few zones[1] where abundant macroscopic fossils occur in abundance, a large part of the 10,000 feet of strata are non-fossiliferous. The lower Blue Mountain Series are mostly without fossils because of the disturbed conditions during their deposition. The upper portion of the Series is likewise mostly barren, owing to the turbulence of the muddy waters in which it was laid down. The deep water Tertiary white limestones, although largely composed of microcopic organisms, contain vast thicknesses of rock with no macroscopic organic remains. This is due to the fact that these limestones were deposited at great depths, where fossil making forms other than Radiolaria were few in number, and the calcareous skeletons of such as did exist were dissolved by deep sea waters.

On the other hand, the many changes of the character of the habitat, such as the introduction into the sea of the material of the Cretaceous volcanic outbreaks and changes of level in the later epochs, have interrupted the continuous existence of such littoral faunas as leave the most abundant remains and which from time to time may have secured foothold around the island prior to late Oligocene time. Thus it is that the few colonies of Upper Cretaceous life which obtained ephemeral existence around the margins of the island were deficient in species; the Cambridge forms, a little more diversified, and the Bowden and later species are numerous, as the surrounding seas afforded more constant and favorable conditions for the life of organisms.

The paleontology of Jamaica is difficult to discuss, because many previously known species have been described from miscellaneous collections (made by others than the describers) by naturalists who had not visited the island and had no conception of the stratigraphic sequence, position, association, or exact locality of the forms. Such studies are valuable so far as they result in the correct naming of species, but they are too often accompanied by an unfortunate duplication of names and conflicting generalizations and deductions. Thus one author referred all the invertebrate faunas of the whole Tertiary and later formations, without a

---

[1] These horizons are marked with an asterisk in the columnar section on page 42.

single detail of stratigraphic or geographic location, to the "Miocene,"[1] in which epoch all the fossils of Jamaica and the West Indies in general, with few exceptions,[2] have been placed. In direct conflict with this opinion, another eminent author in the latest paleontologic publication on the island informs us that "No strictly Miocene strata have yet been discriminated in the Antillean region"[3] and refers the group hitherto so called to the upper Oligocene.[4]

Another serious class of mistakes due to ignorance of the stratigraphic sequence has been the promulgation of erroneous deductions alleging the occurrence in the Antilles of certain forms entirely out of the age position which they were known to occupy elsewhere, such as European Lower Chalk corals in the Jamaican Miocene,[5] of European Cretaceous corals in the Miocene of Haiti,[6] and the occurrence of Eocene Nummulites and Orbitoides in the Upper Miocene of Trinidad[7] and Miocene of Jamaica.[8] The last mentioned class of errors has had a far reaching influence in general paleontologic literature which will require time and patience to correct.

Another source of confusion was the fact that writers ignored the existence in the island of any Tertiary formations of earlier age than the late Oligocene (Miocene of all authors previous to Dall), a theory which arose from the unfortunate errors of the English writers who confused the Bowden beds of the east near the top with the Yellow Limestone of the western parishes at the base of the Tertiaries

Still another cause of misunderstanding was ignorance of the fact which has been pointed out for the first time in our chapters on the stratigraphic conditions, that the great sea depths which separated the island from the continent during its earlier epochs of history — late Cretaceous and Eo-Tertiary times — constituted effective barriers to migration to the site of the littoral faunas of the continental borders. Owing to these barrier depths only a few or none of the shallow water

---

[1] Guppy, On the West Indian Tertiary Fossils, Geol. Mag., Decade II. Vol. I. pp. 404–411, London, 1874.

[2] The two species of Eocene corals from Port Maria and the Rudistes.

[3] Dall, Proc. U. S. National Museum, Washington, 1896, Vol. XIX. pp. 303–305.

[4] Ibid., p. 304.

[5] Duncan, Quart. Jour. Geol. Soc. London, Vol. XXI. p. 12, 1865.

[6] Gabb (Geology of Santo Domingo, p. 88) infers that these so called Cretaceous corals in the Haitian "Miocene" are found in gravel of Cretaceous débris.

[7] Proc. Sci. Association of Trinidad, December, 1872. Port of Spain (1873), Geol. Magazine, Decade II. Vol. I. p. 21, 1874, and elsewhere.

[8] Duncan, Quart. Jour. Geol. Soc. London, Vol. XIX. p. 453.

molluscan species of the adjacent continental borders found habitat in the littoral waters of the island prior to the late Oligocene (Bowden) epoch, when the bottom of the region was sufficiently elevated to permit the migration of shallow water species over wide areas of the tropical seas and to connect the Jamaican littoral fauna with that of the mainland. Forms which abound in the preceding epochs, especially the corals and Foraminifera, are those adapted to wide oceanic migration. These conditions have produced in these earlier faunas a peculiar mixture of genera, comprising oceanic species and a few littoral mollusca which had found accidental foothold and acquired peculiar characters through long isolation, — the whole making a faunal assemblage quite foreign to those known in other typical areas of the world upon which stratigraphic and age classifications have been founded, although retaining generic criteria sufficient for positive age determination. Paleontologists, unaware of these conditions, have naturally failed to obtain in the collections from the island a correct impression of the stratigraphic significance of its fossils.

In view of the confused condition of current published conceptions of the paleontology of Jamaica above set forth, it will be impossible in the present chapter to straighten out the confused synonomy of species, a task which must be left to other specialists. Our principal endeavor will be to point out the true stratigraphic position of the material hitherto described, thereby making it of geologic as well as biologic value, and then, by aid of the larger amount of new material collected by us, present some deductions which may be of service to those who in the future undertake the special task of further advancing the paleontology of Jamaica.

CRETACEOUS.

Blue Mountain Series. Lower Division.

From the occasional limestones and marl beds occurring in the vast thickness of tuffs and conglomerates of the lower division of the Blue Mountains, the following fossils have been collected, most of which have a decided Cretaceous facies.

Foraminifera: Rotalia or Pulvinulina[1]; *Orbitoides (?)[2]; Ellipsactina[1]; *Nummulites (?).[2]

Corals: Cladocora jamaicaensis, Vaughan; *Diploria conferticostata,

---

[1] Identified by R. M. Bagg. Collected by Robert T. Hill.

[2] Identified by Woodward. Collected by Jamaican Surveys.

Vaughan = D. crassolamellosa, Duncan (non Edward and Haime)[1]; *Multicolumnastræa cyathiformis, (Duncan) = Heliastræa exsculpta, Duncan (non Reuss) and Heliastræa cyathiformis Duncan.[1] Cyathoseris haidingeri, Duncan (non Reuss)[1]; Porites reussiana, Duncan[2]; Leptophyllia agassizi, Vaughan.

Echinodermata: Salenia.

Conchifera: Pteroceras[3]; Nerinæa[3]; Cerithium[3]; Turritella[3]; Actæonella[3]; Natica[3]; Amauropsis (?)[3]; Pleurotomaria (?)[3]; Ostrea[4]; Pecten[5]; Inoceramus[5]; Lithodomus[3]; Pholadomya[3]; Barrettia monolifera, Woodward[6]; Radiolites adherans, *R. rudis, R. cancellatus, R. macroplicatus, R. annulosus, Whitfield[6]; *Caprina jamaicensis, Whitfield[6]; Caprinella quadrangularis[6]; Caprinella occidentalis, Whitfield[6]; *Caprinella gigantea, Whitfield.[6]

Fossils marked with an asterisk are also reported from Cambridge beds.

This fauna is peculiar in its generic association, the numerical preponderance of Rudistes and corals, the sparse representation of Pelecypoda, and the almost complete absence of Echini, Cephalopoda, and Brachiopoda, which so largely prevail in the Marine Cretaceous, and its general dissimilarity to Cretaceous faunas elsewhere than in the Great Antilles.

Foraminifera abound in the rocks of the Jamaican sequence from the limestone beds of the lower Blue Mountain Series[7] to the present, and living forms occur in great quantities in the surrounding waters. The fossil forms which will be frequently alluded to in this paper are of many species; some are of great diagnostic value, especially the species of Orbitoides and Nummulinæ, which, as will be shown, are only found doubtfully in the uppermost Cretaceous and Eocene (old usage) beds of the island. A correct appreciation of the stratigraphic occurrence of these and the other Foraminifera in the Jamaican sequence has been greatly confused in literature by the writings of W. J. L. Guppy, who published that they all came from beds of the Miocene age. Inasmuch as his deductions have seriously misled other authorities, like Jones,

---

[1] Identified by T. W. Vaughan. Collected by Robert T. Hill, except the Cyathoseris haidingeri.

[2] Identified by Duncan. Collected by Jamaican Surveys.

[3] Identified by T. W. Stanton. Collected by Robert T. Hill.

[4] Identified by Woodward. Collected by Jamaican Surveys.

[5] Identified by Etheridge. Collected by Jamaican Surveys.

[6] Identified by Whitfield. Collected by Nichols.

[7] The conditions of formation of the lower part of the Blue Mountain Series were in general unfavorable for their occurrence.

Parker, and Dall, it is necessary to give a brief synopsis of them to straighten out the complications.

Soon after the discovery of Orbitoides and Nummulinæ in the Jamaican rocks by the official surveyors, and prior to Jones's studies, Guppy noted the discovery of similar forms in the asphalt rocks of the cliffs at San Fernando, Trinidad.[1] In these papers he also stated that "the same species of Foraminifera had been detected in the Miocene rocks of Jamaica.[2] He said,[3] "I have not detected any other organisms in the same bed as the Orbitoides and Nummulites; but both above and below it are found Tertiary fossils, probably not of more recent date than the Miocene age." Sufficient "to state that the evidence derived from them is not inconsistent with the presumption of the Miocene origin of the deposits in question. We know too little as yet of the Tertiaries of this part of the world to be able to pronounce a more decided opinion; but should the supposition of the Middle Tertiary age of the San Fernando Tertiaries be ultimately established, *we should have here the remarkable phenomena of the association of an Old World with a New World form of Lower Tertiary rhizopod in a deposit of Middle Tertiary age.*" Furthermore he says:[4] "Upon a close examination of the vertical mass [of asphaltum rock[5]] is found to consist chiefly of the remains of Nummulites and Orbitoides, two genera of Foraminifera whose shells, as is well known to geologists and paleontologists, form in various parts of the world thick masses of rock; the Orbitoides being generally characteristic of the Eocene period in the Western Hemisphere, while the Nummulites is regarded as indicative of the Middle Eocene in Europe and Asia. Here, however, we find the remains of both these genera in strata of supposed Miocene age."[6] Thus, with probable correctness, he correlated the Jamaican Orbitoidal beds with those of Trinidad, but erroneously referred both to the Miocene age (old classifications).

In 1863 Jones and Parker described a group of Foraminifera collected by Barrett from the Pteropod marls of Eastern Jamaica of supposed Pliocene and Pleistocene age, and differing entirely both in stratigraphic

---

[1] See Proceedings of the Scientific Association of Trinidad, December, 1872, Port of Spain, 1873. In this paper Mr. Guppy notes that he announced the discovery of these forms in Trinidad at a previous meeting of the society in July, 1863.

[2] See also Proc. Sci. Association of Trinidad, 1867, p. 15.

[3] The Geologist, London, 1864, Vol. I. p. 160.

[4] *Loc. cit.*, p. 159.

[5] Figured on page 38 of Trinidad Reports, 1860.

[6] A Report on the Geology of Trinidad, pp. 33 and 102.

position and in species from the Orbitoidal horizons previously mentioned by Barrett, Woodward, Duncan, and Wall, and Jones himself.[1] In the same Report[2] Jones and Parker described a large foraminiferal fauna dredged from the ocean off Jamaica by Barrett, which consisted of recent species almost identical with those of the Pteropod marls. Neither of these collections contained Orbitoides, Nummulites, or any of the more ancient forms of Foraminifera mentioned in the previous literature. In 1867 Guppy tabulated a few species of Foraminifera from the Pteropod marls above referred to and the Orbitoides and Nummulinæ together, and cites them all as coming from "the Upper Miocene of Jamaica."[3] In 1874 he again tabulated all the Foraminifera from the Pteropod marls and recent dredgings in one group with those from the Orbitoidal and Nummulitic horizons, as coming from the Miocene of Jamaica.[4]

Finally, after successively placing the Orbitoidal and Nummulitic horizons in the Lower Tertiary, the Upper Miocene, and the Miocene respectively, besides mixing them with forms which are definitely known to come from entirely distinct horizons, Guppy in 1892 admitted[5] that the San Fernando (Naparima) Orbitoidal and Nummulitic beds of Trinidad which he originally considered Miocene were probably of Eocene age. Inasmuch as all his references of the Orbitoides beds of Jamaica to the Miocene were based upon their supposed resemblance to these Trinidad beds, this last conclusion clearly cancels his many previous references of the Orbitoidal limestones of the West Indies to the Miocene age.

Fossil Orbitoides were first reported by Barrett in 1860,[6] from the limestones included in our Blue Mountain Series, and these fossils were stated by him to be "of Cretaceous age in Jamaica."[7] Specimens from his collections were sent to England, where they were studied and commented upon by Woodward, T. Rupert Jones, Duncan and Wall, and others.[8]

---

[1] Jones and Parker, British Association Report, 1863, p. 80.

[2] Ibid., p. 105.

[3] Proc. Sci. Association of Trinidad, December, 1867, p. 167.

[4] Geological Magazine, London, 1874, p. 21.

[5] Quart. Jour. Geol. Soc. London, Vol. XLVIII. p. 520.

[6] In a report referred to by the Governor of Jamaica, in the first message of February 7, 1860, printed in Jamaican Reports, 1869, p. 76, he says that Orbitoides are Cretaceous in Jamaica.

[7] Jamaican Reports, p. 76.

[8] See references following.

In 1863 the material collected by Barrett and mentioned by Woodward, was reported upon by T. Rupert Jones.[1] Orbitoides are included in the list of Cretaceous fossils given by Etheridge,[2] and alleged to occur with Nerinæa and Rudistes by Woodward,[3] and Duncan and Wall.[4]

Woodward[5] reported both Orbitoides and Nummulinæ from the "Hippurite limestone" of Jamaica, which "is unlike that of any English stratum. It abounds in small oval bodies related to the Tertiary Nummulites, and also contained Radiolites, Inocerami, a large Nerinæa, and an Actæonella resembling *A. lævis* d'Orb." We have not personally observed Orbitoides in the Jamaican Cretaceous rocks, although they abound in the Eocene, as will be shown on a later page. Cretaceous limestones from Costa Rica, described in our Panama Report, show a mixture of remains very suggestive of the one described. The occurrence of Orbitoides and Nummulites, which abound in the Eocene formation, is more fully discussed on later pages.

Duncan asserted[6] that the corals were mostly European forms, "the majority have very decided facies, . . . suggestive of a close alliance of the great coral fauna of Gosau in the Eastern Alps," while others were alleged to be "common forms in the Kriedensmerle." He also stated[7] that "there is a community of species of corals between the Lower Chalk of Gosau and Piesting and the French Hippurite limestone at Martigues, the Corbières, and Uchaux. . . . It is clearly this assemblage of forms which is represented in Jamaica; and it is an interesting fact that the specimens from Gosau, Mount Hindmost, and Trout Hall present the same mineral aspect; in fact, the specimens are barely to be distinguished." Vaughan, who has recently re-examined Duncan's collections, does not agree with his conclusions, and states that they have no affinities with the Gosau forms. The Gosau (Cretaceous) forms are Senonian, and do not belong to the lower horizon to which Duncan referred them. Furthermore, two of the species mentioned by Duncan from Trout Hall and Upper Clarendon, *Diploria crassolamellosa*, Duncan (non Edwards and Haime) = *Diploria conferticostata*, Vaughan, and *Heliastræa exsculpta*, Duncan (non Reuss) = *Multicolum-*

---

[1] Quart. Jour. Geol. Soc. London, 1863, Vol. XIX. p. 514.

[2] Jamaican Reports, p. 310.

[3] "The Geologist," Vol. V. p. 373.

[4] Quart. Jour. Geol. Soc. London, 1865, Vol. XXI. p. 2.

[5] S. P. Woodward, in the Geologist, London, 1862, Vol. V. p. 373.

[6] Quart. Jour. Geol. Soc. London, 1865, Vol. XXI. p. 11.

[7] Ibid., p. 12.

nastræa cyathiformis (Duncan), are also found in the Cambridge Eocene, and are Eocene species.

There are several species of corals in our collections from Jerusalem Mountain, including, according to Vaughan, a Cladocora, — a genus not hitherto found fossil in the West Indies. Vaughan remarks that there are other undetermined species from the Cretaceous of Jamaica different from those already reported by Duncan. Nowhere in the Continental American Cretaceous, except in Southern Mexico described by Felix and Lenk, is there a diversified coral fauna, and the latter belongs to lower beds. No comparison has been as yet instituted between the Mexican-Jamaican Cretaceous corals, however.

The Mollusca, with the exception of the Rudistes, are very poorly represented. The eight genera of Gastropoda found are all poorly preserved casts, mostly from the Jerusalem beds, with the exception of Actæonella, which also occurs in the Logie Green. The four pelecypods other than the Rudistes are mostly from the upper marls of the Jerusalem beds. This faint representation of Pelecypoda in the Cretaceous of Jamaica is a most remarkable feature. Numerically the fauna is predominantly Rudistean; these forms always occur in all the fossiliferous beds, even when others are unrepresented. They compose the mass of the Jerusalem limestones, and occur singly in the occasional clay beds of the Ballard and Catadupa beds.

Specimens of this Rudistean fauna collected by Nichols have recently been described by Whitfield.[1] It is unique in specific features, being entirely different from that of Europe and North America, especially that of Texas, where Rudistes are very numerous in the Edwards formation of the Lower Cretaceous (unless *R. nicholassi* is allied to a form of the Upper Cretaceous of Alabama and Texas). The absence of the genus Hippurites, so abundant in the Upper Cretaceous of Europe and Southern Mexico, is also noticeable, although this genus is missing from the Cretaceous of the United States. One genus, Barrettia — included in the Rudistes by Woodward,[2] and recently asserted by Whitfield[3] not to belong in this group at all — has no known representation elsewhere with the possible exception of Guatemala, where it has been questionably reported by Sapper.[4]

---

[1] Bull. Am. Soc. Nat. Hist., New York, 1897, Vol. IX.

[2] The Geologist, London, 1862, Vol. V. pp. 372, 377.

[3] Bull. Am. Soc. Nat. Hist., New York, 1897, Vol. IX. pp. 233–246, Plates XXVII.–XXXVIII.

[4] Reported by Sapper from Guatemala. Physical Geography of Guatemala. Petermann's Mitteilungen, No. 113, Gotha, 1894, p. 9.

With this exception not a single species of the fauna has been reported from the North or South American Mainland. Probably the same fauna occurs in Cuba and Haiti, judging from papers by G. F. Matthew[1] and Tippenhauer.[2] It is also possible that it may occur in Guatemala and Costa Rica, or even Southern Mexico, where large unstudied Rudistean faunas abound. As will presently be noted several of these species of Rudistes also occur in the overlying Eocene (Cambridge) beds.

The most numerous and conspicuous forms of the Jamaican Cretaceous fauna are genera which proportionately have but slight representation in the North American Cretaceous, such as the corals, Rudistes, Nerinæa, and Actæonella, while on the contrary there seems to be an almost entire absence in the Jamaican fauna of such forms as Ammonites,[3] Trigonia, Gryphæa, Exogyra, Brachiopoda, and Echinodermata, which are so characteristic of the North and South American Cretaceous of Atlantic sedimentation. The Jamaican Cretaceous fauna, which is the oldest known life of the Great Antilles, is unique. Several Rudistes and two species of corals from these supposedly Cretaceous formations continue upward into the beds which are here placed in the Eocene, indicating a gradation of the faunas of these two epochs, as further discussed on a later page. It may possibly be explained upon the hypothesis that it lived adjacent to an insular land, separated from the continent by great depths of oceanic water which prevented migration to it of the main littoral fauna in its entirety. These beds represent the expiring days of the Cretaceous and can hardly antedate the Senonian in age.

THE EOCENE FAUNAS.

The existence of Eocene strata in Jamaica has hitherto been a question difficult to determine owing to the previous confusion of knowledge of the stratigraphy and paleontology. It is our opinion that the Eocene is well represented by at least two distinct formations, the Richmond and Cambridge, and by three, if the Montpelier formation, which is the equivalent of the Vicksburg stage, is included in the Eocene, as has been customarily done by all American writers until recently, when Heilprin and Dall, following Conrad, have again placed the Vicksburg in the base of the Oligocene.

---

[1] Canadian Naturalist, 1872, Vol. VII. p. 19.

[2] Die Insel Haiti, Leipzig, 1893. See Plate preceding page 381.

[3] Ammonites have been reported in one locality only in Jamaica (page 78), but their occurrence there has not been verified or accepted by the paleontologists of the Survey.

These three formations, although distinct in lithologic characters, grade into one another, the Richmond being a littoral, non-calcareous clastic formation, the Cambridge a mixed calcareous and argillaceous littoral, and the Montpelier a truly deep sea foraminiferal chalk deposit.

De la Beche, the earliest writer on the geology of Jamaica, placed the beds included in our Richmond beds, in his medial, or Carboniferous Series,[1] and included the Cambridge in the base of his "White Limestone," now known to embrace formations from Eocene to recent inclusive, the Miocene excepted. He referred the fossils from the base of this series (our Cambridge beds) to the Eocene, and considered them to "belong to the same age as the London Clay, *Calcaire grossier* of the Paris Basin," and published a figure of one of the large Cerithiums[2] peculiar to it.

Duncan and Wall, and others connected with writing up the Jamaican Reports, referred the beds of our Richmond formation to the Eocene, but expressed many confusing opinions concerning the age of the beds we have placed in the Cambridge and Montpelier, some of the writers having referred them at first to the Eocene, — which conclusion was finally abandoned by Etheridge and others, who confused them with the Miocene strata. These beds, which underlie the white limestones, were at first considered Eocene by C. B. Brown and other field workers in the western parishes, but through the unfortunate miscorrelation on the part of the workers in the eastern parishes, as explained in the Introduction of this Report, they were confused with the Bowden beds, which overlie the white limestones, and all conception of their true position was completely obliterated.

C. B. Brown[3] described the Yellow Limestones (Cambridge beds) with Orbitoides in St. James, "which agrees with descriptions of Claiborne, Jackson, and Suggsville beds." He noted that no provision had been made by the government for a critical examination by a paleontologist; "therefore until such has been made, the subject must remain unsettled." He also referred to a list of fossils from this formation in the Appendix of the Report, but does not give it. It is a singular fact that the species of this fauna were apparently never seen nor studied by the English paleontologists, into whose hands fell the official collections of the Jamaican Surveys.

Sawkins's published views are conflicting. At one time in discussing the "Yellow Limestone of Trelawney" (our Cambridge beds), he de-

---

[1] Trans. Geol. Soc. London, 1826, No. 36, pp. 157–163. [2] Ibid., p. 171.

[3] Jamaican Reports, p. 244.

scribes them as "Orbitoidal limestones, which agree with the descriptions of the Claiborne beds by Sir Charles Lyell and Mr. Dana."[1] In two other places he referred them to the Mid-Tertiary period, on stratigraphic grounds, because they occurred between the Eocene (our Richmond beds) and the White Limestone, the latter of which he (Sawkins) erroneously considered Pliocene.[2] These original opinions on the part of the field workers to the effect that the beds were Eocene were abandoned by the authors of the Summaries of the Jamaican Reports, who, writing in England, confused the identity of the (Cambridge) Yellow Limestone underlying the great White Limestone Series (Montpelier and Moneague formations) with the Bowden Oligocene beds overlying it, and erroneously supposed the latter to be the base instead of the top of the White Limestones. In this manner the identity of the Cambridge Eocene faunas was confused with that of the Oligocene, and the age of the whole Jamaican sequence above the Richmond so jumbled that it has become impossible to obtain a correct knowledge of it from the literature concerning the island, even that of the most recent writers, like Jukes-Browne and Harrison, who have said that the upper division of the Miocene "is doubtless the true place of the Jamaican Yellow Limestone."[3]

So confusing has the literature become that of late years there has been a tendency to deny that the rocks of the Eocene were present in the West Indies. The most recent summary of these formations[4] omits it in this region with the doubtful exception of the Manzanilla beds of Trinidad. One gratifying result of our researches is the presentation of additional proof that the Eocene period is represented in Jamaica, not alone by the doubtful Richmond beds, but also by the Cambridge formation, and that these collectively constitute one of the most distinctive and important formations, not only of this island, but of all the great Antilles, Barbados, Trinidad, and perhaps the Windward Islands, as will be shown in later pages.

The Richmond Beds.

In the Richmond beds animal remains are exceedingly rare. A Natica, a Turritella, and what is probably a large Scalaria associated with two doubtful species of supposedly Eocene corals described by Duncan, have been found in the conglomerate of Point Haldane, at

---

[1] Jamaican Reports, p. 224.
[2] Ibid., pp. 130, 138.

[3] Quart. Jour. Geol. Soc. London, Vol. XLVII. pp. 197, 242.

[4] Dall, "Descriptions of Tertiary Fossils from the Antillean Region." Proc. U. S. National Museum, Vol. XIX. pp. 303, 305. Washington, 1896.

Port Maria. Duncan and Wall have also reported one species of Eocene coral from the black shale of the Blue Mountain Series from the valley of the Yallahs River on the south side of the island, east of Kingston.[1] Etheridge[2] also mentions a Melania and a Turritella from these beds. A small Modiola has also been found in the formation at Arthur's Seat. When the impure turbulent conditions of the sediments are considered, which are very similar to those of the Lignitic group of our Southern States Eocene, this scarcity of fossil remains is not surprising. Plant remains occur nearly everywhere in the laminæ of the clays.

In all, the following species have been reported from the Richmond beds: —

Paracyathus crassus, Ed. & H.;[3] Stylophora contorta, Leym.;[4] Stylocœnia emarciata, Lam. (Duncan),[4] = St. duerdeni, Vaughan; Columnastræa eyeri, Dunc.;[4] Modiola, sp.;[5] Melania;[4] Turritella;[4] Scalaria;[4] Rudistes;[4 6] Caprinella;[4 6] Actæonella;[4 6] Natica phasianelloides.

The supposedly Eocene corals of Duncan, with one exception, were found in the gravel and shale beds of the Richmond formation at Port Maria. They are depauperate forms, which apparently gained foothold with difficulty in the disturbed and muddy waters of the Richmond epoch. Concerning these Duncan and Wall[7] wrote as follows: —

"The specimens from Port Maria are either dark and carbonaceous-looking, or are encrusted on a fine dark purple conglomerate; all are very significant of the horizon, and recall the puny development of the species of the London Clay. The Paracyathus from Yallahs Valley resembles that of the London Clay, being even stained black, like the Sheppy specimens; the *Stylocœnia emarciata* is a well known form in British, French, Italian, and Sindian early Tertiary collections, and the *Stylophora contorta* also. The Stylocœnia and Stylophora are characteristic corals, and denote an Eocene horizon; and they indicate, when unaccompanied by other species, the existence of physical conditions not favorable for coral growth."

Vaughan has described Duncan's *Stylocœnia emarciata* as *Stylocœnia*

---

[1] Paracyathus, sp. Quart. Jour. Geol. Soc., Vol. XXII. p. 8.

[2] Jamaican Reports, p. 311.

[3] Upper Valley of Yallahs River.

[4] Point Haldane, Port Maria.

[5] Arthur's Seat, Clarendon.

[6] Reported by Etheridge (Jamaican Reports, p. 311), who surmised that they were derived from "Hippurite limestone below." No "Hippurite" limestone is known to occur below the beds at Port Maria, or within any reasonable distance.

[7] Quart. Jour. Geol. Soc. London, 1864, Vol. XXI. p. 13.

duerdeni. The association together of species of *Stylocœnia* and *Stylophora*, both being close to Eocene species of Europe, would make the probability in favor of the Eocene age of the beds. Therefore the paleontologic evidence, though not conclusive, supports the opinion of Duncan regarding the age of the beds. Fortunately the stratigraphic position of the Richmond beds is clearly made out, independent of the fossils, so in this case positive paleontologic proof is not essential for determining their position. We studied the locality of Port Maria from which these corals came in order to ascertain their stratigraphic position, which beyond doubt is that of the typical Richmond beds.

Etheridge [1] mentions the occurrence of fossil Rudistes in these beds, but suggests in explanation that their presence might be accounted for upon the hypothesis that they could be water-rolled survivals of the denudation of the lower lying Cretaceous beds. Whether the specimens of "Hippurites," Radiolites, and Actæonellas noted are indigenous to these particular beds or not, we cannot state, not having been so fortunate as to find any of the fauna *in situ*. We question the conclusion, however, that they are derived specimens, because similar forms of Rudistes at least were found by us *in situ* in the overlying Cambridge beds, as will be shown presently. It is probable, as shown in the Ballard bed of the Minho section, that these Rudistean forms appeared in sporadic colonies throughout the thickness of the black shales of the Minho and Richmond beds, and continued into the Cambridge formation. Whoever undertakes the further study of these beds must remember that specimens of free and well preserved Rudistes should not be confused with the rolled pebble of hard crystalline limestone of the Jerusalem type which should also occur.

The presence of the supposedly Cretaceous Rudistean genera would ordinarily invalidate the data upon which the Eocene age of the Richmond beds hitherto depended for establishment, were it not for our positive evidence to be presented that these forms are found *in situ* in overlying beds, associated with undoubted Eocene fossils. The other species are all of Eocene facies and point to their Eocene age, which conclusion we are able to fix with positiveness by the evidence of the overlying Cambridge beds, where a similar mixture is found, whose true nature has hitherto escaped observation.

The Cambridge Formation.

From a paleontologic standpoint these beds mark one of the most interesting and valuable horizons in the whole Jamaican sequence,

---

[1] Jamaican Reports, p. 311.

inasmuch as it contains a distinctive fauna abundant in specimens if not in species, including several species of Cretaceous fossils which have transgressed into the Eocene. The three members of the formation, the Catadupa, Chapelton, and Port Antonio respectively, are paleontologically allied, the only difference being that some of the characteristic corals, Rudistes, and some mollusks of the former, do not range up into the latter.

The Catadupa Beds. — The outcrops along the Montego Bay Railway on the east slope of Great River Valley, on the borders of St. James and Hanover at Cambridge and Catadupa, are by far the best localities we have seen for collecting. We have twice visited these localities for that purpose. The material is very abundant, but most of the Mollusca are poorly preserved. It contains many determinable species of Foraminifera, Echini, and Mollusca, which have been submitted to various specialists.

The fauna so far as studied is as follows: —

(1) From railway cuttings near Catadupa and Cambridge. Foraminifera. — Many small granular Foraminifera, occurring in vast numbers in the shale beds, giving it an oölitic texture on indurating. The following species were determined by Bagg: —

Miliolina subrotunda, Montague, Catadupa; M. cicularis, Borneman, Catadupa; M. seminulum, Linné, Catadupa and Cambridge; M. sp., Catadupa; Textularia trochus, d'Orb., Catadupa; T. barretti, P. and J., Catadupa; T. seminulum, P. and J., Catadupa; Haplostiche soldani, P. and J., Catadupa; Pullenia sphæroides, Cambridge; Miliolina seminulum, var. triangularis.

Corals. — The following corals were determined by T. W. Vaughan: —

From near Cambridge Station, St. James Parish: Turbinoseris jamaicaensis, Vaughan; Turbinoseris cantabrigiensis, Vaughan; Dendracis cantabrigiensis, Vaughan.

From Catadupa: Trochosmilia hilli, Vaughan; Multicolumnastræa cyathiformis, (Duncan); Diploria conferticostata, Vaughan (= D. crassolamellosa, Duncan, non Edwards and Haime); Diploria conferticostata, var. columnaris, Vaughan; Trochoseris catadupensis, Vaughan; Mesomorpha catadupensis, Vaughan.

Echinoderms. — Scutellina,[1] Cambridge and Catadupa; Acrocidaris,[1] Catadupa; Rapinot pneustio,[2] Great River; Diplopodia,[2] Great River; Echinolampus,[2] Great River; Echinanthus,[2] Retrieve.

---

[1] From my collections.

[2] From the collections of the Institute of Jamaica. Macropneustes and Pygorhynchus have also been collected from this formation at Mountain Spring, St. Elizabeth, and Maroontown.

T. W. Stanton of the United States Geological Survey has kindly furnished the following determinations of the Mollusca collected by me: —

(*a*) From near Catadupa: — Ostrea, sp.; resembles young of O. compressirostra. Carolia jamaicensis, Dall; this is an Eocene genus. Caprinula gigantea, Whitf.[1] ?; a fragment. Caprinella occidentalis, Whitf.[1]; a small specimen. Caprina jamaicensis, Whitf.[1]; several small specimens. Radiolites rudis, Whitf.[1]; four specimens (lower valves) that seem to belong to this species. Radiolites adherens, Whitf.[1] ?; one specimen doubtfully referred here. Radiolites, sp.; several fragments of a small strongly plicate species that cannot be satisfactorily identified with any of those described by Whitfield. Caridum, sp.; rather large form. Natica, sp.; casts. Nerita, sp.; a medium sized smooth form. Cerithium, sp.; 1, Cerithium, sp.; 2, fragmentary cast of very large species. Thalassa ? sp.; a Purpuroid shell resembling this genus, represented by a fragment. Cypræa, sp.

(2) From the Railway Cuttings at Cambridge.

The collection from Cambridge is not so large, but it contains enough identical species (marked *) to show that the same horizons are represented as at Catadupa.

(*b*) From near Cambridge: — *Ostrea, sp. Anomia, sp. *Carolia jamaicensis, Dall. Spondylidæ (?) genus undetermined; a peculiar shell having the form of an Ostrea and resembling a Chama in sculpture and shell structure. *Radiolites rudis, Whitf. ? a single small specimen. Protocardia, sp. Cardium, sp. Lucina, sp.; large casts. Nerita, sp. Cerithium, sp.; a very large form resembling one of the huge species from the Paris Basin Eocene.

Several other indeterminate casts of bivalves and gastropods. The genus Cassis was also identfied from the Cambridge collection by Dall. A fragment of a Nerinæa also occurs.

Chapelton Beds. — The upper beds at Chapelton are of later and slightly deeper water origin than the Catadupa, and mark a stage in the great Eo-Oligocene subsidence and a transition between the Cambridge and Montpelier. They are characterized by the same little Alectryonate oyster, large Cerithium and Lucina, which are found at Cambridge. Several large Echinoderms occur in this horizon. None of the other fossils of the Catadupa beds were noticed by us, while a species of Orbitoides (the species referred to *O. mantelli* throughout

---

[1] Forms hitherto supposed to have been peculiar to the Cretaceous beds of Jamaica.

the Jamaican Reports [1]) becomes exceedingly abundant, constituting the larger part of both the marls and limestones.

In all, this fauna has three species of mollusks connecting it with that of Catadupa, but a large number of peculiar fossils characterizing the latter are absent. The molluscan forms occurring in the Chapelton beds are those which have survived from the Catadupa beds, just as the Rudistes of the latter have survived from the lower beds. The difference in the prevalent Foraminifera is one distinction between the beds, Orbitoides, which have not been found at Catadupa, characterizing the Chapelton beds, while the former contains immense quantities of other species as enumerated. At Lower Chapelton the following fossils were collected by me: Orbitoides,[2] Anomia,[2] Lucina,[3] oyster,[3] gastropod.[2]

The same "Yellow Limestone" at Mile Post 17½, Lucea, and Savanna-la-Mar road contains Crustacea,[2] Lucina,[2] Cardium,[2] gastropod,[2] simple Coral,[3] Corbis.

The Port Antonio Beds. — At a locality west of Port Antonio we collected casts of the large Cerithium and Lucina previously mentioned, and a Vulsella, which characterize the Cambridge beds, and also several casts of smaller mollusks, alternating with granular chalks made up of Foraminifera, including some similar to those found at Catadupa. Bagg reports the following species of Foraminifera from this locality: Globigerina dutertrei, d'Orb.; Globigerina bulloides, d'Orb.; Milolina reminulum, Linné; Amphistegina lessonii, d'Orb. (A. hauerii, d'Orb.); Orbitoides fortissii, d'Arch.; O. papyracea; O. complanata; Orbulina universa; Nodosaria; Vaginulina; Nummulites, sp.; Heterostegina; Discorbina.

The material in which these fossils occur at this locality from its lack of color would ordinarily be classed as a white limestone; the beds represent a gradation of one of the formations into the other. The fauna is that of the Cambridge beds (Chapelton and Catadupa), and indicates that either the lithologic nature of the latter has changed from a mixed to a pure oceanic character in this portion of the island, or there is a faunal continuity between it and the base of the Montpelier.

In addition to the forms of the Cambridge beds above mentioned, Etheridge[8] has noted that "A portion only of a Nautilus has been found in the Yellow Limestone of Spring Mount, St. James" Parish in

---

[1] As determined by T. Rupert Jones. See Jamaican Reports, p. 313, and Geol. Magazine, London, 1800, pp. 102, 103.

[2] Found at Catadupa and Cambridge.

[3] No. 81 of Institute collection.

[4] Jamaican Reports, p. 323.

the same valley as Catadupa and Cambridge. This is the only Cephalopod as yet found in Jamaica, and is probably the same form which has been referred to as *Aturia zigzag*. If its position and determination could be verified, it would prove another valuable testimonial to the Eocene age of the beds, as this form is characteristic of the late Eocene of the United States. De la Beche[1] has noted the occurrence of a Nautilus, probably the same as that previously mentioned from Cuba, a Terrebratula, and Nummulinæ in association with other species near Halse Hall House, Clarendon. No other specimens of fossil Cephalopoda have been found in Jamaica.

Of the fossil Mammalia, only a single fossil trace has been discovered in Jamaica, *Prorastomus sirenoides* Owen,[2] a species of Sirenia related to the Manatees of to-day. This specimen was reported from Freeman's Hall Estate in the southeastern corner of Trelawney near the centre of the island. The locality from which this specimen came is a typical outcrop of the Cambridge beds as described by Brown,[3] and Owen's description of the material in which the specimen was embedded conforms also to the lithologic character of that formation. While no final opinion can be expressed without seeing the specimen and locality, the evidence certainly points to the early Eocene age of this animal.[4] Being a marine animal, its occurrence in the rocks of Jamaica is of no significance in tracing previous relationships of Jamaica to other islands.

This fauna of the Cambridge formation is remarkable in several ways. First, for the peculiar mixture it affords at Catadupa of Eocene and Cretaceous genera; and secondly, from its collective dissimilarity to any other known fauna, especially to those of the American continental littoral formations. When a small collection from Cambridge was collected by us in 1896 and submitted to a Tertiary paleontologist of note, it was rejected by him on the ground that it was not of Tertiary age, but Cretaceous, and this too before true Rudistes had been recognized in it. Recognizing its absolute dissimilarity to any known American Cretaceous fauna, we revisited the region in 1897, and discovered

---

[1] Nautilus Cubensis, Lea. Trans. Am. Phil. Soc., 1841, Vol. VII. p. 259.

[2] Quart. Jour. Geol. Soc., 1855, Vol. XI. pp. 541, 543.

[3] Jamaican Reports, p. 224.

[4] Marine deposits of the Cretaceous and early Eocene periods are recognized all over the world, but not a trace of the Cetacea and Sirenia have been found in them. So far as known, these types appear fully evolved at the top of the Eocene. — Nat. Science, October, 1897, page 223.

the more extensive exposure at Catadupa where the Rudistes occurred in great abundance. From this last collection Dall identified the Carolia, hitherto known only in the lowest Eocene of Egypt.

None of the species of the Cambridge beds excepting the Rudistes, the gigantic Cerithium (?), an oyster, and a Lucina, have been reported before from Jamaica. The eight species of corals identified by Vaughan are entirely distinct from the species hitherto reported from the Richmond beds at Port Maria by Duncan; the Spondylidæ (?), Nerita, Carolia, and Cypræa are forms which apparently were not found by the geologists of the British Survey. Not a single one of the species (described or undescribed), is like any of the North or Central American forms, unless it is the small Alectryonate oyster and the Cardita. Some of the corals have European analogues if not specific identity; the gigantic Cerithium-like casts are somewhat similar to forms in the Paris Basin, while the Carolia, as before stated, is a genus hitherto reported from Egypt.

The Orbitoides of the Chapelton beds, which is a comparatively large species from five millimeters to a centimeter in diameter, occurs in vast numbers in the impure littoral sediments. So abundant are these forms in the parishes of St. Mary, Clarendon, and elsewhere, that the formation could well be termed the "Nodular Orbitoidal Limestone," as it was originally designated by Barrett,[1] were paleontologic names still in vogue. Jones was the first to note the occurrence of Orbitoides in the nodular limestone[2] (our Cambridge beds), No. 4 of Barrett's (Woodward's) section,[3] previously specifically reported only in the Hippurites limestone by Woodward and Barrett. He remarked that "In the Western Hemisphere Orbitoides and Nummulinæ are very rare above the Eocene group," and that it may be remarked as a point of interest that the Nummulites and Orbitoides of Jamaica are such as are found in South Europe and India. From these nodular Orbitoidal limestones Jones reported Orbitoides and three or four Nummulinæ. Concerning these he said:[4] "In the Nodular Orbitoidal Limestone of Jamaica [Cambridge beds, R. T. H.] at the base of the White Limestone, . . . I find a few rather small specimens of the same variety of

---

[1] As published by T. Rupert Jones. In the text Jones states that he "understood Mr. Barrett to have informed him that the Orbitoides occurred in nodules in clay just underneath the great White Limestones." Quart. Jour. Geol. Soc. London, 1863, Vol. XIX. pp. 514, 515.

[2] Quart. Jour. Geol. Soc. London, 1863, Vol. XIX. p. 515.

Geologist, London, 1862, Vol. V. p. 373.

Geological Magazine, London, 1864, Vol. I. p. 104.

O. mantelli as that so abundant in the Antiguan flint." He also states[1] that "the Orbitoides are similar to those found fossil in the Upper Chalk of Southern France and the Pyrenees, and in the Nummulites beds of Scinde."

The corals identified by Vaughan are species not hitherto found in Jamaica, and constitute a valuable addition to its fauna, inasmuch as they fix the Eocene position of these beds beyond doubt. He submits the following notes.

"The Cambridge beds can be referred to the Eocene (or possibly Oligocene) on the strength of their containing abundant specimens of *Dendracis.* This genus is not known from rocks older than Eocene or younger than Oligocene. Both specimens and species are abundant in Southern Europe and Northern Africa in strata of these ages.

"The Catadupa beds also appear to be Eocene on the evidence of the *Trochosmilia,* which has a near European relative in *T. acutimargo,* Reuss. The *Diploria* also has a European analogue. *Trochoseris* is a doubtfully Cretaceous genus; it occurs in the Eocene, and there is a recent species.

"The faunas from the Richmond, Cambridge, and Catadupa beds seem quite different from the St. Bartholomew fauna, described by Duncan. Apparently they possess only one species in common, viz. the *Stylocœnia,* identified by Duncan as *emarciata.* The stratigraphic affinities of the Jamaican species for European species are the same as those of the St. Bartholomew corals, and I believe more extensive study and collecting will show considerable resemblance, — especially after a revision of Duncan's types from St. Bartholomew."

Concerning the eight species found by Vaughan, he says that "there is not a strictly Cretaceous form in the collection from Catadupa and Cambridge, . . . so the corals have afforded no evidence tending to prove the Cretaceous age of these beds, but it all, so far as it is definite, points to an Eocene age." They too occurred in muddy waters, but more calcareous than those of the Richmond epoch, and are accompanied by a large molluscan fauna.

The two or three genera and species of Echinodermata submitted to Agassiz were reported by him to be Tertiary forms.

The mollusca of the Cambridge beds, while few in species, as a rule are sufficiently abundant and well preserved to present a distinct faunal aspect. Fortunately these have escaped the non-resident species makers, who have thrown all other Post-Cretaceous Jamaican fossils into the

---

[1] Quart. Jour. Geol. Soc. London, 1863, Vol. XIX. p. 514.

Miocene, and we are enabled to present it for the first time with appropriate stratigraphic data.

In addition to the Rudistes of Catadupa already described, this fauna furnishes many new species of Mollusca, all of which are apparently quite distinct from those of the Eocene beds of the North American Coastal Plain. More of the forms, as Cerithium and Lucina and Cardium, are very large and robust. Of the genera, one at least is new, and still unnamed; another, Carolia, has not hitherto been found in America. The Catadupa beds also afford specimens of the gastropod genera Conus, Cypræa, and Thalassa, which have not been found below the Tertiary. There are many indeterminate casts of gasteropods in the Catadupa beds which have a striking resemblance to those of the Cretaceous beds of Jerusalem Mountain.

De la Beche has frequently noted the occurrence at many localities of the fossils which we now know to belong to the Cambridge beds in the base of his "White Limestone Series," such as the association of Ostrea, Echini, and two large species of Cerithium. In fact, the entire list of species given by him on page 170 of his work most probably came from the Cambridge beds. He figures one of the large species of Cerithium,[1] and states that at one time he "considered that it might have been a cast of a shell analogous to *C. giganteum;* the latter is, however, a much taller shell than the one under consideration, which in general outline resembles more the *C. cornucopiæ* of Sowerby."[2] It is an interesting fact that this fossil also occurs in the Virgin Islands and St. Bartholomew as noted by Cleve.

According to notes kindly furnished us by Stanton, "the evidence as to the age of the molluscan fossils from these two localities is conflicting The forms described by Whitfield under the names Caprinula, Caprinella, Caprina, and Radiolites, are all Cretaceous types, and the genera to which they belong are not known to occur elsewhere in more recent formations. On the other hand, all the other fossils that are well enough preserved to be recognizable, have a more modern aspect, none of them being characteristic of the Cretaceous. The genus Carolia occurs elsewhere only in the lowest Eocene of Egypt. The large species of Cerithium are of Eocene types, and the same may be said of the Cypræa and several other forms. At any rate, similar species are not known from beds as early as the Cretaceous. If the Rudistes and Chamidæ were absent, there would be nothing to suggest a Pre-Tertiary age for the beds.

The presence of Rudistes, supposedly Cretaceous genera, in this other-

---

[1] *Op. cit.*, Plate 21.

[2] *Op. cit.*, pp. 170, 171.

wise Eocene fauna, is a perplexing feature difficult of explanation. The occurrence of Rudistes and Actæonella in the supposedly Richmond Eocene beds of Jamaica, as recorded by the writers of the Jamaican Reports, has already been noted. Their unsubstantiated hypothesis that these might be rolled survivals of the lower beds naturally originates the inquiry if the Rudistes of the Catadupa beds may not be of similar occurrence. The writer can find no foundation for such an hypothesis in case of the Rudistes in the Catadupa beds. Many of the specimens collected were independent or unattached, resembling in appearance the free forms found in the higher occasional horizons of the Minho beds. The single specimens show no signs of having undergone attrition by rolling. The delicate lamellæ and corrugations, such as would be broken by the least possible attrition, are all preserved, as well as the soft chitinous structure of some of the species like *Caprina jamaicensis*, Whitfield. In fact, these forms show no evidence whatever of having undergone such treatment, and are much better preserved than any found in the Jerusalem beds of undoubted Cretaceous origin. In addition to the loose or free specimens, there was a solid stratum two feet in thickness made up of an agglomerate of these shells as thick as coral heads in reef rock, and absolutely *in situ.* Furthermore, it is difficult to see how such forms, if rolled, could have been sorted out and thus segregated without being accompanied by some of the hard enduring igneous pebble of the conglomerate beds of the Minho and Richmond formations, with and below which the lower Rudistes horizons are interbedded.

Elsewhere the lithologic resemblance of the supposedly undoubted Cretaceous beds to the Yellow Limestone has been noted by the Jamaican geologists,[1] and other fossils collected by us from the Minho River section are lithologically and specifically identical in every appearance with those of the Cambridge beds, including two of the typical Cambridge corals, also occur in the Rudistean Cretaceous beds of Logie Green and Trout Hall.

Another fact which reinforces the supposition that the mixture of these Cretaceous and Tertiary forms is natural is that the Jamaican geologists originally described the rocks of the typical Cambridge beds as "the Cretaceous or Hippurite limestone."[2] In fact, we discovered the Catadupa beds while making a vigorous search for the alleged Cretaceous beds which had been described as occurring between Chesterfield

---

[1] Jamaican Reports, p. 233.

[2] Ibid., pp. 245, 246.

and Retreat, and the Catadupa and Cambridge outcrops were the only fossiliferous beds found.

The statement of Barrett,[1] that Orbitoides "are Cretaceous fossils in Jamaica," may possibly have been based upon a knowledge of the association of these forms with the Cretaceous Rudistes.

In view of the facts presented, the writer finds it utterly impossible to accept the "rolled" hypothesis, and he can see no way of avoiding the positive conclusion that the Rudistean forms in the Cambridge beds represent a survival of Cretaceous types into the Lower Eocene. Such an occurrence would in no manner be more anomalous than many other facts connected with the peculiar insular faunas of late Cretaceous and early Tertiary time in Jamaica, mentioned in this Report. Even though the Rudistes should prove to be survivals, this Eocene fauna of Catadupa as a whole shows anomalies comparable to those exhibited by the Jerusalem beds, which mark it as peculiar. As a fauna, nothing exactly analogous to it is known elsewhere.

In view of the apparent mixture of Cretaceous and Eocene forms, question might arise concerning the position of these beds in the geological column. Inasmuch as all the other genera are Eocene, it is our opinion that it will be best to consider the beds of that age and to assume that the Rudistean genera have transgressed into the Eocene.

The fact that these beds are stratigraphically above the Richmond beds is another consideration which leads us to the Eocene conclusion. Inasmuch as the two species of coral from the latter (mentioned on page 126) attest the Eocene affinities of the latter beds, the discovery of the Cambridge formation gives a certainty to the existence of an Eocene system in Jamaica, aggregating at least 1,500 feet in thickness, which, in connection with the Montpelier beds to be described farther on, of supposed Vicksburgian facies, shows the Eo-Tertiary beds of the island to be far more extensive than hitherto supposed. The paleontologic peculiarities of the Richmond and Cambridge formations, analogous to those of the preceding Cretaceous beds, are such as can only be accounted for by geographic environment, and point to the early insularity of the island through Eocene time.

The relations of this fauna to other regions of the world is anomalous. Its affinities in some respects seem more analogous to those of the southern portions of Europe than to those of the United States, but we do not dare at present to make positive conclusions except to agree with Moore

---

[1] Jamaican Reports, p. 76.

that "the fauna of the West Indian seas in those remote times appears to have been as remote from that of the shores of the United States as it has lately been shown by Mr. Bland to be at the present day."[1]

Fossils of the Montpelier White Limestone.

As a rule, the Tertiary White Limestones which succeed the Cambridge beds, although almost entirely of organic origin, are singularly free from macroscopic fossils, especially the lower half of the Series. There is a current impression that the white limestones, as a whole, are richly fossiliferous, owing to the fact that many shells from the Bowden horizon have been described as coming from the "White Limestones of Jamaica," but, as we have shown, the Bowden beds are not White Limestones, but gravels and argillaceous marls. De la Beche notes many shells from the White Limestones, but all came either from the underlying Cambridge beds or the overlying Post-Tertiary White Limestones of the Coastal Series which we have separated from the true Tertiary White Limestones.

Minute search for such fossils in hundreds of exposures has generally been without success. Except the beds at Port Antonio, which are of Cambridge affinities, the Moneague beds and a few places in the Bog Walk section, the great mass of the White Limestones are barren of such remains so far as we have observed them. This noteworthy absence may in some instances be due to secondary alteration of the rocks, but, in general, it is owing to the fact that the material originated at depths beyond that in which the abundant littoral molluscan life occurred. Notwithstanding the absence of macroscopic remains, the Montpelier beds, which compose the lower 500 feet of the White Limestones, are almost entirely made up of foraminiferal remains, — Orbitoides, Nummulinæ, and Miliolidæ at the base, grading up into Globigerinal deposits. These beds are very free from remains of shallow water corals, — a fact which further supports the theory that they were deposited at great depths beyond that at which these organisms could flourish. The great subsidence of this epoch undoubtedly must have extinguished most of the dense molluscan life, which does not appear again until the Bowden epoch.

Radiolaria are rare in the Jamaican rocks, our specimens from the Montpelier beds usually showing only a few traces of them, — certainly

---

[1] T. C. Moore, Quart. Jour. Geol. Soc. London, Vol. IX. p. 131.

no well defined forms, — although a minute fragment or two in some of the collections are very much like Radiolarian tests. Nowhere on the island have rocks been found made up nearly entirely of these forms such as occur in Barbados, Haiti, and near Baracoa, Eastern Cuba. W. B. Hill has stated[1] that "one or two Radiolarians can be seen in outline in a rock in which Globigerinæ are conspicuously abundant," from Hanover Parish, — where the Montpelier beds occur.

The lower White Limestones of the Oceanic Series are composed of chalk making Foraminifera, deposited in deeper waters than the preceding beds, and of these there are several distinct horizons each composed of a different character or association of Foraminifera.

Globigerinæ appear in great number, composing the chalky strata of the Montpelier beds on the north coast near St. Margaret's, the hill at Montpelier hotel, and the rocks underlying the northern side of the plain back of Savanna-la-Mar, Westmoreland.

W. B. Hill[2] has also described a specimen of white limestone from Hanover County, which he asserts is an "oceanic deposit," in which "thick-shelled Globigerinæ similar to those of the Barbadian rocks" are very abundant. Jukes-Browne and Harrison[3] have said that Colonel Fielden, who sent this specimen from Hanover, reported that flints were abundant in the formation. I do not hesitate from our acquaintance with this region to state that this specimen is from the Montpelier formation.

Orbitoides and Nummulinæ, which have already been noted as occurring in the Cambridge beds, continue into the Montpelier, as Bagg's studies of our specimens show, and from the specimens described by T. Rupert Jones the stratigraphic position of which we have been able to identify, thanks to his having given localities of material studied by him from Jamaica.

Bagg reports the following Foraminifera in our collection, from the Montpelier Formation.

Flints from Montpelier Hill (No. 75): — Orbitoides dispansus, Sowerby; abundant, Eocene. Orbitoides mantelli, Morton, rare; uppermost Eocene and lowest Oligocene. Orbitoides papyracea, Boubée, Eocene. Nummulites, probably.

These flints are Eocene.

Bluff at Dover: — Orbitoides mantelli, Morton. Orbiculina adunca, Fichtel and Moll. Amphistegina sp.

---

[1] Quart. Jour. Geol. Soc. London, 1892, Vol. XLVIII. p. 180.

[2] Ibid., p. 280.

[3] Ibid., p. 219.

Mile Post 74, Falmouth road: — Orbitoides and Nummulites.

Highgate, St. Mary Parish: — Orbitoides dispansus; Orbitoides sp.; Textularia; Pulvinulina; Nummulites.

Port Antonio, Slide No. 13: — Globigerina dutertrei, d'Orb.; Globigerina bulloides, d'Orb.; Miliolina seminulum (Linné), also Catadupa; Nummulites; Amphistegina lessonii, d'Orb. (A. hauerii, d'Orb.); Orbitoides fortissii, d'Arch.; Nodosaria; Vaginulina; Orbitoides papyracea, (Boubée); Discorbina.

This bed is Eocene.

Port Antonio, Slide No. 23: — Nummulites sp.; Orbulina universa, d'Orb.; Globigerina bulloides, d'Orb.; Heterostegina sp.; Orbitolites complanata, Lam.

This bed is Eocene.

13. Port Antonio: — Nummulites; Amphistegina lessonii, d'Orb.; Orbitoides fortissii, d'Orb.; Orbitoides papyracea, (Boubée); Nodosaria; Vaginulina.

This is Eocene.

Buff Bay "near Tunnel." (Montpelier Formation at base of Section.) — This limestone contains an abundance of Globigerinidæ, also many Nodosariæ.

Globigerina: — Truncatulina wuellerstorfi, Schwager; Eocene to recent. Nodosaria raphanistrum, Linné; Cretaceous to Tertiary. Nodosaria pauperata, Cretaceous to Tertiary; recent. Nodosaria (D) aciculata, d'Orb. Nodosaria farcimen, (Soldani); Permian to recent.

We suspect this to be a Tertiary limestone, since Truncatulina wuellerstorfi begins with Eocene beds. The Globigerinidæ and Nodosariæ prove nothing here, as their range is so great.

In addition to the localities given, the following have been observed from our own collections.

Port Antonio (Collection No. 13), a foraminiferal marl made up of Nummulinæ and Orbitoides, with one Rotalia-like form.

Flint beds of Dover (Collection No. 36): — (1) Section of flint. Mostly opalescent amorphous groundmass, — a few spicules and one Rotalia-like form. (2) Chalk: Globigerinæ mostly, with several species of Orbitoides. (3) Another chalk, mostly Rotalia-like forms.

Belmont, St. Elizabeth, clear crystalline calcite, in which are outlined many Foraminifera, Orbitoides being the predominating form.

One mile south of Port Antonio, in upper part of Richmond beds grading into Cambridge. Nummulinæ ? and Orbitoides.

Flints at foot of Montpelier Hill: — These are incrusted with silicified tests of Orbitoides, Alveolina?, and Miliolidæ, while the interior mass of one flint clearly shows the silicified outlines of these remains.

Concerning these species Bagg comments as follows: —

> "The limestones and flints with numerous Orbitoides must belong to the Eocene period, because this genus Orbitoides though sparingly found in Upper Cretaceous beds did not become prominent until Eocene time, and, furthermore, it did not survive the Miocene age and only a few occur in the Miocene. Its geologic range is as limited as almost any other single genus in the Foraminifera group.
>
> "The species of Orbitoides called *dispansus*, Sowerby, is easily recognized by its internal structure and its external mammillated surface. This species is one of the essential constituents of the Eocene rocks of Scinde and also occurs in the Eocene of Southern Germany and Italy.
>
> "Nummulites is another genus almost equally important, being limited in range to the Tertiary period and rarely found now. We have lately discovered this genus in the Eocene beds of Vicksburg, Mississippi.
>
> "The Globigerina limestones of which 48*b* is a good example, are fine illustrations of a rock composed almost entirely of these microscopic organisms. It is, however, impossible to state with certainty its age upon this occurrence. Since *Globigerina cretacea* seems to be absent from these limestones we presume the rock is to be placed in the Tertiary period."

Nummulinæ, so characteristic of the Eocene of Europe and North Africa, but missing in the Eocene of the United States, except in the Vicksburg formation of Florida and Mississippi, where they have recently been identified by Bagg, have been noted in Jamaica, first by De la Beche, next by Woodward, and more fully identified by T. Rupert Jones,[1] supposedly from the Orbitoidal beds, in association with Orbitoides, and also in the flint bearing beds of the Montpelier formation, which erroneously, as in the case of Orbitoides, owing to the stratigraphic misconception, were referred by Jones[2] and Guppy to the Miocene. Operculinæ are also reported by Jones in the flint of Preston, St. Mary, and Brimmer Hill, associated with Nummulinæ, characteristic localities of the Montpelier beds.

In two papers, Prof. Jones[3] describes the material and gives the localities of certain specimens sent from Jamaica in a manner that, after our personal studies of the island, we found no difficulty in recognizing

---

[1] See papers of these authors previously cited.

[2] Geol. Magazine, London, 1864, Vol. I. pp. 102, 106.

[3] The Relationship of Certain West Indies and Maltan Strata, etc., by T. Rupert Jones. The Geologist, January, 1864, Vol. VII. No. 73, pp. 104, 105.

their true stratigraphic position in the general section. This material and its occurrence as given by him is as follows: —

1. In a piece of gray flint from the base of the White Limestone at St. Thomas, Jamaica. Numerous Orbitoides, mostly *O. mantelli*, though some may be *O. dispansus*.

2. Orbitoidal limestone, Hopewell, Metcalf. Flint with Orbitoides and Nummulinæ, Orange River, Metcalf.

3. Limestone with Operculinæ and Nummulinæ, and the same silicified, Brimmer Hill, St. Mary.

4. Flint with Operculinæ and Nummulinæ, Preston, St. Mary.

5. Orbitoidal limestone, Carron Hall, St. Mary.

6. Alveolina limestone, Crofts, Clarendon.

7. Orbitulina rock, Vere.

8. A specimen of hard yellowish limestone at Clarendon, largely composed of the Heterosteginæ, and further noted in this Part under the head of Bowden beds.

Of the above list Nos. 1, 2, 3, and 4 are undoubtedly from the flint and chalk beds of the Montpelier formation; No. 5 is probably from the Cambridge beds; No. 6 from the Moneague; No. 7 comes most probably from the Cobre limestone overlying the Bowden beds.

From these collections, 1 to 5 inclusive, he identified *O. mantelli*, mixed with numerous forms referred to *O. dispansus* and *O. fortissii*, associated with Nummulinæ. Jones also says[1] that the "*Orbitoides mantelli* of Morton, of stronger growth than the variety found in Jamaica, Antigua, and Malta, characterizes some of the Tertiary beds of Alabama, Nummulites being absent, it is supposed."[2]

To this statement we might add that *O. mantelli* is especially characteristic of the Vicksburg horizon of the Upper Eocene (now lower Oligocene of Dall) of the Southern United States, and has been identified from this horizon by Dall from our collection from the beds of this age in Costa Rica. According to Bagg, *O. fortissii*, "a typical Eocene form," also occurs in Panama lower down in the Eocene.

Jones, accepting the current stratigraphic conceptions, was misled into the serious error of concluding that these forms, notwithstanding their world-wide habitat, were Miocene in Jamaica. This opinion was largely due to the publications of J. Lechemere Guppy.

Fossils of the Moneague Beds. — The limestones of the Moneague beds abound in moulds of Mollusca. Fossils of this character from

---

[1] *Loc. cit.*, p. 105.

[2] Since discovered by Bagg. Letter to author.

Retreat consist of single pieces of a delicate branching, indeterminate coral, a Conus, resembling *C. solidulura* Guppy,[1] a Tellina, and large Tubula casts of a Teredo?

The only fossils from these beds which I have been able to have identified are the Foraminifera, of which Bagg has recognized the following species from Cinnamon Hill: *Orbitoides dispansus*, Sowerby; *Orbitoides* sp. undetermined; *Operculina complanata*, Defr.

Of these species Bagg says that the first is Eocene, and the third rare in the Cretaceous and abundant in the Eocene. He remarks that Brady has said that the "Miocene" of Jamaica contains the latter form. Inasmuch as we have shown that the "Miocene of Jamaica" of previous writers meant anything from Eocene to recent, this determination is of no value. Bagg adds that "This bed is Eocene."

Careful collecting should be made from these beds, although the material is of such a poor character that paleontologists to whom it has been shown consider it too poor for determination. The fossils and the material in which they occur are of comparatively deep water character, — more shallow than the Montpelier, but deeper than the Bowden.

The position of these beds below the Bowden clearly indicates that they antedate the latter in age, and for the present we can only say that their affinities are with the Montpelier beds of Eocene age.

The conditions of subsidence which made the deposition of the Montpelier and Brownstown white limestones possible were undoubtedly sufficiently great to drown the pre-existing littoral faunas of Jamaica; and this epoch ended the old insular life conditions of the earlier epochs and separated it from that of the later and succeeding epochs, which assumed a more cosmopolitan character.

The fossils of this horizon practically embrace all the forms which hitherto have been described by the English paleontologists, from the "White Limestone," the "Yellow Limestone," the "Upper Miocene," "Lower Miocene," "Miocene," and Bowden Beds, by Moore, Etheridge, Duncan, Guppy, and perhaps others, and referred to the Miocene, Upper Miocene, and Lower Miocene age by those writers, and finally placed in the Upper Oligocene by Dall.

In résumé we can now say that the hemera of the Orbitoidal fauna of Jamaica is as follows: Orbitoides have been reported in the Hippurites limestone of the parish of St. Thomas by Barrett, Woodward, Jones, and Etheridge, and we have shown their occurrence in abundance in the

---

[1] Quart. Jour. Geol. Soc., Vol. XXII., Pl. XVI. Fig. 1, 1866.

TIME.	SERIES.	FORMATION.	MATERIAL.	FOSSIL REMAINS.	EVENTS.	GEOGRAPHIC CONDITIONS.
Late Pleistocene and Recent.	Coastal.	Bogue Island.	Mangrove mud.		Successive elevations, aggregating less than 500 feet.	Slight peripheral expansion of area to present outline.
		Montego.	Alluvial.			
		Falmouth.	Littoral marl.	Marine Mollusca, reef coral, etc.		
		Coast Soboruco.	Elevated reef rock.	Reef coral.		
		Barbican.	Elevated reef rock.	Reef coral.		
		Hopewell.	Elevated reef rock.	Reef coral.		
Pliocene.		Manchioneal.	Littoral marl.	Marine Mollusca, Foraminifera, Brachiopoda.	Subsidence, submerging margins of the island.	Island contracted to back coast borders.
		Kingston.	Old aggradational material.			
Miocene or Late Oligocene.	Bowden.	May Pen.	Impure lime.	Marine Mollusca, Echinoids, simple corals, Foraminifera, and Bryozoa.	Submergence by subsidence of the margins of the island.	Contraction of island by subsidence.
		Bowden.	Conglomerate and marl.	Same as above, and fresh-water shells.		
Middle Oligocene.		Break.			Mountain folding. Elevations to 10,000 feet or more. Intense erosion of surface and intrusion of "granitoid" rocks.	Area expanded beyond present limits; probable connected Antillean land.
Early Eocene to Early Oligocene.	Oceanic.	Cobre.	White limestone and marl.			
		Moneague.	White limestone.	A few mollusks and simple corals.	Rising bottom.	All of island submerged except a few points of highest mountains.
		Montpelier.	White chalk with flints.	Foraminifera and Radiolaria.	Profound oceanic subsidence.	
		Chapelton.	Yellow-white limestone.	Mollusca, corals, Echinoids, and Foraminifera.	Initiation of Montpelier subsidence.	
		Catadupa.	Nodular limestone in clay.			
Late Cretaceous.	Blue Mountain.	Richmond.	Alternation of clay and sandstone.	A few mollusks and corals.	Erosion and deposition of muddy sediments.	Lowering of land by erosion.
		Minho.	Volcanic tuffs.		Active vulcanism.	
		Ballard.	Black bituminous shale.	Rudistes, corals, and mollusks.	Erosion and muddy depositions.	Volcanic summits rising out of the Mesozoic sea.
		Logie Green.	Yellow marls.	Rudistes, corals, and mollusks.	Irregular deposition during a general period of erosion.	
		Jerusalem.	Irregular beds of limestone.			
		Frankenfield.	Irregularly bedded lavas, tuffs, and conglomerates of hornblende andesites.	Rudistes, corals, and mollusks.	Active vulcanism.	

Cambridge, Montpelier, and Moneague Eocene formations. They are missing in all subsequent strata.

It is also now apparent that Dall's recent statement,[1] based upon Guppy's material from alleged Miocene beds (Oligocene), to the effect that "*Orbitoides mantelli* has not been found in the West Indian species," is incorrect, and we must accept the occurrence of this species as identified by those eminent authorities, T. Rupert Jones[2] and R. M. Bagg.

Concerning the other Foraminifera of the Cretaceous and Eocene strata it can be said that Alveolina is a genus which elsewhere "begins in the Cenomanian, continues in extraordinary profusion, and becomes a most important rock builder in the Eocene[3] of the Paris Basin, Libyan Desert, and Greece, is also reported by Jones in "Alveolina limestone" from Crofts in the northeast corner of Clarendon, — a locality of the White Limestone which we have not had the opportunity of visiting.

The Orbitoides, Nummulinæ, Alveolina, Operculina, and Globigerinæ are Foraminifera which have been found only in the Blue Mountains, Montpelier, and Cambridge beds of the Cambridge section. These genera, with the exception of Globigerina, which ranges extensively through geologic time, from the early Mesozoic to the present, have their typical and highest development elsewhere in the Vicksburg stage of the Eocene Tertiary. In accordance with Dall's usage, the Vicksburg beds, to which the Montpelier beds are undoubtedly equivalent, are now considered the base of the Oligocene. When we consider the stratigraphic evidence concerning the containing formations, there is no reason to believe that their occurrence in Jamaica is later than in this epoch.

The Mid-Tertiary Antillean revolution, with its mountain making, expansion of land areas, and rearrangement of barriers and enclosures, which closely followed after the Montpelier subsidence, seriously affected the conditions of life and produced changes of environment affecting the molluscan and other faunas of the whole Tropical American region. After this revolution, the littoral mollusca, as it next appears in the Bowden formation, presents new and distinct facies, characterized by the appearance in Jamaican waters of species which also occur on the continental borders, many of which are still living. This fauna constitutes the chief bench mark in the whole system of Jamaican Neo-Tertiaries, just as the Cambridge does for the Eo-Tertiaries.

---

[1] Proc. U. S. Nat. Mus., 1896, p. 329.

[2] The Geologist, London, 1864, Vol. VII. pp. 103-105.

[3] Eastman's "Text Book of Paleontology," by Karl A. von Zittell, London, 1896, p. 26.

Fauna of the Bowden Beds. — The Bowden coral fauna was published by Duncan. What is apparently the Bowden molluscan fauna was studied by Carrick Moore,[1] and later by Guppy.[2] Etheridge [3] has also written extensively on the fauna. Most of the English writers except Duncan, in discussing the Miocene fossils, have given no specific localities nor any stratigraphic details concerning their occurrence. Duncan gives Bowden, Vere, and the district of Vere, Clarendon Parish, as the localities of his species of Miocene corals.

Some of these early writers give references which indicate that the original source of their material was a collection of fossils brought over by Barrett in 1862,[4] and deposited in the British Museum. Guppy has also described many species collected by Vendryes, who still lives at Kingston. Moore stated [5] that they came from "some beds which were referred to in the Geologist for 1862, page 373." Upon consulting the volume and article quoted, which is Barrett's original article [6] on the Cretaceous rocks of Southeastern Jamaica, no reference to these beds was found. In the Jamaican Reports, however,[7] Barrett notes that in the gravel at Bowden "are beds of the most perfect Tertiary shells yet known on the island, a list and description of which will be found in the Appendix, after critical examination." This brief note is the only clue to the locality of the numerous molluscan fossils usually discussed by most of the British paleontologists from "The Miocene" and "White Limestone" of Jamaica.

From Barrett's short description, given on previous pages, it will be seen that he clearly recognized the conglomeritic nature of the beds at Bowden, and nowhere speaks of the fossils as occurring in the "White Limestone," or "Yellow Limestone," as they were later made to appear by others. His death prevented his further elucidation of these beds, but the above citations undoubtedly give the locality of the Tertiary fossils collected by him and sent to England, to which Moore, Guppy, Woodward, and Etheridge have alluded, and which is the same as that from which Simpson and Henderson (in 1893–94) and the writer (in 1896) made the abundant collections mentioned in this paper.

---

[1] Quart. Jour. Geol. Soc. London, 1863, Vol. XIX. pp. 510–513.

[2] In many papers previously cited.

[3] Jamaican Reports, pp. 319–338.

[4] See Quart. Jour. Geol. Soc. London, 1866, Vol. XXII. p. 281.

[5] Ibid., 1863, Vol. XVI. p. 510.

[6] Ibid., 1860, Vol. XVI. p. 381.

[7] *Op. cit.*, pp. 44, 45.

It is not necessary to repeat the details, elsewhere stated in this report, of how the original gravel beds of Barrett at Bowden became the "Yellow Limestones" of Etheridge and Duncan and Wall through their miscorrelation by the latter with the entirely different "Yellow Limestones" of Brown in the western part of the island, which we have described as the Cambridge beds and "White Limestones" of some other writers. By easy stages this error grew into a great chain of misinterpretations. Through Etheridge, Barrett's conglomerates became "an outcrop at the base of the White Limestone";[1] next the "Miocene" and the "Yellow Limestone,"[2] as contradistinguished from the "White Limestone," then the "Miocene Limestone" of Woodward,[3] and finally the White Limestone, in general, of the whole Antillean region. It was in this manner, through literary imitations, that the restricted molluscan fauna of a single bed of Jamaican gravel became the fauna of the White Limestones.

Guppy[4] refers back to the articles above cited, and also to the paper of Duncan and Wall,[5] in which, as we have previously shown, the relations of the beds are erroneously given, and wrongly states that "the formation from which the Mollusca to be described consists of shales, sands, and marls exposed *in several parts* of Jamaica."[6]

Concerning the localities of a few Miocene fossils identical with the Bowden forms which have been accredited to "Clarendon" and "Upper Clarendon," it can be stated that these probably came from a point on the seacoast at Round Hill, near Bath, in the extreme southwest corner of the district of Vere, the fossils of which, collected by Sawkins, were said by him to be "nearly all the same genera and species as those found at Bowden, Port Morant, St. Thomas-in-the-East."[7] The reference to "Upper Clarendon" was no doubt an error originally made by Etheridge in citing the field workers. The only allusion made by the latter concerning this locality was in connection with the occurrence of older formations.

Dall has lately published a paper[8] which belongs to a more recent

---

[1] Jamaican Reports, p. 311.

[2] Ibid., p. 311.

[3] The Geologist, London, 1862, Vol. V. p. 373.

[4] Quart. Jour. Geol. Soc. London, 1866, Vol. XXII. pp. 281, 282.

[5] Ibid., 1865, Vol. XXI. pp. 1-14.

[6] *Op. cit.*, p. 282.

[7] Jamaican Reports, pp. 162, 163.

[8] Descriptions of Tertiary Fossils from the Antillean Region. Proc. U. S. Nat. Mus., Vol. XIX. No. 1110, Washington, 1896.

epoch than the contributions of the class of writers previously mentioned. His information was supplemented by the recent field work of Simpson and Henderson and myself. In this paper he describes Guppy's collections, which are accompanied with no information concerning their locality, except that they were collected by Vendryes. We have made inquiries of Mr. Vendryes, through Professor Duerden, concerning the locality of his collections, and he has stated, in a letter dated October, 1897, that they were made at Bowden.

It is sufficient to state, as far as the described species of the so called Miocene and Oligocene Mollusca are concerned, that, instead of having wide and general distribution in Jamaica, they are known to occur in only one or two restricted localities, one of which, Bowden, has furnished all the recorded species.

In but few other places in the world are fossils so beautifully preserved, so representative of diverse orders, or so numerous in species, as in the gravels of the Bowden beds at the foot of Captain Baker's hill, Morant Bay. These occur only two or three feet above sea level, in the bluffs of the highway where it starts up the hill. A single barrel of this material, recently collected, has yielded more than three hundred species of marine Mollusca, in addition to land and fresh water species, besides twenty-six species of corals, five species of Foraminifera, and traces of Bryozoa and Echinodermata.

In the Bowden beds an entirely new foraminiferal fauna appears, and one which occurs under entirely different conditions from those of the Montpelier beds, representing for the second time in the Jamaican history a shallow water foraminiferal fauna. These are of large macroscopic texture, are found in the Bowden gravel beds, and are of contemporaneous origin with them. Following is a list of the genera collected by me from this horizon at Bowden, as determined by Bagg: —

Foraminifera. — Haplostiche soldanii (Parker and Jones); abundant in Tertiary. Textularia barrettii (Jones and Parker); Miocene to Recent. Textularia trochus, d'Orb.; Cretaceous to late Tertiary, Recent. Orbiculina adunca (Fichtel and Moll); Miocene to Recent. Orbiculina compressa, d'Orb.; Miocene to Recent. Cristellaria cultrata (Montfort); chiefly Tertiary. Cristellaria cassis (Fichtel and Moll); Cretaceous to Recent. Cristellaria calcar (Linné); Miocene and Pliocene chiefly. Gypsina globulus (Reuss); very abundant in Miocene. Gypsina vesicularis (Parker and Jones); same range as G. globulus. Cuneolina pavonia, d'Orb.; Cretaceous (?). Cuneolina sp.; perhaps new. Vaginulina legumen (Linné); Trias to Recent. Nummulites ramondi, d'Arch., Eocene to Miocene rarely; this is not very abundant. Amphistegina lessonii, d'Orb.; Tertiary and rare Recent. Synonymy, A. vulgaris, A. hauerii, d'Orb.; Miocene.

This bed at Bowden must be Miocene. The material from Bowden, Jamaica, is undoubtedly Miocene.

Concerning these Foraminifera Bagg says: "The Foraminifera from Bowden, Jamaica, are essentially tropical species which existed in rather shallow waters of less than 300 fathoms, while many occurred at depths of only a few fathoms and still exist. I have recognized the species *Orbiculina adunca* in the Pliocene deposits of the Caloosahatchie River, Florida. This species, though ranging throughout the Tertiary period, did not become plentiful until Miocene time. *Cristellaria calcar,* Linné, another shallow water form, is remarkable for its large size, reaching nearly $\frac{3}{16}$ in. in diameter in the Bowden specimens.

Gypsina globulus, Reuss. This curious little fossil, round, as its name implies, and as large as double B. B. shot, is very abundant in the Bowden material. This is the genus described as Tinoporus, Ceriopora, etc. Professor Brady in the Challenger Report says of this form, and its relative *G. vesicularis,* "Both have been obtained in the fossil condition from the Miocene formation of Austria and Hungary, Malta and Jamaica, and from the Pliocene of Costa Rica, and, according to Parker and Jones, from the Tertiary beds of Palermo, Bordeaux, and San Domingo."

The species *Textularia barretti* is still living in shoal waters off the West Indies. It is a curious type of the genus, being compressed at right angles to the usual plane of compression.

Haplostiche soldani is the form described as *Lituola soldani,* but is now placed by Brady under the genus Haplostiche. It still lives off the West Indies, but was most abundantly developed during the Miocene period.

There are numerous specimens from the Bowden gravel which have an aspect which might be, and probably have been, mistaken for Orbitoides.[1] Jones has also reported Orbitolina from Vere,[2] where other Bowden fossils are found, and from the supposed Pliocene Pteropod marls of Jamaica.

---

[1] Jones has said that "Orbitoides have long been, and still sometimes are, mistaken for Nummulinæ, Orbitolites, and Orbitolinæ, — all very different one from another; and even when they are recognized, it is often difficult to get at their specific characters." — The Geologist, 1864, Vol. VII. p. 106.

[2] Ibid., p. 104.

There are also two or three specimens of a large form which are either Operculina or Heterostegina. Jones has reported[1] the latter genus from the same horizon as that of the "shells and corals lately brought to England by L. Barrett, and described by J. Carrick Moore and Duncan," in a collection which was clearly from the Bowden formation.

Bryozoa. — The Bowden gravel bed contains numerous specimens of a species of Lunulites, associated with the corals, Foraminifera, and Mollusca. This form attains a maximum size of half a centimeter. Dall has also reported[2] *Membranipora savorti* Audovon, from the "Oligocene of Jamaica."

In the Bowden beds is a varied fauna of simple corals. These in association with Foraminifera, Bryozoa, Pteropods, and other Mollusca occur in vast quantities in the gravel and marl at the foot of the bluff at Bowden, and sparsely in the marl at Buff Bay. They have also been reported by Duncan from Vere, the Clarendon coast, and from Navy Island off Port Antonio; and erroneously reported from "Upper Clarendon" by other writers.[3]

During our expeditions we made a large collection of corals from the Bowden locality and these have been carefully restudied by Vaughan, who adds several to the number of species. He reports the following species from Bowden: Thysanus excentricus, Duncan; Thysanus elegans, Duncan; Placotrochus costatus, Duncan; Placocyathus barretti, Duncan; Placocyathus moorei, Duncan; Trochocyathus profundus, Duncan; Lithophyllia ponderosa (Duncan), (non Montlivaltia ponderosa, Edwards and Haime); Circophyllia walli, (Duncan); Asterosmilia sp.; Teleiophyllia probably grandis, Duncan; Porites sp. cf. furcata; Porites sp. of the astræoides type, but with larger calices; Madrepora sp.

In addition to the species of coral previously described from Bowden by Duncan, Vaughan notes that our collection "is especially interesting because it contains two determinable species of Porites and one of Madrepora, none of which have previously been described," and "which, if *in situ*, contribute rather important information concerning the conditions under which the Bowden beds were deposited."

Concerning the corals collected by us from the Bowden horizon at Buff Bay, Vaughan reports that "it contains a specimen of *Placocyathus barretti*, Duncan, and an undescribed species of Dendrophyllia."

---

[1] The Geologist, 1864, Vol. VII. p. 105.

[2] Proc. U. S. National Museum, Washington, 1896, Vol. XIX. No. 1110, p. 329.

[3] See Appendix to Jamaican Reports.

According to Duncan,[1] the Bowden corals (his Miocene) comprise forms common to the Miocene of Europe and species peculiar to the Indian seas, while many of the genera now exist in the Pacific Ocean. He said that one species of Montlivaltia is found fossil at Travanocore.[2] He also states:[3] "Corals from Vere, Bowden, and Navy Island off Port Antonio have no general resemblance to those from the Eocene and Cretaceous strata, but present the appearance of the common specimens of the various Miocene shales and marls of San Domingo and the European Miocene; and all are absent from the existing coral fauna of the West Indies. The comparative absence of compound corals from the Jamaican Miocene is very remarkable; and equally interesting, in reference to the deep sea nature of a part of the coral fauna, is the abundance of Foraminifera which crowd amongst and fill up the interstices of the specimen."

Etheridge states[4] that twelve of the nineteen species worked out by Duncan are common to the Miocene (old usage) of Jamaica and Europe, while eleven of the species are said to be still living, but Gregory and Vaughan cast doubt upon the validity of Duncan's conclusion, as he seems to have confused species from the elevated reefs with those from entirely different horizons. It may not be out of place to add that this fauna is totally distinct in genera and species from another West Indian "Miocene" coral fauna described by Duncan from Antigua. Duncan has also stated that a majority of these species indicate deep water.[5] This fact seems to be borne out by the studies recorded in the "Three Cruises of the Blake."

It is an important fact that only three closely related compound species of corals, such as composed the elevated and modern reefs of the Caribbean region, were found by me in the Bowden beds, and these may have been pieces of recent beach débris. This indicates that true reef building corals had not made serious appearance in Jamaica at the time of the deposition of these beds. The Bowden corals have been frequently cited as reef making forms.

Moore recognized[6] seventy-one species of marine Mollusca from these beds, twenty-eight of which were alleged to occur in the San Domingo beds, and twelve of which are living in the adjacent seas.

---

[1] Quart. Jour. Geol. Soc. London, 1863, Vol. XIX. p. 454.

[2] Ibid., p. 456.

[3] Ibid., 1865, Vol. XXI. p. 14.

[4] Jamaican Reports, p. 309.

[5] Quart. Jour. Geol. Soc. London, 1868, Vol. XXIV. p. 12.

[6] Ibid., 1863, Vol. XIX. p. 511.

Guppy has described 250 species of "Tertiary fossils of the West Indian region" without giving definite localities or horizons, but we have reason for believing that a large majority of these come from the Bowden beds. Dall has recently described[1] forty-eight additional species from the "Oligocene of Jamaica," which are all from the Bowden locality.

No detailed list of the molluscan fauna of Bowden as a whole has been made,[2] although such a catalogue would be most important and valuable, for with it the discussion of all great questions concerning the West Indian later Tertiary paleontology would be made intelligible, while now this subject is in a stage of mist and chaos. Dr. Dall has in his hands the material for such a catalogue, and it is sincerely hoped that he will make one at an early day. It is a well known fact that a large percentage of these Bowden forms have persisted through later times and are at present living in West Indian waters, and that deductions concerning the Pliocene or Pleistocene age of the succeeding beds can be made only on the percentage of many forms. Without a census of the Bowden molluscan fauna, it must be evident that all such deductions as have been or will be made concerning this fauna are unstable.

Dall correlates[3] this molluscan fauna with the "Chipola, Tampa, and Chattahoochee horizons of Florida, corresponding to the Aquitanian of France." He also notes the wide occurrence of this fauna in the Antilles, Trinidad, and Curaçoa, and on the mainland of Panama. A large percentage of these forms still exist in the adjacent seas and represent the ancestral conditions of the present life.

No traces of Pteropods were found in my examinations of any of the rocks below the Bowden beds. In the latter numerous specimens of small Pteropods about five millimeters in length appear. In these beds there are also many specimens of a craniate shell attaining a diameter of half a centimeter which may belong to this order. Bagg has kindly identified the species as follows: Hyalæa gibbosa, Rang; Hyalæa limbata, d'Orb.; Hyalæa (Diacria) vendryesiana, Guppy.

The land and fresh water Mollusca of these beds stand out strong and clear, thanks first to the admirable studies of Simpson.[4] He enumerates

---

[1] Proc. U. S. Nat. Mus., Vol. XIX. pp. 303–331, Washington, 1896.

[2] I have heard that G. F. Harris, British Museum, is now working on one.

[3] Proc. U. S. Nat. Mus., Vol. XIX. p. 304, Washington, 1896.

[4] Distribution of the Land and Fresh Water Mollusks of the West Indian Region and their Evidence with Regard to Past Changes of Land and Sea. By Charles Torrey Simpson. Proc. U. S. Nat. Mus., Vol. XVII. pp. 423–450, Washington, 1894.

the following fossil species from the beds at Bowden: Neocyclotus (Ptychocochlis) bakeri, Simpson; Lucidella costata, Simpson; Pleurodonte bowdeniana, Simpson; Thysanophora; Opeas; Succinea.

In the marginal land derived material of the upper part of the Blue Mountain Series and Cambridge beds, no remains of land or fresh water mollusca have been found, and if they existed in late Cretaceous or early Eocene times, it is singular that no trace of them can be found in beds so peculiarly adapted for their occurrence. Even if they previously existed, their absence in the deep water marine beds of the Montpelier and Moneague beds would be natural, for they are never met with in such formations.

In the Bowden series, however, land shells do appear for the first time, several species having been sorted out of the great fauna of Foraminifera, Bryozoa, Hydroids, corals, and Mollusca of this peculiar littoral formation which occurs in the midst of the great White Limestone Series. Their appearance here fits in beautifully with the facts of the Mid-Tertiary land expansion elsewhere given, and thoroughly satisfies the facts of the present known distribution of their descendants in other islands and in Central America, as elsewhere explained. Simpson has found a probably fossil land shell in the succeeding Cobre limestone of Bog Walk.

A few traces of fish teeth have been found in the Bowden formations.

In résumé, it can be said that the Bowden fauna as a whole marks a most important horizon in Jamaican history, representing the reappearance of molluscan life after the long hiatus intervening since the Cambridge epoch, and presents the beginnings of the littoral fauna which have since prevailed around the border of Jamaica in the later Tertiary, Miocene, and Pliocene-Pleistocene, and recent time.

The Cobre Beds. — The Cobre (White Limestone) which may be a synchronous but deeper water formation than the Bowden beds, is largely composed of Foraminifera mixed rarely with débris of Mollusks, simple corals and Echinoidea. Mollusca are almost entirely missing from this formation, except at its immediate base near Bog Walk village, where many imperfect casts may be found, all of which have a superficial resemblance to the Bowden and later forms. In these beds we found two or three specimens of Echini. The main portion of this limestone is almost entirely foraminiferal.

Our microscopic sections of the white limestone of this formation, from the convict quarry east of Kingston and Bog Walk, show a large number of small Foraminifera of many species, but in which Nummulinæ, Orbitoides, etc., of the Montpelier and lower beds are entirely absent. To this formation belongs the collection of specimens described[1] by William Hill from Mile Gully, Manchester Parish, containing Amphistegina.

Probably this is the limestone largely composed of Heterosteginæ from Clarendon Parish, described by T. Rupert Jones,[2] which he says "corresponds to the same horizon as that of the shells and corals [Bowden] brought to England by Mr. L. Barrett and lately described by Mr. J. Carrick Moore and Dr. Duncan."

Bagg reports as follows upon the Foraminifera of limestones collected from the Cobre formation.

No. 80. Yallahs: *Globigerina bulloides*, d'Orb.; Cretaceous to Recent. Orbulina universa, d'Orb.

The apparent absence of *Globigerina cretacea* makes it very probable that the rock is to be placed somewhere in the Tertiary period, but *Globigerina bulloides* occurs abundantly in many horizons.

No. 58. Rock Quarry, one mile east of Spanish Town: Amphistegina, (also at Bowden); Nodosaria; Globigerina; *Textularia trochus* (also at Bowden); Textularia (2 sp.); Rotalia or Discorbina.

No. 62. Retreat, Clarendon, Operculina (?); Textularia (also at Bowden); Cuneolina (?) (also at Bowden); Gypsina (also at Bowden).

No species of corals have as yet been identified with certainty from the Cobre limestone beds. Only two or three imperfect specimens of what were apparently simple corals were found in our close examination of hundreds of outcrops of this formation, but they were too imperfect for specific identification. They resemble very much the simple forms of the Bowden beds.

Duncan has reported three species from "the hard white limestone" which may have come either from the Cobre formation or the white limestones of the Coastal Series. One of these, *Alveopora dædalæa* is known to occur in formations of later age than the Bowden beds, in Antigua; another, *Cyphastræa costata*, a doubtful species, is said to occur in the Post-Pliocene (presumably Pleistocene) beds of the island of Barbuda.[3] The third, *Astrocœnia decaphylla*, he says, is a Cretaceous

---

[1] Quart. Jour. Geol. Soc. London, 1891, Vol. XLVII. pp. 248, 249.

[2] *Op. cit.*, pp. 104, 105.

[3] "*Cyphastræa costata*, Duncan. The type from Barbuda is a piece of the small caliced West Indian *Orbicella* — *O. aeropora* Linn. (Gregory) *O. annularis*, Dana, of Pleistocene, late Tertiary or recent age. The other specimen, from Santo Domingo, and labelled *Cyphastræa costata*, is a *Solenastræa*, therefore the name *Cyphastræa costata* must be dropped from coral nomenclature. Gregory's *Cyphastræa costata* are *Orbicella acropora*."— Vaughan.

coral of Europe. Probably the stratigraphic occurrence of the latter in Jamaica was not properly represented to Duncan, and it may have come from the Cretaceous formations of that island, in which some of the limestone (notably of Clarendon) is as "hard and white" as any of the other white limestones.

Fauna of the Pliocene Formations. — In the Pliocene, Manchioneal, and Mulatto River beds of the Coastal Series, we have the first undoubted appearance of the modern reef building compound corals in the Jamaican sequence. In these two localities of supposed Pliocene age, the forms occur sparsely as single heads in the former, and as a thin stratum of true reef rock about one foot thick in the latter.

Vaughan has recognized an *Orbicella*, probably *radiata*, and a *Meandrina* from these beds.

In discussing a species of *Terebratula* reported by Guppy from Trinidad, Etheridge[1] distinctly notes that "none occur in the Tertiary of Jamaica, although careful search was made through the collection." De la Beche says,[2] "At Manchioneal Harbor the white marl contains corals, spines of Echinites and Terebratulæ, besides casts of other shells." Barrett, in a note which was published by Woodward in the "Critic" of February 1, 1863, also noted the occurrence of Terebratulidæ in the new Tertiary of Jamaica.

We were fortunate to find in these beds at Manchioneal two Terebratula forms which have been determined by Schuchert to belong to the genus Liothgrina. Most of the specimens are *L. vitrea*, Borne, and one specimen is probably *L. bartletti*, Dall. The former is not known as a living species in the West Indies, but is a common species of the Pliocene of Sicily.

There is also a single specimen of a large and beautiful *Caviolina*, about one centimeter long, very much resembling the figured specimens from the Pliocene of Italy. From the so called Pteropod marls, which are probably allied in age, Etheridge reports[3] three genera of Pteropods, to wit, *Cleodora, Creseis,* and *Cuvieria.* The Manchioneal beds contain but few other molluscan remains, only a few moulds and casts having been found by me. Barrett, who collected more thoroughly, is said to have found sixteen species of recent Mollusca belonging to the surrounding seas in this marl.[4]

The "Pteropod Marls" of Barrett — our Manchioneal beds of supposed Pliocene age — contain still distinct foraminiferal fauna, the species

[1] Jamaican Reports, p. 318.

[2] Ibid., p. 181.

[3] Ibid., p. 319.

[4] Ibid., p. 313.

of which, as determined by T. Rupert Jones and W. K. Parker, are nearly all identical with those dredged by Barrett in the adjacent sea at depths which indicated at least 100 fathoms.

The species determined by Jones and Parker[1] are as follows: Nodosaria raphanus; Nodosaria raphanistrum; Dentalina acicula; Frondicularia complanata; *Cristellaria calcar; *Cristellaria cultrata; Cristellaria rotulata; Cristellaria italica; *Orbitolina (Gypsina) vesicularis; Bulimina ovata; *Lituola (Haplostiche) soldanii; Vertabralina striata; *Cuneolina pavonia; Vagulina acumen; Vagulina striata.

Eight of these species have been found living in the adjacent waters by Barrett. Five of the species (marked *) are the same as those identified by Bagg in the Bowden beds. Those genera which are specially characteristic of the Oceanic White Limestone and Cambridge beds, such as Orbitoides, Nummulinæ, Operculina, Heterostegina, and Amphistegina are absent here,[2] as well as from the Bowden beds.

In the Falmouth beds of the north and south coast of the west end of the island, the third, last, and most recent horizon of abundant well preserved fossil remains of Post-Pliocene Mollusca are met. They include Lucina, Cardium, Arca, Solen, and many other genera of bivalves, and among the Gasteropoda forms of Turbo and Strombus, such as abound off the present coast, and great numbers of a small Bulla, which is especially abundant in similar deposits of Yucatan, Barbuda, and other West Indian localities. This sub-recent or Pleistocene fauna is well worthy of careful study and analysis by those interested in the study of the paleontology of the Mollusca.

Fauna of the Elevated Coral Reefs. — In the elevated reef of the Coastal Series, corals are everywhere found, either as the chief material of the elevated reefs, as previously described, or as single specimens or fragments in the contemporaneous marls.

Vaughan has identified the following species of coral in the various Soboruco collected by us.

"7. Barbican Bay, Jamaica, twenty-five foot reef; Siderastræa radians, (Pallas); Siderastræa siderea, (Ell. and Sol.); Porites porites (Linn.); Orbicella acropora, (Linn.).

"13. Bluff east of Port Antonio, Jamaica; Orbicella acropora (Linn.).

"16. Soboruco, Port Maria, Jamaica: Lower Soboruco; Orbicella acropora, (Linn.); Siderastræa siderea, (Ell. and Sol.).

"38. Tryhall, Jamaica; Lower Soboruco: Orbicella acropora (Linn.).

---

[1] British Association Reports, 1863, p. 80.

[2] Noted by Etheridge, Jamaican Reports, p. 313.

"39. Hopewell, lower reef between Lucea and Montego, Jamaica: Meandrina, sp.; Siderastræa radians, (Pallas); Orbicella acropora, (Linn.); Porites porites, (Linn.); Madrepora muricata, Linn., *forma* cervicornis, Lam.

"50. Soboruco cut in railway, Orange Bay, old Soboruco: Orbicella radiata, (Ell. and Sol.).

"54. Soboruco, Runaway Bay: Orbicella acropora, (Linn.).

"71. One mile west of St. Ann Bay; Lower Soboruco: Orbicella acropora, (Linn.); Siderastræa sp.

"93. Corals from stratified limestone, Mulatto Bay, (Manchioneal Beds): Orbicella acropora, (Ell. and Sol.); Orbicella radiata, (Ell. and Sol.); Meandrina, sp.

"Manchioneal Bluff, 'same as other reefs.'"

PART IV.

Geologic and Topographic Evolution of the Island.

In the preceding chapters we have set forth the general geographic features and the details of composition, structure, and paleontology, and arrived at conclusions by whose use the events accompanying the geologic and geographic evolution of the island can be more intelligently reviewed.

Upon the table (page 143) we have summarized this history in a manner that will enable the reader to follow what will now be set forth in detail. A short sketch of the principal events of its history will now be given, including, first, a brief outline of the events, next, an interpretation of their magnitude.

The known history of Jamaica begins with the expiring days of the Cretaceous period. What part the present locus of our island played in the earlier events of the battle between sea and land preceding this epoch cannot at present be stated, but we do know that in late Cretaceous time its crests appeared above the waters, and that in succeeding epochs grew more and more conspicuous.

The vast accumulation of rolled igneous pebble of hornblende-andesites and volcanic tuffs, which constitute the oldest known rocks of Jamaica, prove clearly that in late Cretaceous time volcanic eruptivity was active at or near the island during their formation, while the colonies of peculiar fossils interbedded at intervals in these rocks fix the time of their origin as the latest epochs of the Upper Cretaceous period. Furthermore, the species themselves, their faunal assemblage, and the circular arrangement of the colonies around the nuclei of the Blue Mountain and Clarendon ridges may possibly indicate that there were several centres of this eruption. The débris of this event was enormous. The thickness of that portion which now survives can be assumed to be at least five thousand feet. The former extent and relations of these late Cretaceous volcanic outbreaks in the Antilles is now concealed by the coatings of later formations, but they were not peculiar to Jamaica alone, as shown later in this Report.

The next event in Jamaican history was the degradation of the nucleal volcanic heaps by erosion, — a fact recorded in the sediments of the upper part of the Blue Mountain Series, especially the Richmond beds. The thickness of these sediments, aggregating 1,500 feet or more, attests the existence of a high pre-existing land, and the abundant plant remains they contain show that it was thickly covered with vegetation. The nature of the sediments themselves, which are of impure land-derived material, carbonaceous clays, sandstones of volcanic débris, and beds of the older igneous pebble reassorted, and the scarcity of animal remains, indicate rapid erosion and deposition. The uniform alternations, the wide extent of the formation, and the occasional presence of marine fossils, show that the material was sorted in shallow waters. This fact, together with the presence of a few pebbles of foreign origin, the absence so far as known of any distinct delta or estuarine deposits, and the widespread occurrence of similar formations in the West Indies, suggests the existence in the region at that time of larger land areas than the mere nucleal summits we have described.

There is also evidence that subsidence accompanied this deposition, and that the two events were so compensatory that the depth of bottom did not materially change. These events were also closely followed by folding of the strata, — a process which was repeated at intervals until the close of Miocene time throughout the Antillean region.

The strata of the Richmond beds are not only everywhere folded, but near Lucea, in the western end of the island, they are closely flexed, and are completely overthrown, as shown in the illustration on Plate XXII. The epoch of this folding could be easily assigned to a later disturbance, such as that at the close of the Miocene, were it not for the fact that none of the overlying and succeeding strata exhibit such intensity of disturbance. The latter occur in gentler and more open folds.

There is also some evidence of unconformable deposition of the later beds upon the Richmond. On the south side of the Clarendon Mountains the Chapelton beds of the Cambridge formation rest directly upon the Minho beds of the Blue Mountain Series, without the intervention of the Richmond beds; the Catadupa beds at Catadupa are interpolated between the Richmond and Chapelton beds; at other places, on the north side of the island, the Chapelton beds rest directly upon the Richmond.

Furthermore, the older beds of the Blue Mountain Series, the Cretaceous limestones and Richmond beds, are all turned up together in this older and more complicated system of foldings, and inseparably constitute the summits of the Blue Mountain Ridge, which between the altitude of 3,000 and 7,325 feet now protrude 4,325 feet above all the later Eocene and Oligocene formations. These facts, especially the different nature of the folding, strongly suggest an interruption of sedimentation and a corrugation of the strata after the close of the Richmond deposition period, and also indicate that mountain making movements were operative in Mid-Eocene time, which may have been the initiation of the uplifts, which had far reaching importance in Antillean history, accompanied by active vulcanism in the Isthmian and probably Windward regions. We are not prepared to interpret fully this particular event without further examination of the region. If, on the other hand, this folding did not occur at this particular epoch, then the Richmond beds may mark the initiation of a great subsidence so clearly traceable in the succeeding epoch.

Lime making fossils begin to appear in the upper part of the Richmond shale where the Cambridge beds begin, — such as Foraminifera, corals, and Mollusks, — and the lime they produce has been taken into solution and segregated into masses and strata of nodular limestone, occurring in the shale. These impure limestones of the Cambridge beds represent the transition between the terrigenous littoral deposits of the Richmond and the deep oceanic chalks of the Montpelier epoch, and are a step in the great subsidence that was then progressing. The "Yellow Limestones," like the Richmond beds, are undoubtedly of Eocene age, corresponding to the later portion of that period.

The rapidity with which the impure nodular limestones of the Cambridge grade into Montpelier chalks, composed of Globigerinæ and void of molluscan fossils, indicates that the subsidence, initiated as above stated, continued to profound depths, 1,200 fathoms or more, accompanied in adjacent localities with great deposits of Radiolarian earths.

This subsidence was one of the most important and far-reaching events in all Antillean history as we shall show in our next Part. For present purposes, however, it is best to consider how far it involved the pre-existing land topography of Jamaica. Canyon cuttings through the collar of the limestone plateau which now encircles the peaks of Blue Mountain structure show that the latter extends down to sea level and nearly everywhere out to the present margin of the island. The limestone deposits of this subsidence encrust this mountainous core to a height of 3,000 feet, and hence only the portion of the summits above that altitude could have been dry land when this subsidence was at its maximum. This land, then, was restricted to an area of what is now the upper slopes and summit region of the Blue Mountain ridge proper. The remaining parts of the island, including the limestone plateau and the Clarendon and Jerusalem Mountains, were completely submerged. The culmination of this subsidence can be fixed by the paleontologic evidence at the close of the Eocene period, Vicksburg epoch.

The next event in Jamaican history was the re-elevation of the sea bottom and the restoration of the land area to proportions far beyond its present outline, connecting it with the adjacent island of Haiti on the east and possibly the Central American region to the south of west. This elevation is attested, first, by the shallowing nature of the upper limestone Moneague formations of the Oceanic Series, in which simple corals and Mollusca appear; and, secondly, by the emergence of these strata into land during another period of mountainous folding, accompanied by great laccolithic intrusions of igneous granitoid rocks.

This emergence of the island to beyond its present outline is evident. This emergence brought up with it that portion of the old presubmerged mountainous topography now encrusted by a coating 1,000 feet or more of oceanic chalks. That the land extended still farther beyond its present margins than at present is shown by the truncated termination of the formations of the back coast topography, and the unconformity of the later formations against their eroded bluffs, the submerged benches of the island, and the biologic proof that dissemination of the land Mollusca between the islands took place at this time.[1]

This emergence was dominated by a low east and west fold through the geographic centre of the island, which caused its present elongate

---

[1] Distribution of the Land and Fresh Water Mollusks of the West Indian Region. Proc. U. S. Nat. Mus., Vol. XVII. pp. 423–450, 1894.

shape. This constituted a gently arched openly folded anticlinal structure, inclining north and south. This broad fold is marked in its course by numerous short secondary wrinkles or miniature low anticlinal folds, as is so beautifully shown in many places, notably near Catadupa and Montpelier. (See Figs. 18, 19, 20.)

Accompanying this uplift was a great intrusion from below of the deep seated granitoid and dioritic rocks we have described. The central location of this mass below the limestone, now so beautifully exposed by subsequent erosion in St. Mary, the metamorphism which the overlying Montpelier beds have suffered, and the numerous dikes protruding from it through the oceanic limestones and Blue Mountain Series, indicate that this laccolith was contemporaneous with this epoch, and corroborate the belief that, if it was not the direct cause, it was at least intimately associated with this Mid-Tertiary (Oligocene?) uplift of Jamaica.

The higher terraces or levels, between 1,000 and 2,100 feet, seem to have been during or immediately following this emergence epoch, and previous to the next subsidence to be described. We shall also show that this event was not peculiarly Jamaican in its effects, but had a wide reaching influence in Antillean and Central American geography.

The next event in Jamaican history was a renewal of subsidence and a contraction of the land to its present back coast borders. This subsidence, recorded in the Bowden formation, involved at its conclusion only the margins of the present island area, which at its beginning was probably expanded beyond its present borders. It was initiated by the deposition of the land derived littorals of Bowden gravels, found only in the north and south coasts of the eastern portions of the island, and probably culminated in the deposits of the shallow marls. The amplitude of this movement was probably less than one third that of the great Montpelier subsidence. The Bowden and Cobre beds encrust the pediments of the island up to a height of less than 300 feet. The land area during this epoch again became insular in character.[1]

Succeeding the Bowden epoch there was another upward movement of the island. The larger portion, which had remained land during the Bowden subsidence, including much of the Limestone Plateau and the

---

[1] The probable absence of these formations from the western half of the island, if true, and the immediate east coast if proven after further research, may indicate that the Jamaica-Haiti land connection continued to exist during their deposition, and that the more extensive lands existed to the south and west in the vicinity of the Pedro Banks or beyond.

Blue Mountain ridges, was elevated some 500 feet or more, bringing up with it, not only the present marginal border composed of the new made sediments of the Bowden epoch, but a now slightly submerged area towards the south, which extended at least as far as the present 500 fathom line, embracing the Pedro banks and keys. This upward movement, while accompanied by slight deformation, was less orogenic than those of the preceding epoch, probably representing the last throes of the Antillean uplifts. It is very certain that the large area of Jamaica was expanded during this epoch (late Miocene) beyond its present borders at least as far as the present 500 fathom line.

Accompanying or closely following the time of this elevation in late Miocene or early Pliocene time was a period of great erosion and denudation, which largely produced the minor relief of the surface configuration of to-day. During the Pre-Bowden elevation the headwaters of the marginal drainage of the south coast, which then flowed out to sea across the present submerged banks, were actively engaged in cutting out, as headwater amphitheatres, the embryo embayments of the present Liguanea type of plains, and the older sink-holes in the summit of the limestone arch by dissolving through the soluble limestone. In the Post-Bowden epoch the sink holes were cut downward to the insoluble strata, underlying the limestone, producing the first of the present great interior basins, which also commenced to expand laterally by erosion of their soluble margins. Meanwhile, the coastal drainage rapidly extended interiorward by headwater erosion, and the country adjacent to its lower portions became extensive base-levelled plains, and included then what are now the submerged benches of the island, and which were veneered with the aggradational Kingston formation during a subsequent subsidence. This period of erosion was late Miocene or early Pliocene, corresponding in time almost exactly with the great Pre-Lafayette erosion epoch of the North American continent.

During this late emergence the middle series of terraces (now from 200 to 700 feet high) were cut around the coastward face of the back coast country.

Possibly there was another subsidence in late Pliocene time, — the first of a cycle of epeirogenic oscillations that characterized the later history of the island. The island once more underwent partial subsidence; the pre-eroded coastal plains and base-levelled bights bordering the island became in their seaward extension submerged platforms, while their interior borders constitute deeply indented estuaries at the mouths of the great rivers of the south coast and Montego Bay of the north side. The platforms were covered with littoral formations and the estuaries filled with aggradational débris. This submerged the island to the foot of the back coast country. It clearly took place during the late Pliocene and beginning of Pleistocene time.

The next and last event was the epeirogenic elevation, or series of elevations, which have continued until the present time, restoring to the island the belt of land now forming the fringing coastal border, including the elevated reefs.

The continuity of this uplift may have been interrupted by a minor subsidence in early Pleistocene time. Unfortunately paleontologists have not sufficiently analyzed the West Indian marine faunas to enable us to discriminate between the Pliocene, Pleistocene, and recent faunas, especially the last. Hence the differentiation of the stages of Post-Pliocene chronology is still vague. As the pre-submerged platforms of the preceding epoch of subsidence were brought up within the zone of reef coral growth, the first true coral reefs began to fringe the island and formed outlying and fringing reefs. As elevation progressed, the oldest of these were first raised above the sea into a bench of Soboruco, while new living reefs were installed upon that portion of the submerged platform which the elevation in turn brought up to a position favorable for reef growth. Thus successive reefs were elevated into coastal benches, while living reefs continued to grow in the adjacent waters, as are found to-day. In this manner, as the island was constantly rising, the terraces of reef rock now found at altitudes of 60, 25, and 15 feet, as described in the geologic portion of this paper, were made. Similar living reefs continued to grow as now in the adjacent waters, which in turn may some day be elevated into marginal terraces. Inasmuch as the elevated reefs are made up entirely of living species, there is no reason to assign this elevation to a more remote period than late Pleistocene and recent time.

Accompanying their elevation the lagoonal débris behind the barrier reefs was also converted into low coastal swampy lands, and the streams renewed their channels to the sea across the old alluvial plains. This elevation completed the geographic evolution of Jamaica into the land area it presents to-day.

From the foregoing statements it will be seen that the evolution of Jamaica has resulted from varied processes of land construction, including, first, piling up of volcanic ejecta in the beginning of its history, which we shall not further mention at present; and two kinds of uplifts, orogenic and epeirogenic movements respectively.

These movements have collectively constituted the great oscillations whereby, since the close of Cretaceous time, the land and sea bottom have moved up and down, resulting in the expansion or shrinking of the respective areas in harmony with these movements.

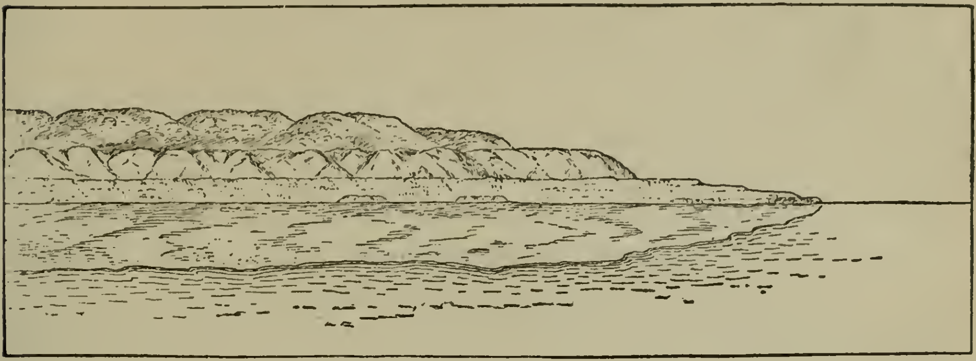


FIGURE 39. Coast Benches, Trelawney.

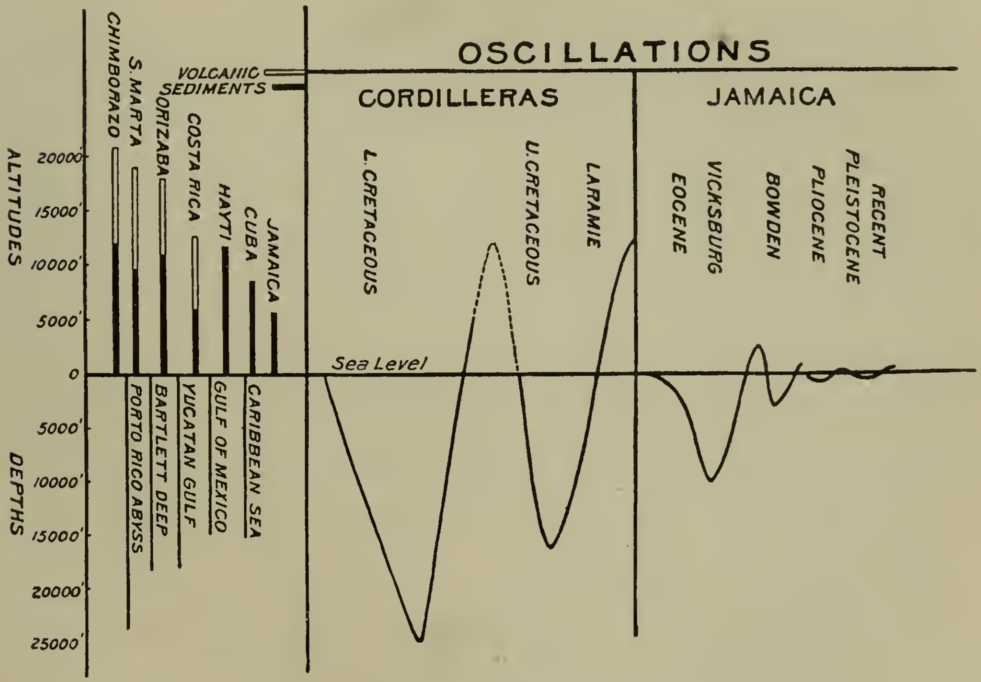


FIGURE 40. — Changes of Level in the West Indian Region.

These oscillations, as summarized upon the accompanying diagram, have comprised three complete cycles of movement, each of which embraced a period of depression and elevation, the downward movement of which may be termed the Montpelier, the Bowden, the Manchioneal, and the Pleistocene subsidences, and the succeeding elevations the Mid-Oligocene, the late Miocene, and the early Pleistocene, or recent elevations respectively. It is interesting to note that these movements are each successively smaller in amplitude than the preceding, like the dying strokes of the pendulum.

The orogenic or mountain folding movements were especially characteristic of the earlier of the middle periods of its history, while the epeirogenic events mark the later stages. The Post-Richmond, Post-Moneague, and Post-Bowden uplifts were all of an orogenic character, but each successively consisting of broader arching and less closely folded deformation. Thus it is that the Richmond beds are closely folded and overthrown, the Cambridge, Montpelier, and Moneague beds arched and gently wrinkled, the Bowden beds only tilted. Collectively, they probably represent the initiation, culmination, and expiration of the great Antillean mountain uplifts. The elevated reefs recording the epeirogenic movements were horizontally elevated without visible deformation.

An interesting fact of the structure of Jamaica, as well as the Antilles in general, are the two lines of orogenic dominant trends, one extending northwest and southeast, and the other east and west. Whether these trends can be each associated with a peculiar effort of mountain making we cannot form definite conclusions at present. It is very probable, however, that all of the structure was originally dependent upon an ancient early Mesozoic orographic uplift or buttress, which had an east and west axis through the Great Antilles and the Guatemala-Chiapas region, the only trace of which is now preserved in the old Post-Paleozoic mountains of the latter region and possibly Western Cuba. It is certain, however, that the earliest movements visible in the present structure of Jamaica had a northwest and southeast trend conformable to the direction of the present Blue Mountain ridge, and conformable to similar trends in the combined coast line of northeast Cuba and Haiti and the outer margin of the Bahama Banks. The later movements have east and west trends (which might be called Antillean), as shown in the secondary axis of the elevated limestone ridges of Jamaica, Cuba, Porto Rico, and the structure of the base of the Yucatan peninsula, the mountains of Eastern Honduras, the Isthmus of Panama, and the Venezuelan coast. It may be well to note here that it is impossible at present to fit into either of these systems of trends — the Bahaman or Antillean — all the Windward Islands or their submarine platforms.

To the physicist who estimates the amplitude of these oscillations there is apparently only one available datum plane, — the position of sea level relative to that portion of the island now protruding above the water. This is an imperfect bench mark, however, for a large portion of the former island surface is now submerged, and sea level may have changed. Fortunately, we have in the geomorphology, stratigraphy, and paleontology of the present land area, and the knowledge of the submarine topography and bathymetric distribution of living marine organisms, important collateral data which give valuable facts for estimates.

The first or great primary oscillation was that embraced in the cycle of the Cambridge-Montpelier descending, and the early Oligocene ascending movement. This subsidence was certainly 3,000 feet, as can still be measured by the height to which the bases of the old pre-existing mountain summits are plastered with its deposits. When we remember that the present land surface of Jamaica is only the crest of a larger Jamaica still submerged, it would be no stretch of the imagination to believe that the movement was from twice to thrice the amount given. In fact, there is very direct evidence which leads us to the latter conclusion.

The purity of the Montpelier chalks and their dominant composition of Globigerinæ would indicate that they were deposited like the deep sea oozes of to-day at depths of 1,200 and 2,300 fathoms. The fact that in the eastern end of the adjacent island of Cuba the stratigraphic and time position of these beds is occupied by Radiolarian earths which are now known to abound from 2,000 to 4,000 fathoms (12,000 to 24,000 feet) justifies us in premising that the Globigerina beds of Jamaica were laid down in very deep waters. It would not be at all unfair to assume the average between the minimum and maximum of the Globigerina and Radiolarian depths as 1,750 fathoms, or over 10,000 feet, as the mean of this subsidence at Jamaica. The assumption of a minimum depth has additional support in the fact that the Jamaican Globigerina deposits were close to the slope of the nucleal islands which persisted as tips of land during this epoch.

The succeeding Post-Montpelier upward movement brought up the bottom not only to sea level (± 10,000 feet), but raised it at least 3,000 feet above it, which would equal an elevation of 13,000 feet. As the highest mountain peaks of Jamaica now stand 4,325 feet above the material deposited in the Montpelier subsidence, they must have reached at the culmination of this elevation altitudes of over 17,000 feet above the sea. As great as these heights may seem, they do not greatly exceed that of the summit of the Sierra de Santa Marta, which now stands beside the Caribbean shore of Colombia, and of other known high peaks like Orizaba and St. Elias adjacent to the Pacific shore lines of our own continent.

So grand a subsidence and elevation as this must surely have left some record in the present submarine topography of the whole region, and we cannot contemplate maps of such phenomena without coming to some very definite opinions which will be elucidated in Part V. Neither could the maximum of elevation have failed to expand the areas of the Antillean lands, and to unite many of the islands or even the mainland together, especially had their geographic areas been greater then than now, which hypothesis seems tenable.

The amplitude of the Bowden subsidence could hardly have exceeded, if it reached, 3,000 feet (500 fathoms). The data for this conclusion are as follows: — The upper and lower limits of the deposition beds of this epoch are now practically visible. While they have, no doubt, been attenuated by erosion and their thickness has not been finally measured, they do not exceed 500 feet in thickness. The lithologic and sedimental character of the beds indicate a rapid gradation from off-shore to moderate oceanic depths. The fundamental beds are gravels, much water worn, embedded in marl, but contain no plant remains or other indications of ultra shallow deposition, although land shells do occur sparingly in them. The fauna could not have lived at depths of over 500 fathoms.

The presence of nearly four hundred species of Mollusca in a single horizon of one of the basement beds at first suggests immediate littoral conditions. Their mode of occurrence in the gravel, however, indicates slightly deeper or off-shore conditions or origin, for had this gravel been near the beach line the delicate shells would have been ground and broken into breccia by wave action, and it is probable that they were too deep to be influenced by any such action. The mollusca are such as live at present at depths of less than 100 fathoms. The several species of Foraminifera, Bryozoa, and corals, especially the last, which are all simple non-reef-building species of the type which Pourtalès has mentioned[1] as having probably lived at an average depth of 450 fathoms, indicate *abyssal* or *continental* deposition. These facts indicate that the basal Bowden beds, now exposed at sea level, were slightly below sea level at the beginning of the Bowden subsidence, and that the amount of the depth must be subtracted from the total thickness of the Bowden to ascertain the true submergence, which could not have exceeded 500 fathoms.

[1] Cited by Agassiz, "Three Cruises of the Blake," Vol. II. p. 19.

The Post-Bowden (Miocene) emergence equalled the combined thickness of the Bowden beds, the depth of deposition and their present altitude above sea level of about 300 feet, or a total not exceeding 1,000 feet. This movement was to a certain extent orogenic, resulting in deformation by tilting and differential elevation, the rocks being inclined as high as twenty degrees in places.

The amplitude of the Pliocene subsidence, if there was one, judged from the thickness of the Pliocene deposits, could not have exceeded the interval between the present 100 foot contour of the land to about the 100 fathom line of the sea, or a total of 700 feet. It was probably much less. This was sufficient, however, to restrict completely the island to its present insular condition.

The Pleistocene-recent emergence in Jamaica can be measured by the position of the top of the emerged Pliocene rocks above the sea (200 feet), and a conjectural supposition that they were deposited at a depth of over 100 fathoms, or a total of at least 800 feet.

The foregoing estimates platted upon the diagram (Figure 40) are not given with any idea of finality, but as a preliminary contribution — the mere entering wedge — to a subject which future studies will improve, amplify, and correct. They sufficiently approximate the truth to be considered of greater value than mere guesses.

The number and amplitude of these great oscillations, and the radical revolutions in geography which they produced, not only appal the mind by their magnitude, but have taken place with rapidity, — all having practically occurred in the Cenozoic era. They present a flashing panorama of gigantic changes. Yet there is reason to believe that these movements were not catastrophic in character, but of that dignity which accompanies all the great isostatic changes. They are merely further illustrations that geologic time is long, notwithstanding our incapacity for conceiving the fact.

The amplitude of each of these movements, if known with exactness, would be an important key note not only to Jamaican history, but also would throw important light upon the whole of the Tropical American region which participated in them, and of which it is the geographic centre.

PART V.

Relations of the Jamaican Formations to those of Adjacent Regions.

Having given every known evidence of paleontology, geologic structure, and geomorphology bearing upon Jamaican history, and having presented the conclusions in the preceding Part, this work would not be complete without an attempt to point out the extension of the described phenomena throughout the adjacent Great Antilles and other regions of Tropical America, where similar or related geological formations and topographic features of the land and sea should be found. While the facts to be set forth in the present Part make no pretensions to finality or completion, they will be a further contribution to the subject which will assist whoever may hereafter take up and continue these investigations.

I must leave the discussion of the biologic and oceanographic phases of the question to others, and in this place I shall endeavor to discuss only the testimony of the stratigraphy and structural geology, presenting a brief conspectus of the extent throughout the adjacent regions of formations similar to or identical with those found upon the island of Jamaica, together with remarks on the source of the material. In Part VI. I shall review the history of the deformation, including the evidences of elevation, subsidence, and degradation, which often occurred synchronously in different parts of the region, and finally make an inquiry as to their influences upon the present land and submarine configuration of the West Indian region.

The regions with which comparison will be made will be: (1) The Great Antilles proper, including the Virgin Islands and the Bahaman Plateau; (2) The Caribbee Islands; (3) Barbados; (4) The Venezuelan coast of South America, including Trinidad; (5) The Central American region, including the Isthmus of Panama and Yucatan peninsula, and the Guatemala-Chiapas or Tehuantepec Province; (6) The Coastal Plain of Mexico and the United States.

In these presentations I shall be able to show that the Jamaican sequence, so far as it reaches backward in time, is remarkably like that of all the Great Antilles, and may be distinctly termed the Antillean type. This type presents great lithologic variation from that of the peripheral coast lands of the American Mediterranean, yet their relations are harmonious. I shall also be able to show a remarkable difference in some respects between the formation of the Great Antilles and the Caribbee Islands.

In Cuba and Haiti alone of the West Indies (excepting Trinidad, which is as much South American as is Long Island a part of the New England coast) is it at all probable that Pre-Cretaceous or older rocks than in Jamaica are exposed, although theoretically it is even possible that the submerged portions of all the West Indies including Jamaica may have a Paleozoic foundation. Cuba and Haiti it should be remembered, with Porto Rico and the Virgins, are in the main axial line of the Antillean uplift, and it is highly probable that older rocks occur in them, while Jamaica is an outlier or offshoot of this main axis.

The Cuban rocks also contain some mica schists and other classes of rocks which as yet have not been found in Jamaica except in the later débris. Hennoken,[1] and perhaps others, have described micaceous schists of supposedly Pre-Cretaceous age in San Domingo. Duchassaing[2] has described a Paleozoic coral (*Favosites Dietzii*) from St. Thomas. Cleve,[3] however, was inclined to believe that this specimen is not native to the island.

Castro and Salterain[4] consider that in Cuba there occurs a considerable range of Pre-Cretaceous rocks, some of which were questionably considered and mapped as Paleozoic. Salterain has referred certain formations, notably in the western province of Pinar del Rio, which the writer has not had opportunity of personally studying, and an area near the city of Trinidad, to the Paleozoic, Triassic, and Jurassic periods.[5]

With the exception of the foregoing, and certain observations of Frazer and Bergt to be noted later concerning the islands of Cuba and Haiti, there are no records of exposures of any Pre-Cretaceous

---

[1] On Some Tertiary Deposits of San Domingo. Quart. Jour. Geol. Soc. London, 1853, Vol. IX. p. 115.

[2] Mem. della Acad. dell. Scien. di Torino, 11 ser., Tom. XIX. p. 84, 1860, and Ibid, 1866, Tom. XXIII. p. 199.

[3] Geology of the Northeastern West Indian Islands. By P. T. Cleve. Stockholm, 1871.

[4] Croquis de la Isla de Cuba, 1869–1883.

[5] Lea has also described from near Havana two Brachiopods, *Terebratula poeyana* and *Rhynchonella tayloriana*, which are very similar to certain forms from the Jurassic of Mexico and South America. See Trans. Amer. Phil. Soc., Phila., 1841, Vol. VII. pp. 258–260, Pl. X. Figs. 12 and 13.

rocks in the West Indies, and while we are willing to grant that they may have occurred, their exposure has been so completely covered by the more recent events of sedimentation, vulcanism, and diastrophism that the interpretable history of the islands may be said to commence with Cretaceous time. The rocks and general section of the Great Antilles all present otherwise a great resemblance to those of Jamaica, as will now be shown.

Clastic rocks composed of water deposited tuffs and volcanic débris, with occasional Cretaceous fossils of the type of the Blue Mountain Series, constitute the basement formation of the interpretable geologic series in all the Great Antilles as in Jamaica, and form the summit masses of high mountain topography, showing that the present configuration at least has largely been produced since the Cretaceous period.

Rocks of the character of the Blue Mountain Series, which constitute the fundamental formations of Jamaica, have wide occurrence throughout the other Great Antilles, Cuba, San Domingo, and Porto Rico, and the Virgin Islands of St. Thomas, St. John, Tortola, Iost Vandyck, Sandy Key, Guana, Camanoe, Scrub, Mosquito, Prickly Pear, St. James, Dog, Savanna, and Inside Bras; also on the islands of St. Croix and St. Bartholomew,[1] where they constitute the oldest rocks. In some of these localities these rocks of the clastic basement group have not been separated from the overlying Richmond and Cambridge formations.

In Cuba these clastic rocks constitute the high divides of the Oriente, and occur to the westward below the limestones in insular spots as in Jamaica. In addition to the hornblende-andesite gravel which predominates in Jamaica, the Cuban and San Domingo beds contain débris of the older rocks not found in Jamaica.

In the Republic of San Domingo[2] formations analogous to the Blue

---

[1] Geology of the Northeastern West Indian Islands. By P. T. Cleve. Stockholm, 1871.

[2] The geology of the island of Haiti or San Domingo has been partially studied by several geologists. These studies have been largely confined to the eastern Republic of San Domingo. So far as we are aware, there is hardly a single published contribution to the geology of the western Republic of Haiti. We have in our possession, however, some important unpublished minor manuscripts by Gabb.

Those who have made researches of the island since 1804 were Schomburgk (1851), Don Manuel Fernandez de Castro (during the Spanish annexation), Henneken (about 1859), Prof. Gabb (about 1870), and the geologists of the United States Commission, W. P. Blake, J. S. Adams, and A. R. Marvine (1871), and L. Gentil Tippenhauer. Of these it may be said that the researches of Schomburgk, Mountain Series have great development where they constitute the highest mountain summits, the Pico del Yaqui, reaching an altitude of 9,684 feet (2,955 meters) according to Schomburgk. They are also probably the nucleal material of the Republic of Haiti, and its two westward extending peninsulas. This formation has been described by Gabb[1] as the Sierra group, and his descriptions in every way coincide with it as it occurs in Jamaica, except that it contains some gravel of different material.

The occurrence of these rocks in the islands to the east of San Domingo is based upon the descriptions given by Cleve in his excellent work on the Northeastern West Indian Islands.[2] He has described, as the "Bluebeache" from St. Thomas,[3] a formation fully 6,000 feet in thickness consisting of stratified conglomerates and tuffs largely made up of hornblendic igneous material, which he says also occurs beneath the white limestone formations, on the north side of Porto Rico,[4] and which he considers probably of Cretaceous age. He has also described the same formation from the Virgin Islands to the eastward.

This formation, which is over 5,000 feet in thickness in Jamaica and 6,000 feet in St. Thomas, is the most important landmark in

Henneken, Gabb, and Tippenhauer present prospective views of the general geology successively controverting in a more or less degree the previous observations.

Gabb's report on the Geology of San Domingo, notwithstanding its value, presents a confusion of data concerning the Tertiary sequence and the white limestones in general, very similar to that concerning allied formations in Jamaica. After careful study of the work I am of the opinion that he has failed to interpret correctly the stratigraphy of these formations. There can be no doubt that he has confused the two great littorals, the equivalents of the Richmond and Bowden, and classified with the Coast Limestone all the limestone formations from the Montpelier to the elevated reefs inclusive. Furthermore, these errors upon his part have led to some very broad generalizations which are utterly untenable.

Of these writers Gabb has given by far the largest and oftenest quoted report, while Tippenhauer gives the latest and best general summary (Die Insel Haiti, Leipzig, 1893). The recent researches of Bergt, noted on a later page, alleging the possible existence of an older plexus of Pre-Cretaceous rocks were not published at the time of Tippenhauer's contribution. While Tippenhauer's age conclusions are not always reliable, the sequence which he gives of the rocks is the first logical presentation thereof, and presents a remarkable analogy to the general Jamaican sequence as set forth by us, as will be seen by the section on page 172.

[1] Topography and Geology of San Domingo, p. 83, and unpublished manuscript in the library of the U. S. Geological Survey.

[2] Kongl. Svenska Vetenskaps-Akademiens Handlingar, Bandet 9, No. 12, 1870.

[3] Geology of the Northeastern West Indian Islands, 1871, p. 4.

[4] Ibid., pp. 14, 15.

GEOLOGIC SEQUENCE OF HAITI, BY TIPPENHAUER.

AGE.	FORMATION.	MATERIAL.	THICKNESS.	EQUIVALENTS TO JAMAICAN SECTION. R. T. HILL.
Post Tertiary.	Alluvium.	Lime, sand, chert, red iron earth, vegetal humus, muck.	Feet. 328	Various coast formations of Jamaica.
	Coast limestone.	Limestone and marl with masses of corals and mollusks.	65.60	Soboruco.
	White marl.	White or yellow marl with some limestone lumps.	295.20	Manchioneal, Pliocene.
Tertiary.	White limestone (Post-Pliocene) = Vicksburg Oligocene.	Chalk marl with red soil.		Cobre.
		Compact limestone; limestone breccia.		Moneague and Bowden.
		Thin chalky strata with intercalated white marly layers which often contain flints. Thinner sandy strata of limestone mixed with clay.	2,624	Montpelier.
	Yellow limestone (Miocene) = Eocene.	Yellow clay and sand; compact yellow limestone alternating with yellow clay and marl. Thin blue strata.	656	Cambridge.
	Eocene conglomerate; later clay strata and sandstone; thinner clay strata.	Green, brown, or dark gray strata between thin layers of fine-grained sandstone (lignite).	984	Richmond beds. Blue Mountain Series; upper part.
Secondary.	Cretaceous Formation.	Yellow marl and clay; yellow-brown limestone; more blue limestone, all containing fossil Hippurites.	656	Antillean, Cretaceous, equivalent to lower part of Blue Mountain Series.
	Metamorphosed Conglomerate.	Metamorphosed clays; sandstones, conglomerates composed of syenite, granite, diorite, much broken.	3,280	
	Plutonic rocks intruding into above.	Syenite, porphyry, granite, and diorite.		

Antillean history, representing as it does the commencement of a consecutive sequence of events from late Cretaceous time to the present. It is clearly the débris of a vast volcanic extrusion which in late Cretaceous time completely obliterated and revolutionized all the antecedent relief. The age of this eruptive epoch is clearly late Cretaceous.

In San Domingo,[1] St. Thomas,[2] and Porto Rico, these formations are associated with limestone beds and Cretaceous fossils in part, resembling in species and faunal associations those of Jamaica, and in part containing species not found in the latter island. In Cuba[3] both the Jamaican and continental types of Cretaceous faunæ are found.

The data seem to point to the fact that the whole region of the Great Antilles proper, including the Virgin Islands, St. Croix, and St. Bartholomew, was the site of active vulcanism in late Cretaceous time.

The extent or outline of the Antillean volcanic disturbance of late Cretaceous time cannot be delineated. It is an important fact that no Cretaceous fossils or formations analogous in age to the Blue Mountain Series are known to occur in the Caribbee Islands proper and Barbados. There is slight evidence, however, that the Cretaceous rocks and fossils of Central America are of the Antillean facies. The sparsely developed Cretaceous formations of Central America known to occur only in the Chiapas-Guatemala district as reported by Sapper,[4] and the San Miguel

---

[1] From San Domingo, Gabb has reported a serrated oyster, Trigonia, Turritella, Ancillaria, Pugnellus (?), Mactra, Pterocera, Cucullæa, Lima, an Ammonite, and Baculites from beds of limestone in the River Maniel. Tippenhauer (*Op. cit.*, pp. 84, 85) gives the following note on the Cretaceous of San Domingo: "The San Juan valley on Samana, the Pico Gallo on the Central range, the region of Tablasas in the south, are types of this secondary formation. These masses, up to 300 m. thick, form a zone around the highest elevations. Besides vast, compact gray-blue and dark limestone masses, there occur marl and sand strata. The ordinary fossils are Hippurites, Nerinea, and Actæonella. The compact limestone often encloses Radiolites up to seven feet long. In places the limestone has been strongly metamorphosed by the influence of plutonic rock; in such cases it resembles serpentine, is exceedingly dense, and has lost almost all its fossils by obliteration; it is also for the most part whiter."

[2] The beds of St. Thomas, according to Cleve, contain the fossils Nerinæa, Actæonella, Ammonites, Trochus, Pectunculus, Limopsis, Opis, Venus, Astarte, Corbula, etc., of Cretaceous age. Geology of the Northeastern West Indian Islands, 1871, p. 5.

[3] In Cuba the Cretaceous fossils, according to Salterain, are Holectypus, Discoidea, Cassidulus, and Codiopsis; and, according to G. F Matthew, Ostrea, Exogyra, Inoceramus, from a locality in the Cienfuegos road, and a Hippurite limestone composed of Caprinella and Caprotina, corals, a large Oliva, a Conus, an oyster of the type of *O. cristati*, Echini, and sponges from Limones.

[4] Grundzüge der physikalischen Geographie von Guatemala, p. 9.

beds of Costa Rica,[1] are of a clastic nature, and intermixed with volcanic débris, and contain a little studied fauna of Rudistes quite suggestive of the Antillean type. The oldest known formation of Panama is an unfossiliferous andesitic tuff of Pre-Tertiary and probably Cretaceous age.

No Cretaceous formations interbedded in igneous deposits analogous to these are known to exist on the coast of the North American continent north of Tehuantepec, although, as has been shown, active vulcanism was in progress during the Upper Cretaceous period in the vicinity of Austin, Texas, and southwestward. Whether or not this was the most northern extent of the volcanic phenomena which were especially active throughout the Central America, Isthmian, Antillean, Andean, and Venezuelan regions at that time cannot be stated.

The northern portions of the South American continent — Colombia, Venezuela, and the outlying islands of the Venezuelan seaboard — possess Cretaceous faunas of a South American type, including beds of older epochs than those found in Jamaica. Pteroceras, Cerithium, Turritella, Trigonia subcrenulata, Arca, Cardium, and Echinus have been reported by the official Trinidad Survey[2] from Cumana, on the mainland near Trinidad.

Stratified formations of the type of the Richmond beds, composed of impure land derived carbonaceous shales and sandstones grading upward into calcareous beds representing the initiative of the great Mid-Tertiary subsidence, also have wide occurrence in the West Indies, although but few attempts have been made at differentiating them from the preceding group with which they are continuous.

In San Domingo and Haiti, as in Jamaica, this formation undoubtedly has extensive development. It has been clearly described by Gabb,[3] but confused with the equivalents of the Bowden beds. It is most probable that the uptilted coarse sandstones, conglomerates near Bao and Yagui, and the shales into which they grade as described by him, are the equivalents of the Richmond beds. They have a thickness between 1,200 and 1,500 feet. Tippenhauer's[4] description of the Eocene conglomerates of Haiti conforms perfectly with the nature of

---

[1] Geological History of the Isthmus of Panama and Portions of Costa Rica. Based upon a Reconnoissance made for Alexander Agassiz, by Robert T. Hill. Bull. Mus. Comp. Zoöl., Vol. XXVIII. No. 5, 1898, pp. 226, 227.

[2] Report on the Geology of Trinidad, by G. P. Wall and J. G. Sawkins, London, 1860, p. 166.

[3] *Op. cit.*, p. 94.

[4] *Op. cit.*, pp. 85, 86.

the lower part of the Blue Mountain Series, and the Richmond beds of Jamaica. Concerning these he says: —

> "The Eocene conglomerates consist of sandstones, clay slates, and stratified conglomerates. The latter predominate decidedly. The constituents of nearly all these beds are almost exclusively of volcanic origin, and are to be attributed to the decomposition and erosion of the porphyritic and syenitic rocks, especially the former. The porphyritic constituents have in the main imparted the red color to this formation. The débris forming these conglomerates is granite, especially syenite and porphyry, also trap, more rarely gneiss; they are united by a siliceous cement. Alongside of them are found limestone pebbles, whose blue-gray or black color and Hippurite and Nerinea fossils indicate that they belong to the Jurassic (?) limestone. The texture of the various beds is loose, where no plutonic masses have exerted a hardening influence. The sedimentary origin, however, remains recognizable in the lines of stratification and in the flat rounded pebbles. The strata, varying in thickness from a few inches to several feet, always appear in regular arrangement. At the surface this formation is frequently decomposed into local clays, shining ochres, kaolin, various siliceous stones, agates, amethysts, and quartz. Such surfaces, either high plateaus or mountain crests, always have a dreary red appearance. The clay slates often show a well marked purple color. At the base of this formation occur dark colored clay slates; they seem to extend back into the epoch of the Jurassic limestone. There they also grow more rich in fossils, and show traces of plants, marine shells, and calcspar veins. Lignite beds of small extent lie between the slates. The sandstones bear impressions of leaves and stems. The higher clay slates are light brown or reddish, and form thin beds of friable conglomerates, resting on massive gray sandstones. In the vicinity of eruptive rock the sandstone is hardened, becomes crystalline and transformed into quartz; elsewhere it is soft and friable. The slate has been still more changed by heat, having become porphyritic. When exposed to the air, it crumbles, the sulphur, iron, and lime being separated and forming with the aluminum two differently colored clays, red and gray, used in industry."

In Cuba the bituminous plant-bearing shales of Esperanza and other points in Santa Clara province and in the vicinity of Havana, previously noted by the writer[1] and others, occupy a position below the great White Limestone Series corresponding to that of the Richmond beds. So far as is known the outcrops are not widely developed.

In Porto Rico, the Virgin Islands, and St. Bartholomew, no attempt has been made to separate this formation from the overlying equivalents of the Cambridge beds, or to distinguish it from the Bluebeache, but doubtless future study will reveal its presence there.

[1] Notes on the Geology of the Island of Cuba, Cambridge, 1895, p. 246.

In the islands of Antigua, Guadeloupe, and Martinique, of the Windward Island group, which are quite different in generic structural character from the Antilles and Virgin Islands, there are vast deposits of stratified tuffs which belong to several epochs. The lower portions of these are suggestively like the Richmond beds in arrangement, although entirely different in composition. We are not prepared, however, to assert their identity at present, although there is some evidence of synchronous origin, as some of them in Antigua clearly underlie fossiliferous beds similar to those elsewhere overlying the Richmond. The whole structure of the island of Barbados below the veneering of reef rock is composed of an intensely folded land-derived formation of littoral land-derived shales and sandstones (the Scotland beds) which closely resemble the Richmond Eocene formation of Jamaica and the other localities mentioned, and in our opinion is identical in age with them, as will be shown in a future paper.

The widely distributed occurrence of such beds of land-derived material at the base of the Tertiary in the Great Antilles and Barbados, is suggestive of the existence and destruction of extensive land areas concerning which I can now state but little. Furthermore, these formations are remarkably similar in general character to the synchronous deposits of the continental littoral, as will now be shown.

Along the continental margins of North, Central, and South America there are thick formations of approximately synchronous age which have a remarkable and suggestive lithologic and structural resemblance to the Richmond beds of the Antilles, being composed like them of impure unwashed land derived material accompanied by plant remains and bituminous material, everywhere occurring in uniform wide extending alternations of sands and clays indicative of shallow marginal deposition within the limits of tidal action, and marked by the absence of limestones of organic, oceanic, or other than segregational secondary origin. Of this nature are the lower and by far the greater portion of the Eocene beds of the Southern Coastal Plain of the United States, — the Great Northern Lignite Group of Hilgard, — which extends as far southward as the Tropic of Cancer in Mexico, and the similar formations which characterize the closing days of the Cretaceous and beginning of the Tertiary throughout the great Rocky Mountain front. The lithologic resemblance of the older Tertiaries of the Central American, Isthmian, and Colombian coasts of South America to those of the Antilles is equally striking. In Trinidad and Venezuela the Eocene formation is also represented by a land-derived formation, the Naparima beds, which coincides in character with the Richmond formation of Jamaica.

The wide extent in latest Cretaceous and Eocene time of these impure shallow water land-derived deposits, so alike in sedimentary character, is an evidence of changes of level during these epochs when rapid erosion and deposition were going on. Around the continental margins, except in Panama, the source of the material can be traced to an adjacent back land, but all geologic record of the lands whence the Antillean deposits came are destroyed.

There is also evidence of wide occurrence in the Antilles of stratigraphic horizons corresponding to the Cambridge beds of Jamaica, marking the rapid transition from the underlying land-derived shales into the overlying Oceanic White Limestone deposits of the Montpelier type and characterized by its peculiar invertebrate fauna.

In the islands of Anguilla and St. Bartholomew the shales and conglomerates allied to the Richmond are overlain by or intercalated with limestones and marl beds. The faunas of the two islands, as reported by Cleve,[1] are somewhat different. The fossils of these probable Eocene horizons from Anguilla, as enumerated by Cleve, consist of many species of molluscan genera, only one of which, *Natica phasianelloides*, W. J. G., is also reported from the Richmond beds of Jamaica. These Anguilla beds were originally referred to the Miocene by Guppy.[2] Following the latter author, Cleve, in describing the fossils, referred them to the Miocene. This conclusion was fortified by the identity of the fossils characteristic of the San Fernando beds of Trinidad, which Guppy at that time also considered Miocene. Guppy in his latest papers has referred the San Fernando beds, together with those of Anguilla,[3] to the Eocene, and the latter age must now be accepted for the Anguilla beds, which are worthy of further investigation.

In St. Bartholomew certain beds referred to the Eocene by Cleve[4] and Guppy[5] have a most decided Cambridge aspect. Nearly every fossil genus mentioned from them is identical with those found in the Cambridge and Catadupa beds, including the peculiar gigantic Cerithium, Terebratula, and the Echinoderms Macropneustes and Echinolampus, — genera which were found by me in the Cambridge beds of Jamaica.

---

[1] *Op. cit.*, pp. 22–26.

[2] Quart. Jour. Geol. Soc. London, 1866, Vol. XXII. p. 297.

[3] Geol. Magazine, London, September–October, 1874, p. 2.

[4] *Op. cit.*, p. 44.

[5] Geol. Magazine, London, September–October, 1874, p. 2.

There is no evidence that beds equivalent to the Cambridge are represented at all in the other islands of the main chain of the Windward Islands, unless the Orbitoides and Nummulinæ of Antigua, described by Jones[1] from an unknown stratigraphic horizon, belong here. I am disposed to consider them not later than the succeeding Montpelier horizon.

In Barbados and Trinidad it may be possible that the Cambridge horizon is represented by a certain formation characterized by *Nucula schomburki*, which is closely associated with the base of the equivalents of the Montpelier beds next to be described.

In San Domingo, as described by Gabb,[2] the Yaqui shales, like the Richmond shales of Jamaica, grade up into 400 feet of locally varying beds, which, like the Cambridge, are "yellowish or brown or buff color," and like them contain corals and Orbitoides. Many of the fossils noted by Gabb, especially the Orbitoides and Nummulinæ, are similar to those of the upper part of the Cambridge beds of Jamaica, where they grade into the Montpelier beds. Conrad[3] has previously asserted the Eocene character of the fossils of this formation, which Gabb erroneously included in his Miocene.

Tippenhauer[4] has more clearly described the Haitian equivalent of the Cambridge than Gabb. His description of the beds leads me to believe that they are identical with the Cambridge beds of Jamaica in age, composition, thickness, and fossils, thereby indicating a similar geologic history during this epoch in the two islands. His descriptions are as follows: —

> "The yellow limestone lies above the conglomerates and below the white limestone. Its peculiar yellow ochreous color makes it readily recognizable. Bright yellow marls and blue gray clay also occur in this formation. The boundary line between the white and yellow limestone is very indistinct, except that the white limestone is poor in fossils, while the yellow is exceedingly fossiliferous. It is very rich in Foraminifera, Ostrea, and Echini. Instead of the great compact masses of the higher-lying white limestone, the yellow limestone shows series of distinctly stratified thin beds. For the most part these strata consist of yellow, sandy, or clayey marl. In some places the limestone is compact and crystalline. In such cases it forms a fine marble; in others it is impure and verges toward sandstone. The total thickness of this for-

---

[1] The Geologist, London, January, 1864, pp. 102–106.

[2] *Op. cit.*, p. 94 *et seq.*

[3] Smithsonian Miscellaneous Collection No. 200, p. 37, and Proc. Phila. Acad. Nat. Sci., 1852, p. 198.

[4] *Op. cit.*, pp. 85–87.

mation may be about 200 meters. The formation of the yellow limestone, essentially marine in character, seems to have been terminated by river-mouth deposits, since its highest strata consist of shells and carbonated clay slates, containing brackish water. At this period the formation must have been almost on a level with the surface of the sea, but after it, during the deposition of the white limestone, there was presumably a great epoch of depression ; the yellow limestone must have descended to considerable depth to allow the formation of 800 meters of white limestone. A remarkable peculiarity becomes apparent at the surface of the yellow limestone. After the primitive forest has been cut down, no other trees grow on it, but only a graminea (*Anatherum bicorne*). This phenomenon is so characteristic that it indicates the boundaries of this formation. Owing to the extraordinary porousness of the white limestone, water readily seeps through it, and, unless carried off by underground flow, it descends until it reaches the impervious clay of the yellow limestone, and there, under appropriate conditions, gushes out of the ground.

"Among the common fossils of this formation are Cardium, Ostrea, Trochus, Natica, Cerithium, Conus, Serpula, Echinocyamus, Echinolampus, Orbitoides, and Corals."

Every detail above noted corresponds exactly with the character of the Cambridge beds of Jamaica.

Formations allied to the deep water Montpelier beds of Vicksburg age (late Eocene of old writers, early Oligocene of Heilprin and Dall) constitute an especially important landmark in Antillean history, and have wide occurrence. White limestones made up of Globigerina chalks or white siliceous deposits composed of Radiolaria occur in Cuba, Haiti, Barbados, and Trinidad. In Barbados the Globigerina chalks grade down into pure Radiolarian earths, constituting with them a related and continuous formation, which in turn overlies the older Eocene Scotland formation, composed of land derived sediments like the Richmond beds, and are folded together with them in the most complete mountain structure. This association of the Globigerina and Radiolarian beds in Barbados establishes the intimate relations of the deposits.

At Baracoa in the northeast part of Cuba, and Port Jérémie, on the north coast of the southeastern peninsula of Haiti, Radiolarian earths occur in great abundance. I was so fortunate in my explorations of Cuba as to ascertain the exact stratigraphic occurrence of these Radiolarian earths unconformably beneath the late or Bowden Oligocene, then called Miocene by Dall.[1] In the light of my later researches in Jamaica,

---

[1] Notes on the Geology of the Island of Cuba, Bull. Mus. Comp. Zoöl., Vol. XVI. No. 15, Cambridge, 1895, p. 253, Pl. I. Fig. 5.

I have no hesitation in considering this bed synchronous in age with the Montpelier chalk of Jamaica.

In Cuba foraminiferal white limestones of the Montpelier type have wide extent, especially in the western and central portions of the island, notably in Havana and Matanzas.

The Eocene system of Cuba, as described by Castro,[1] Salterain,[2] and Valentin Peleterro,[3] undoubtedly includes the equivalents of our Cambridge and Montpelier beds. Among the characteristic fossils are *Orbitoides mantelli* and *Aturia zigzag*, Sow., the latter from La Criolla, near Havana, and from the Sierra de Santiago.[4] According to Salterain, this is also the same species as that called *Nautilus cubaensis* by Lea.[5] These fossils occur in a white limestone very much like that of the Montpelier beds of Jamaica, and have wide occurrence.

That the Cambridge and Montpelier beds have extensive development in Haiti and San Domingo there can be no doubt. This the reader can readily ascertain, if, after reading this report, he will peruse the descriptive portions of Gabb's Geology of San Domingo, although Gabb does not differentiate the white limestones of the upland or interior from that of the coast formations, but confuses them together under the head of the Coast Limestone, in the very untenable thesis on pages 103–112. In numerous places in the descriptive portion of his report the upland limestones are described in a manner that leaves no doubt not only as to their existence but also their differentiation into the several kinds we have described from Jamaica and Cuba. He notes in many places the occurrence of Orbitoides, and says,[6] "It has more than once proven of great value to me in distinguishing these limestones from the overlying Post-Pliocene calcareous beds." Furthermore, on page 144 of his report, he speaks of a Nummulite form which is found throughout the Dominican "Miocene from the blue shale at its base to the top of the series." In his unpublished manuscript in the Library of the United States Geological Survey, entitled "Additional Notes on the Topography and Geology of San Domingo," he further comments on

---

[1] Pruebas Paleontologicas, etc.

[2] Apuntes para una Descripcion Fisico Geológica de la Habana y Guanabacoa, Madrid, 1880, pp. 30–40.

[3] Apuntes Geológicos referentes al Itinerario de Sagua de Tanamo a Santa Catalina de Guantanamo. Boletin de la Comision del Mapa Geológica de España, Tomo XX. pp. 89–98, Madrid, 1895.

[4] Salterain, *loc. cit.*, p. 37.

[5] Trans. Am. Phil. Soc., 2d Series, Vol. VII., Plate X. Fig. 15.

[6] Page 96.

the occurrence of the *Nummulinæ* as characteristic of the otherwise unfossiliferous lower Miocene and its discovery in Haiti. From his details there can be no doubt that the Post-Cretaceous sequence of Haiti and Jamaica are identical in lithologic and paleontologic character, consisting of Richmond-like shales at the base with *Orbitoides* passing up into Montpelier-like limestones with *Orbitoides* and *Nummulites.* In the chapter on "The Geology of the Monte Cristo Range," pages 162–173, he shows that the Orbitoidal White Limestone, as in Cuba and Jamaica, occurs to heights of 2,530 feet. This limestone at Monte Cristo is foraminiferal and of great purity, and like the Montpelier of Jamaica does not weather into red soils. It is also interesting to note that in San Domingo as in Jamaica the *Nummulinæ* and *Orbitoides* occur in the limestone, and the latter extends down into the shale.

Tippenhauer has described the white limestones of Haiti more fully than Gabb, but like the latter refers them to a more recent age. Under the head of the "White Limestone" which he says covers five eighths of the island, he describes several varieties which perfectly conform with the descriptions of the Jamaican rocks. Unfortunately, however, he includes the coast limestone or elevated reef rock in this category and assigns the whole to the Post-Pliocene.

Concerning the Haitian Radiolarian beds nothing is known regarding their stratigraphy, the material being known commercially only from St. Jérémie. From the similarity of geological structure and sequence of that end of the island, and in the absence of information to the contrary, we can at least infer that the Radiolarian beds of this locality are closely related to those of Cuba and the Montpelier chalks of Jamaica.

The Radiolarian and Globigerina earths of Barbados have been made the subject of extensive researches by Jukes-Browne and Harrison,[1] Gregory,[2] and others, and the geology of this island has been recently thoroughly restudied by the writer.

The details of this structure are elaborated with great minuteness in the publications of Jukes-Browne and Harrison. With the exception that they referred the Radiolarian earths and the underlying Scotland beds to newer epochs by one stage than that to which I think they belong, their reports are in general correct.

In Trinidad beds of Radiolarian and Globigerina chalks occupy the

---

[1] Quart. Jour. Geol. Soc. London, 1892, Vol. XLVIII. p. 193.

[2] Paleontology and Physical Geology of the West Indies. Quart. Jour. Geol. Soc. London, 1895, Vol. LI. p. 293.

same relative position above folded terrigenous formations as in Barbados and Jamaica. These beds, variously called San Fernando and Naparima by Guppy, contain the characteristic *Globigerinæ*, *Orbitoides*, and *Nummulinæ* of the Cambridge and Montpelier beds of Jamaica, and in Guppy's latest papers are referred by him to the Eocene,[1] although for many years he placed them in the Miocene. The position of the white Radiolarian marls above a great series of clays and sandstones resembling the Scotland rocks of Barbados (Richmond beds of Jamaica) has been later confirmed by the observations of Harrison.[2]

Extensive deposits of Radiolarian earths occur nowhere, so far as we are aware, adjacent to the eastern side of the American continent. The occurrence of these apparently synchronous oceanic beds in the widely separated West Indian localities of the Antilles, Trinidad, and Barbados, indicate deep water conditions in each of the regions.

The Vicksburg-Jackson formation of the Gulf States Tertiary is in my opinion synchronous with that of the oceanic beds of the Montpelier epoch of the Antillean region, and are probably the northern shallow attenuation of the oceanic beds of the West Indies. They are characterized by the species *Orbitoides mantelli*, and in Florida *Nummulinæ* also occur. Although composed largely of oceanic material they are shallower beds than the Antillean formations. The visible effect of the Antillean subsidence reflected in the sediments of the Tertiaries of our southern coast was to change their character from the non-calcareous nature observable in the Claiborne to more calcareous deposits of the Jackson and Vicksburg beds. In Alabama and Mississippi the Vicksburg beds, with the overlying Jackson, are white limestones, the combined thickness aggregating about 500 feet. In Florida the Vicksburg beds outcrop in the northern portion of the State. Beneath the Pliocene coating of Southern Florida the Vicksburg beds, as exposed by well drillings, have a thickness of 200 feet, and contain the characteristic *Orbitoides* and *Nummulinæ*. Their microscopic nature has not been investigated. These beds are characterized by the three genera of Foraminifera, *Orbitoides mantelli* (the Orbitoides limestone [3]), *Nummulinæ*,[4] and *Milolidæ*,[5] which are so abundant in the lower part of the Montpelier of Jamaica and Southern Mexico.

---

[1] Quart. Jour. Geol. Soc. London, 1892, Vol. XLVIII. pp. 519-524.

[2] Quart. Jour. Geol. Soc. London, 1892, Vol. XLVIII. p. 218.

[3] Dall, Bull. 84, U. S. Geological Survey, page 101.

[4] Heilprin, cited by Dall, Bull. 84, U. S. Geological Survey, pages 103, 104.

[5] Ibid., p. 104.

Beds of the Vicksburg horizon have not been discovered between Yucatan and the Mississippi. Agassiz[1] has reported the beds of the Vicksburg epoch as constituting a ridge along the southern peninsula of Yucatan. Orbitoidal and Nummulitic limestones form a belt of strata in Chiapas and Yucatan back of the later marginal coast formations. A. Agassiz's observations, notwithstanding Heilprin's denial, have been confirmed by the more recent explorations of Dr. Karsten, J. Felix, and H. Lenk.[2] These authorities show the existence of Orbitoidal and Nummulitic limestones in the vicinity of the ruins of Palenque and other localities, and prove according to them the existence of marine Eocene strata of the Alpine Nummulitic and Orbitoidal limestone facies in Yucatan, Mexico.

The only known locality of this formation around the margin of the Caribbean is in the uptilted beds at Guallava, Costa Rica, 150 feet above the sea, which Dall has identified from collections made by the writer, as reported in my work on the Isthmus of Panama. In Costa Rica at least, the Vicksburg beds are of an impure non-oceanic nature, occurring as in the Antilles above igneous derived rocks.

Although the Bowden fossils are reported to have wide extent in the tropical region[3] by paleontologists, the formation has not been clearly defined stratigraphically. According to Dall the molluscan element of the fauna is homotaxially equivalent to the Chipola, Tampa, and Chattahoochee beds of Southern Florida, and occurs also in Trinidad and Curaçoa. It also occurs around the continental perimeter along the Carribbean side of the Isthmus of Panama, where the formation has been described by the writer as the Monkey Hill beds[4] of Panama and back of Chiriqui lagoon. There can be little doubt, however, that the sediments of this age have considerable extent along the Talamancan, Panamic, and Colombian coasts of this general Isthmian region.

The equivalents of this formation are known in Cuba, and its fossils from Haiti. It has great development along the north coast of Cuba especially towards the eastern end, where it is composed of the yellow clays and gravel beds called Miocene (after Dall) in the writer's papers on that island,[5] and is well developed at Matanzas, Nuevitas, Gibara, and Baracoa. I now have little doubt, in the light of later experiences,

---

[1] Three Cruises of the Blake, Vol. I.

[2] Neues Jahrbuch für Mineralogie, 1895, Bd. II. pp. 207, 208.

[3] Proc. U. S. Nat. Mus., 1896, Vol. XIX. p. 304.

[4] The Geological History of the Isthmus of Panama, p. 176.

[5] Notes on the Geology of the Island of Cuba, Cambridge, 1895.

that the medial limestones of my section at the entrance to the great amphitheatre of Matanzas is also of this formation.[1]

From the numerous paleontological descriptions of Duncan, Gabb, Guppy, and others, this formation is the classical "Miocene" of Haiti and San Domingo, although careful search of the writings of all these authors fails to reveal any stratigraphic data concerning it other than that many of the species came from certain beds near Nivajé.

There is also reason to believe that the Bowden beds are progressively more shallow in nature from Jamaica towards Haiti. Gabb there encountered this character of formation in contact with the similar appearing Richmond and Cambridge beds, and confused them together, — a mistake which has been made by nearly all first workers in regions where aggradational terraines of similar composition are in contact without a conspicuous intervening deposit. Gabb himself notes the duplication of sedimentation cycles in succeeding epochs[2] and these very conditions may have confused him in San Domingo, as they have others in Jamaica.

It is probable that they may occur in Antigua and other Windward Islands, but exploration has not sufficiently progressed to justify a positive opinion. Beds of Antigua which we consider of a later age than the Bowden beds of Jamaica, and usually discussed with them under the general head of the Miocene by Guppy, Duncan, and others, may prove to be identical with the Bowden. In these islands the vast formations of sedimentary volcanic tuffs were probably being made during this epoch.

Close studies convince me that these beds are lacking in Barbados, their position being occupied in the latter island by the unconformity between the oceanic (Montpelier) beds and elevated (Pleistocene) reefs during which time land existed there.

According to Dr. Dall the later or true Miocene is unrepresented in the fossil faunas of the West Indies, during which time the island areas may have had greater expansion than at present. He refers all the formations hitherto called Miocene to the Upper Oligocene. It is my opinion that the differentiation of the faunas of these two epochs needs much research. In Antigua and Porto Rico undoubted Miocene exists.

Vast aggradational deposits of the Kingston type similarly laid down on pre-eroded troughs, benches, interior basins, or other erosion sur-

---

[1] Notes on the Geology of the Island of Cuba, Plate I. Fig. 4.

[2] *Op. cit.*, p. 156.

faces, are present in Haiti upon even a more extended scale than in Jamaica. They are well developed in Cuba. They are probably absent from the Windward Islands so far as I can ascertain and especially Barbuda, Barbados, Martinique, Dominica, and Antigua, which I have especially studied. In Antigua there is some evidence in the configuration of the Pre-Kingston erosion epoch which is still largely submerged. No formation comparable to the Kingston has been recognized on the mainland of Panama. In the Coastal Plain of the United States and Northern Mexico the so called Lafayette formation of McGee and its extension into Arkansas (the Plateau Gravel) and Texas (the Uvalde formation) is identical in method of origin, although of course not continuous in extent with it. These beds are an important landmark in the physical history and relations of the Antillean region.

The Manchioneal (Pliocene) marls of Jamaica cannot be positively correlated with other regions, owing to the vagueness of the criteria for determining beds of this age. That marginal Pliocene formations exist in Cuba, Haiti, and Porto Rico is well known, while the beds of Moen, Costa Rica,[1] and certain formations of Trinidad, Guadeloupe, Antigua, and other of the Windward Islands may be contemporaneous. Formations of this age have also been reported as extending far inland towards the foot of the central summits of Tehuantepec.[2] Marine formations of supposed Pliocene age are also extensively developed in Florida and South Carolina. Catalogues of Tropical Pliocene invertebrate faunas are given by Gabb in the Appendix to his San Domingo Report, and of Florida and Yucatan by Heilprin[3] and Dall[4] from Tehuantepec.

Elevated reefs, fossiliferous calcareous marls of the Falmouth type, and aggradational deposits of Pleistocene or later age have wide and extensive development in the marginal regions of Tropical America. These are all connected phenomena dependent for their origin upon the submergence and re-elevation of the pre-existing platforms and benches, and owe their present position to elevations in late geologic time.

The Falmouth formation, composed of clastic shell limestone, principally molluscan, is synchronous in origin with the elevated reefs. Littoral and lagoonal débris and beach wash preserved as marls and white limestones of this character are extensively developed in Haiti

---

[1] W. M. Gabb, Journ. Acad. Nat. Sci. Phila., 2d Series, Vol. VIII. No. 4, p. 349.

[2] J. W. Spencer, Bull. Geol. Soc. America, 1897, Vol. IX. pp. 13–34.

[3] Proc. Phila. Acad. Nat. Science, December, 1890.

[4] Bull. Geol. Soc. America, 1897, Vol. IX. pp. 13–34.

and Cuba, and probably San Domingo, having been well described from the last named island by Gabb. The shell formation underlying the coastal swamps of Panama, although having a matrix of land débris, is also of similar age.

A. Agassiz has described at length in his chapter on the Florida Reefs[1] the wide extent of somewhat similar formations which constitute the small keys and reefs of Florida,[2] as well as the whole of the eastern and western coasts of the southern end of the peninsula.[3] He has also shown that a large part of the peninsula of Yucatan is composed of similar material.

These formations are also largely developed around some of the Virgin Islands, and the peculiar island of Barbuda, which the writer has recently studied, is composed entirely of similar rock occurring at two well marked levels 5 and 125 feet above the sea.

This material in the Antilles, Virgin Islands, Yucatan, and Barbuda, is characterized by many beautifully preserved Mollusca embedded in a white limestone chalky matrix. A small species of *Bulla,* still living in the adjacent waters, is specially abundant, sometimes almost entirely composing the mass.

The true elevated reefs of Jamaica are related to kindred phenomena in many parts of the West Indian region. The term reef rock in this paper is restricted to those strata which are composed almost entirely of compound coral heads of modern reef building genera, such as *Porites*, *Siderastræa*, *Orbicella*, *Meandrina*, and *Madrepora*, and does not include other white limestones not of unmistakable reef origin. The genera and species of these elevated reefs, with two exceptions in Barbados found one each by Gregory and Vaughan, are all the same as those of the growing reef of the region today. The living reefs have been reconnoitred and described very minutely by A. Agassiz, and he has noted the elevated reefs in numerous places along the Central American coast, the Tortugas, the Great Antilles, Windward Islands, Barbados, and Florida. He has also shown that these reefs were formed on shallow submarine banks of less than fifteen fathoms, and there can be no doubt but they formed the West Indian region during periods of elevation.

Elevated reefs similar to those of Jamaica are known to border a large portion of the island of Cuba. There, as in Jamaica, they occur only in benches immediately adjacent to the sea, nowhere a hundred

---

[1] Three Cruises of the Blake.

[2] Ibid., Vol. I. p. 54.

[3] Ibid., Vol. I. p. 62.

feet above its level — in fact not over fifty — although the whole of the white limestones of that island rising to heights of 2,000 feet or over, have been erroneously attributed to coralline origin by various writers.[1]

Similar low elevated reefs occur completely around the island of Haiti, as described by Gabb in a manuscript in the library of the United States Geological Survey, which recounts the results of a second visit to the island after his large report on San Domingo had been published, in which he had erroneously attributed all the white limestones of the region to coral reef origin. The writer has seen many of these reefs on the coast of San Domingo, and they are in general analogous to those of Cuba and Jamaica, although the three subsiding stages of the latter island have not been differentiated. Concerning Porto Rico and the Virgin Islands we have no data proving the existence or non-existence of elevated reefs around their borders. According to Cleve's description of the Virgin Islands,[2] and my observations of Barbuda, the geological position of the elevated reefs of the Great Antilles is generally occupied in these islands by the granular white limestone with molluscan remains previously described. Sombrero, as described by Julien,[3] however, is an exceptional locality in this general region, as it is composed of elevated reef rock, the Bulla limestones and lagoonal material. There is some evidence in the reports of McClure[4] and Henry[5] that elevated reefs occur on the island of St. Croix.

The elevated reef phenomena of the Lesser Antilles are varied and peculiar, presenting different aspects in Barbados and on the leeward and windward sides of the Caribbee Islands. On the windward side of the Caribbees true elevated reefs of the modern type are found bordering Desirade, Marie Galante, and Grand Terre-Guadeloupe, as noticed by Maclure in 1817.[6] Here they occur as in the Western Antilles as simple undeformed benches of reef rock standing from six to ten feet above the level of the sea. The reefs of Guadeloupe were described by Duchaissang in 1847,[7] and were considered by him to be recent in age, and synchronous with the upland formations of that island which contain the remains of fossil man.

---

[1] Gabb, Crosby, and others.

[2] Cleve, *loc. cit.*, p. 18.

[3] On the Geology of the Key of Sombrero, W. I., Annals of Lyceum of Nat. Hist. of N. Y., Vol. VII. pp. 251–278.

[4] Trans. Phila. Acad. Nat. Sci., 1817, Vol. I. p. 138.

[5] Amer. Journ. Sci., 1839, Vol. XXXV. p. 73.

[6] Jour. Phila. Acad. Nat. Sci., 1817, Vol. I. p. 135.

[7] Bull. Soc. Géol. de France, 2d Series, 1842, Vol. IV. Pt. 2, pp. 1093, 1094.

In Antigua and Porto Rico there is a reef rock entirely different in mode of occurrence, assemblage of species, and lithologic character from the class of modern elevated reefs we have just described, and belongs to an older geologic period, — probably the Miocene or early Pliocene Tertiary. Furthermore, it is evident that these older Antiguan reefs were elevated by orogenic or volcanic uplifts at a period prior to the later epeirogenic elevation of the true modern reefs described.

True elevated reefs — normal unaltered reef rocks raised by epeirogenic elevation to heights not exceeding 100 feet above the sea — do not occur near sea level in the leeward margin of the Caribbee Islands. The main or inner chain of these islands is in general a mass of volcanic débris almost void of sedimentary rocks. In St. Kitts,[1] St. Eustatius,[2] Martinique, Dominica,[3] and Granada,[4] "reef rock" is alleged to be found tilted at high angles interbedded with volcanic débris, and occurring as high as 500 feet above the sea, but we are not able to state whether these are identical with the true elevated reefs.

On the Central American and Panama (western) coasts of the Caribbean Sea, the modern elevated reefs also occur sparsely at Colon and Limon,[5] but not so highly elevated as in the region adjacent to the Windward Passage, standing hardly five feet above the level of the sea. The same may be said of the elevated reefs of Southern Florida and adjacent regions described by Agassiz,[6] where heights of eight feet are recorded.

In the island of Barbados, which geologically belongs neither to the Caribbee nor Antillean type, the modern elevated reefs attain their highest and most perfect development, and rise to exceptional altitudes of over 1,100 feet above sea level or 1,000 feet higher than elsewhere known. This dome-shaped island is composed of a nucleal mass of rocks allied to the Richmond and Montpelier formations, which are covered by a veneering of true reef rock nowhere exceeding one hundred feet in thickness, which extends to the very summit of the island, and presents numerous benches and terraces, — the old surfaces and escarpments of the reefs which have been elevated without local de-

---

[1] Geology of the Northeastern West Indian Islands, 1871, Stockholm, p. 21.

[2] Maclure, Jour. Acad. Nat. Sci. Phila., Vol. I. Part I. p. 147.

[3] Cleve, *loc. cit.*, p. 45.

[4] Harrison, "The Rocks and Soils of Granada," London, 1897, reports beds of coral sand and mud 150 feet above the sea at extreme north end of the island.

[5] Three Cruises of the Blake, Vol. I.

[6] The Elevated Reefs of Florida, Bull. Mus. Comp. Zool., Vol. XXVIII. No. 2, 1896.

formation above the adjacent waters, in which similar reefs with the same kinds of escarpments are now growing. The altitudes of these reefs in Barbados are so distinctly greater than those of the rest of the West Indian region that they can be accounted for only on the theory that the synchronous movement which has produced this result was there of much greater amplitude than elsewhere, as will be more fully discussed in Part VI.

A discussion of the formations of Tropical America would be incomplete without a consideration of the igneous extrusions which, from time to time, have assisted in producing the radical changes in the geography of the land and sea bottom, and broken into the sequence of sedimentary events. Yet there has been so little systematic study of the various volcanic and intrusive rocks that I take up the subject with great diffidence. Since the time of their intrusion is only determinable by their association with fossiliferous sedimentaries, it is evident, in the light of the facts we have given concerning the latter, that we have some data for at least approximating with more accuracy than has hitherto been attempted the history of the vulcanism.

Dr. Persifor Frazer has asserted[1] that there is strong reason to believe that the axial range of the entire islands, and of Cuba, Jamaica, San Domingo, Porto Rico, and the Windward Islands, instead of being igneous extrusions of the Tertiary period, and later, are in reality crystallines of much earlier date, and may not be entirely volcanic.

The considerations which he advances to support his view are as follows: that microscopic analysis "of the rocks which form the nucleus of the spurs of the Sierra Maestra of Cuba shows immense alteration to have taken place, and consequently a very long period to have elapsed; that the complexity of the congeries of rocks forbids the hypothesis of their having been derived from one mass; that the associated characters are those which one finds united in very many Archæan regions throughout the world; that the products of alteration are similar to those in other Archæan districts, etc.; and that the rocks are diabases or diorites with epidote, porphyry, actinolite, felsite, orthofelsite, and porphyry like that of the South Mountain of Southeastern Pennsylvania. Professor Frazer adds that a number of the first petrologists of Europe who have examined his slides are disposed to consider the specimens of not later than Paleozoic age, while none are willing to deny that they may be earlier.

---

[1] British Association for the Advancement of Science, Bath, 1888, pp. 654, 655.

While failing to see on what ground Dr. Frazer extended his conclusions, based upon examination of a single locality in Cuba, to Jamaica, Porto Rico, and the Windward Islands, it may be possible that some of the rocks of the Sierra Maestra range of Cuba are of a Pre-Cretaceous age, although Kimball has shown that the diorites have overflown the Tertiary. Personally, I have failed to find any Pre-Cretaceous crystallines in the localities cited.

Dr. W. Bergt has also strongly advocated the existence of an Archæan plexus at the foundation of San Domingo,[1] another of the Great Antilles. Unfortunately, while his argument is strong, like Frazer's it is largely hypothetical, and not founded upon extended field work. The substance of his conclusions is as follows.

Bergt had before him the following rocks from the southern and southwestern parts of San Domingo: — Crystalline schists: hornblende gneiss; pyroxene granulite; fine-grained typical hornblende schist; chloritic hornblende schist, thin laminated, phyllite-like, folded; garnet amphibolite, augite-bearing, eclogite-like; chloritic schist, etc.

Older eruptive rocks: normal mica granites, having the appearance both of mountain granite and vein granite; protegene granites with the most distinct evidences of pressure; hornblende granites, even macroscopically so rich in large quartz grains that it is impossible to confound them with syenite; syenite subordinate; diorite, quartz-diorite, "Bluebeache"; diabase; quartz-diabase; picrite, olivine rock, serpentine.

Younger eruptive rocks: basalts in doleritic, anamesitic, and basaltic development, the latter compact and of the nature of a finely porous lava; andesites; on the small island of Alta Vela also trachytes.

He concludes that, "while according to Gabb, San Domingo forms an exception, showing none but young eruptive rocks with very old appearance, the above series shows quite normally the well known petrographic and geologic contrast between older and younger eruptive rocks. The eruptive rocks designated above as 'older' differ plainly by their state of preservation, by transpositions and new mineral formations, from the volcanic rocks; they do not even resemble the transition rocks distributed all over America (propylites, Andes diorites, etc.)."

Bergt also concludes that the older eruptive rocks of San Domingo are not the causes of the mountain movements, but, on the contrary, were themselves subjected to such movements, and bear the traces of

---

[1] On the Geology of San Domingo, by Dr. W. Bergt. Sitzungsberichte und Abhandlungen der naturwissenschaftlichen Gesellschaft Isis in Dresden, Jahrgang 1897, Juli bis December, Dresden, 1898, pp. 1–7.

them in the form of so called dynamometamorphic phenomena; "accordingly they have to be regarded as 'older' until their younger age has been unassailably demonstrated, which is hardly to be expected. The crystalline schists, the last of which might be given considerably greater fulness by collections and observations not merely occasionally, but systematically, bear in no wise the character of contact metamorphism; they have to be regarded as normal Archæan rocks, though, like the older massive rocks, they are in part altered by mountain pressure and folded on a small scale."

Thus, according to Bergt, in San Domingo, besides the younger strata of the Cretaceous and the Tertiary, as the bed rock, there is possibly Archæan plexus.

Bergt and Frazer's conclusions, as far as they apply to Santo Domingo and Cuba, may be correct, for there are other reasons for believing that here and there in the main Antillean chain there are evidences of a Pre-Cretaceous buttress, but there is absolutely no stratigraphic evidence as yet unearthed to warrant the assertions that similar rocks occur in Jamaica, Porto Rico, or the Windward Islands, where as yet no such rocks have been found, although, except in the last named, the clastic and terrigenous nature of the basement exposures certainly indicate the pre-existence of rock masses of older age than those now known *in situ.* The younger eruptive rocks of San Domingo enumerated by Bergt are most probably of Cretaceous and Tertiary age.

Omitting from further consideration the Pre-Cretaceous crystallines, the interpretable volcanic phenomena of the West Indian Islands and the bordering continental lands may be classified for historical purposes into the following time categories: —

1. Regions where there are no visible signs of vulcanism: Eastern Coastal Plain of the United States, Bahamas, Barbados.
2. Regions where vulcanism existed prior to the beginnings of the later Mesozoic: The Cordilleras of North America, Guatemala, Oaxaca, and Andes, and possibly Cuba and Haiti.
3. Regions in which vulcanism was greatest in late Cretaceous and early Tertiary time: Mexican Plateau, Western Coastal Plain, Panama, north coast of South America, Great Antilles.
4. Regions where vulcanism was active in middle Tertiary time, since which it has been quiescent: Panama, north coast of South America, and Antilles.
5. Regions of recent volcanic activity: Southern Mexico, Central America, Northern Andes, and Caribbee Islands in part.

1. There is no evidence that vulcanism has in any way affected the Atlantic Coastal Plain east of the Sabine within the periods of geologic history bearing upon our problems, and hence the northern border region of the American Mediterranean may be considered as having been beyond the zones of volcanic disturbances affecting the Caribbean region.

2. Vulcanism in Cretaceous time undoubtedly affected all the peripheral regions of the American Mediterranean except the Coastal Plain of the Gulf, including the Great Antilles and Virgin Islands, in which detrital igneous rocks similar to those we have described as constituting the oldest formations of Jamaica occur under similar conditions. I have seen these old Cretaceous igneous rocks in Cuba, Gabb has described them from San Domingo, and Cleve has pointed out their wide extent in Porto Rico, the Virgin Islands, and St. Bartholomew. In all these Antillean localities, as in Jamaica, the rocks are of a hornblendic nature, occurring largely as conglomerate and tuffs. In fact, the closing days of the Cretaceous were essentially marked by vulcanism in the Great Antilles. In my report upon Panama I have shown that an old rhyolitic or andesitic tuff of probable Cretaceous age, but not hornblendic, there constitutes the oldest discovered formation.

The occurrence of vulcanism in Cretaceous time in the Andean and Central American region has been shown by many writers. In the Cordilleras and plateaux of Northern Mexico the closing days of the Cretaceous were marked by vast extrusions of volcanic rocks, while volcanic action also sparsely occurred in Trans-Pecos, Texas, and perhaps as far north as Little Rock, along the interior margin of the Coastal Plain during this epoch.

In Eocene time vulcanism was especially violent in the Isthmian, Central American, and Colombian regions, and along the south margin of the Mexican Plateau. The volcanoes of the Caribbee Islands were also most probably active in this period.

There is no evidence that vulcanism occurred in the Antilles or Virgin Islands during the Eocene epoch. On the other hand, all data tend to show that the great eruptive activity of Cretaceous time in the Antilles was followed by epochs essentially marked by placid sedimentation.

The chief Panamic eruptions ceased at or soon after the close of the Eocene, although vulcanism continued in the adjacent Costa Rican and Andean provinces, and along the Mexican volcanic belt, until the present time. On the eastern slope of Costa Rica the Vicksburg fossils of the Gualllava formation are interbedded with contemporaneous basic eruptive débris.

Some time during the middle of the Tertiary time — probably between the Vicksburg and Bowden epochs, as we have elsewhere shown — the great intrusion of granitoid and dioritic porphyritic rocks occurred in Jamaica. The dioritic dikes were probably slightly subsequent to the granitoids in sequence, but they are both so intimately associated as to be practically inseparable, and hence may for discussion be considered as a unit. There is little evidence, excepting in the case of the Low Layton basalt, that the igneous rocks of this epoch ever protruded to the surface in Jamaica although they may have done so elsewhere. In Cuba there is evidence presented by Kimball[1] that eruptive diorites overflowed the old Eocene limestones (called corallines by him) of the Sierra Maestra. In the vicinity of Havana the Vicksburg limestones are also cut by Tertiary intrusives.

There is abundant evidence that the Mid-Tertiary vulcanism was far reaching in extent and affected all the Great Antilles, Virgin Islands, Yucatan, Costa Rica, and the Panamic, Colombian, and Venezuelan coasts of the Caribbean. A brief outline of the distribution of these phenomena on the mainland has already been presented in my Panama report.[2] Kimball[3] has described with considerable detail their occurrence on the Santiago coast of Cuba. Descriptions of San Domingo by Gabb,[4] and of Porto Rico, the Virgin Islands, and St. Bartholomew by Cleve,[5] also confirm this opinion. Rocks of this general age also occur in St. Martin, Burks, Coopers, Georges, Round Rock, St. Croix, St. Thomas, Tortolu, and Salt Islands. Cleve doubtfully refers them to the Cretaceous or Eocene; but after reading his observations in the light of our own researches, there can hardly be the least doubt that they are of the same age as the similar phenomena of the Antilles.

With the possible exception of the Low Layton stock of Jamaica, which may or may not have been an accompanying event, these rocks represent the last indications of vulcanism in the Great Antilles and Virgins — where there is no evidence of igneous activity — in the subsequent epochs of late Miocene, Pliocene, Pleistocene, or recent time.

The Caribbee Islands constitute a unique and peculiar volcanic province, the discussion of which, with their general phenomena, can now be briefly considered. To those who first look at the map and have not considered their minute geology, the Lesser Antilles, extending across the east end of the Caribbean from Porto Rico to South America

---

[1] Amer. Jour. Sci., Vol. XXVIII. pp. 419, December, 1884.

[2] *Loc. cit.*, p. 251.

[3] *Loc. cit.*, pp. 416, 417.

[4] Geology of San Domingo, p. 83.

[5] *Loc. cit.*, p. 47.

appear as the members of a kindred archipelago. The Virgin Islands at the north are Antillean, while all south of Grenada are South American in natural relations. Barbados may also be distinctly related to the latter category. Even after detaching these termini the remaining islands of the archipelago lying between the Anegada Passage and Tobago, constituting the Caribbee group, present almost as complicated compositions. Some of the northern islands, such as Santa Cruz and St. Bartholomew, are also Antillean in structure, and were it not for the deep Anegada Passage, which almost severs the latter from the submerged platform of the Antilles and their presence on a similar platform at the north end of the Windward Channel, they might probably be considered as Antillean.

The Caribbee chain, however, south of the Anegada Channel and north of Trinidad, constitutes a distinct geographic and geologic type, which may be classified by composition into three general sub-types as follows: (1) Volcanic islands composed entirely of igneous material; (2) Islands composed entirely of organic oceanic sedimentary débris; and (3) Compound islands, with a higher summit region of volcanic rocks of the first mentioned class, with added areas or benches of sedimentary rocks. These three types are exemplified in Martinique, Barbuda, and Antigua.

The Caribbee chain is divisible into two parallel belts extending the length of the archipelago. The innermost of these, facing the Caribbean, including Saba, St. Eustatius, St. Christopher, Nevis, Montserrat, Basse Terre, Guadeloupe, Dominica, Martinique, St. Lucia, St. Vincent, the Grenadines, and Grenada, are composed almost entirely of purely volcanic summits. These islands constitute the newest and highest summits of the Windward chain, attaining heights approximating 4,000 feet in all the islands mentioned except the two most northern, Saba and St. Eustatius, which rise to 2,820 and 1,950 feet respectively, and the Grenadines.

The eastern belt, composed of the sedimentary and compound type, includes Sombrero, Dog, Anguilla, St. Martin, St. Bartholomew, Barbuda, Antigua, the Grande Terre of Guadeloupe, Marie Galante, and Desirade.

Barbados perhaps belongs in a class entirely by itself, lying to the eastward of the chains mentioned.

The arrangement of the islands as borne out by the stratigraphy shows that the axis of volcanic extrusion was the main chain, or belt of islands on the Caribbean side, and that the other islands of organic accumulation represent portions of the windward sea bottom which was brought up by uplifts of the main chain.

This main or interior chain is composed of piled up volcanic débris, and upon the islands of Guadeloupe and St. Vincent there have been active volcanic eruptions in historic time, 1797 in the former and 1812 in the latter. Soufrières, hot springs, etc., show that this activity is only slumberingly quiescent in nearly all these islands. Besides most of them still possess upon their summits one or more true craters, while Saba and St. Eustatius are composed of simple crater cones now quiescent. While these facts attest recent eruptivity in the islands, there is much evidence presaging the conclusion that the present vulcanism is merely the survival of that which began much earlier in geologic history.

The configuration and structure show that their history extends back to considerable antiquity. In the first place while the protuberance of all these islands is largely due to extrusive piling up, the present detailed configuration expressed in steep coastal bluffs, benches, slopes, and canyons, is produced by erosion, which has required considerable time for development. True crater shapes, except in St. Eustatius and St. Christopher, are exceptional, and are merely secondary summit features in the other islands, occurring parasitically upon masses of old eroded volcanic débris reaching a height of 4,000 feet. Secondly, they are all composed largely of vast piles of old tuffs and trachytic débris of many eruptive epochs, like the volcanic heights of the Costa Rican plateau, which indicate long continuation of the volcanism since comparatively remote geologic epochs, reaching back most probably to the Eocene time.

In St. Christopher, St. Eustatius, Guadeloupe, Martinique, St. Lucia, and Granada, disturbed fossiliferous beds of Pleistocene or recent age are found interbedded in volcanic débris of the lower slopes at altitudes of two or three hundred feet above the sea, showing that uplifting as well as extrusion has in part produced the present eminences, and that vulcanism existed in Pleistocene time.

The fossils mentioned are hardly older than Pliocene, and are most probably Pleistocene, and their border-like position shows that the greater mass of the islands were ejected in previous epochs.

So much for the main chain of the Caribbees considered by themselves, but the eastern belt, of the compound type, owe their present position above sea level to the orogenic uplifts which affected the Caribbean area in later geologic time. Guadeloupe and Antigua are the two islands which throw the greatest light upon the age of the vulcanism of the Caribbees.

In Antigua the older massive volcanic rocks constitute a high mountainous region on the south side of the island, while to the northward for miles these are overlapped by a vast thickness of stratified tuffs, evidently the ejecta from the vents of which the massives are the remnantal stocks. This material must be thousands of feet in thickness. It contains beds of thin lime deposits of marine origin, including a bed of older massive consolidated crystalline limestone less than ten feet in thickness, and an old coral reef. Towards the north end of the island the tuffs are overlain by conglomerates grading up into chalk marls with fossil Mollusca of possible Miocene age. In the tuffs there are also beds of chert with vast quantities of fossil wood, land shells, and silicified reef building corals (but no reef rock), which also extend into the marls. Finally there is a small area of elevated reef rock. Of these stratified formations none in my opinion, except of the Orbitoidal crystalline limestone, can be of older age than Pliocene or late Miocene. The latter may possibly be Vicksburg — an opinion based upon the occurrence therein of Orbitoides and Nummulinæ, described by T. Rupert Jones. Upon the erroneous correlation of others he referred these beds to the Miocene, but they are older in age than the Bowden beds of Jamaica "Miocene" with which they have been confused by many writers. These facts show that the volcanic tuffs of Antigua were being formed before the Vicksburg epoch, and that the Caribbean vulcanism was then active.

In Guadeloupe we have somewhat similar evidence concerning the evolution of the volcanic range and the mass of sedimentaries. This island is composed of two parts of about equal area, separated by a shallow creek, Rivière Salée. The most western of these islets (Basse Terre) is a typical volcanic pile of the main Caribbee chain, and is thoroughly mountainous. The most eastern area, Grande Terre, is an elevated cut plain, composed of sedimentary formations of Pleistocene age underlain by a platform of volcanic tuffs, etc., derived from the volcanic débris of Basse Terre. Still to the eastward of Grande Terre is the small island of Desirade, composed entirely of organic material, which, with several other islets, stands above a shallow submerged platform extending out from the south east end of Grande Terre and Basse Terre. To the southward of Grande Terre is the island of Marie Galante. This island is of the same topographic and geologic type as Grande Terre.

Owing to an outbreak of yellow fever the writer's studies of these Gaudeloupean islands were limited to the briefest reconnoissance of their general features as above enumerated, but they were sufficient to warrant the deduction that the following details of the geology as set forth by Duchassaing were in general correct.[1]

These beds consist of three formations, the oldest of which are fossiliferous tuffs called by Jones[2] and Duchassaing the "Pierre à ravets" and "sables volcaniques remaniés par la mer." This is composed of yellow tuff very similar to the oldest stratified rocks of Antigua, with few fossils, and the sands contain three species of Mollusca which Cleve asserts with the enclosing strata greatly resemble the Eocene beds of St. Bartholomew.[3] Above these beds of sedimentated igneous material there is a hard ringing limestone containing Terebratulæ. Still above the latter, and constituting the surface formation of most of the Grande Terre are tufaceous marls very much resembling those of Antigua, containing Foraminifera, Lunulites, and many Mollusks, which Mr. Duchaissaing considered to be "older Pliocene in age." In these beds also occur three species of Echini which were not considered as living in the adjacent waters. The latter beds at oldest cannot antedate the Bowden or late Oligocene. Above these in places are non-marine deposits of land wash in which were found the famous human remains, and which also contain many fossil species of land shells.

The next and latest formation is the "Formation Madréporique" of Duchaissaing. This is true elevated reef rock or Soboruco, and borders all the coasts of Grande Terre as well as constitutes the outlying islands of Marie Galante and Desirade.[4]

These formations of Eocene and later age all overlie the detrital tuffs of the old volcanoes of the Caribbee chain, and demonstrate the antiquity of the vulcanism.

These facts above presented lead me to the following conclusions concerning the Caribbee Islands. Their geomorphology is entirely different from that of the Antillean province except in those features on the Windward side recording the events of the last epochs of geologic time. No

---

[1] Bull. Soc. Géol. France, 2d Ser., 1847, Vol. IV. Part II. pp. 1093–1100, and 2d Ser., 1855, Vol. XII. pp. 753–757.

[2] Histoire physique des Antilles française, Paris, 1822.

[3] *Op. cit.*, p. 44.

[4] The reef formation of these two islands was also described by Maclure in 1817. See Journ. Phila. Acad. Nat. Sci., Vol. I. p. 135.

similar phenomena indicating harmony of elevation and submergence in previous epochs can be made out. The cut plains of the north half of Antigua and the Grande Terre of Guadeloupe clearly show that regional elevations have taken place after the close of Miocene time, followed by erosion epochs and a Pliocene or early Pleistocene subsidence somewhat analogous to the Lafayette events. The bordering reefs formed on the rising platforms at Marie Galante and Desirade, and the double terrace structure of Barbuda show that these islands participated in the general Post-Pleistocene elevation of all the West Indies. Prior to the latest Miocene the details of composition and history were entirely dissimilar, and unlike the events of Eocene and Oligocene history of the Great Antilles.

During all these epochs from the Eocene to the present the volcanoes of the Caribbee chain have been piling up the vast heaps of stratified tuff that form not only the eminences but much of the extensive submarine platforms of the region.

The island of Barbados, standing 125 miles east of the main Windward circle, and separated from it by over 2,000 fathoms of water, is entirely unlike the Antillean, Windward, or Central American provinces in history and geomorphology. It has no known volcanic rocks.

These facts concerning the geology of the Lesser Antilles clearly show that piling up of volcanic material began there as far back as the Eocene epoch, and that the islands have participated in the later epeirogenic movements of Pleistocene or recent time. Hence we may conclude : —

1. The Windward Islands represent a distinct volcanic province, dissimilar in lithologic composition from the older volcanic phenomena of the Antillean province, and somewhat similar to the volcanic summits of Central America.

2. Their visible history dates back at least as far as Eocene time, and their periods of greater eruptivity ceased in the Pleistocene.

PART VI.

Changes of Physiography in Tropical America, bearing upon the History of the West Indian Islands.

The interpretation of the present configuration and history of the Antillean and Central American regions is a difficult task, and involves the analysis of many groups of data, embracing several distinct fields of research. Biology, paleontology, oceanography, structural geology, diastrophism, orogeny, and physical geography, must all be considered. The past and present distribution of life of all orders, both land and marine, their paleontologic history, the part which the débris of their skeletons, extracted from the liquid sea, has played in accumulating strata upon the submerged slopes and bottoms or building coral reefs are also important factors. The possibilities of the great Equatorial current and Gulf Stream, as carriers of sediment, corrosive agents, and the effect on the distribution of lime-making organisms is also a most important consideration.

There are several important conditions which make all attempts at final interpretation of Antillean and Tropical American history more or less hypothetical. The first of these is the fact that the submarine configuration suggests that large areas of land now submerged may have existed, not only in the immediate basins of the American Mediterranean, but also in the Atlantic and Pacific waters off the present continental borders. These submerged areas are now so covered with accumulations of organic and oceanic débris that their geologic composition can never be approximated even by soundings. Much of the older sedimentary strata of the present land masses have also been as completely concealed by burial beneath vast accumulations of volcanic ejecta, especially in Central America, the southern end of the Mexican Plateau, and the Caribbee Islands.

Notwithstanding the incompleteness of the record, the general configuration, and the geologic structure and paleontology of the land areas, and the distribution of the present life of the land and sea, afford much data of a fragmentary nature which can be so placed together as to throw some light upon the geologic evolution of the region. The discussion of the biologic and hydrographic phases of the question must be left to others, and in this chapter only the testimony of the structural geology and the configuration will be discussed.

The geologic composition and arrangement of the rock sheets relative to one another record in a manner changes of level, relative depth of deposition, and position of land areas. Variations in the physical and chemical composition of strata, when traced over wide areas, enable us to judge with a degree of conjecture the location of the land from which they were derived or the extent of their basins of deposition, and to construct hypotheses of former bathymetric variations. Features of land configuration by which events of elevation, degradation, and subsidence can be traced, should present harmonious and parallel conclusions with the interpretation of the fossils and the strata. Many writers of excellence, by failing to correlate the threefold testimony of configuration, biology, and geology have been led into serious errors of deduction.

Vague indeed is knowledge of the history of tropical regions prior to the Cretaceous period. Rocks of an earlier epoch are but sparsely and imperfectly exposed, being concealed even where they probably occur by the overlay of later sediments and volcanic ejecta. We know that the Appalachian and allied regions of the United States, as far west as the 98th meridian, since Paleozoic time, have been great bulwarks of land, against the southern front of which the northern waters of the Gulf of Mexico extended in Cretaceous and Eocene time, and that these old lands prior to their degradation and burial in late Mesozoic time occupied much of the southern and eastern Coastal Plain. There are also areas of old Mesozoic land of smaller dimensions in the Cordilleran regions of northwestern Mexico and the southwestern United States. In southern Mexico, Guatemala, and possibly Cuba and Haiti, there are long east and west ridges of Paleozoic rock, which may have had some fundamental relation to the east and west trends so largely dominating in the tropical region, or possibly foreshadowing the present outlines of the Great Antilles. In northern Venezuela another stretch of Paleozoic or Archæan rocks is reported to extend from the Andes north of east to the Caribbean coast and through the island of Trinidad. Paleozoic rocks also probably occur beneath the volcanic débris of Central America in Nicaragua, Honduras, and Costa Rica. The oldest rocks of Cuba and Haiti have been doubtfully considered of Paleozoic origin. Such are the earliest foundations of the great tropical amphitheatre in which during Mesozoic and Cenozoic times conflicts between land and ocean have continued, and from which amidst the vicissitudes of migrating shore lines, great oscillations of level, and volcanic extrusions, the present configuration of land surfaces and ocean bottoms have been evolved. In all of these localities south of the United States the events of Paleozoic and older Mesozoic history have been obliterated by the overwhelming phenomena of Cretaceous and later time, — buried beneath the oceanic sediments or volcanic ejecta, so that the interpretable history of the region may be said to begin with Cretaceous time.

There is some evidence that during the long period between the Appalachian revolution, after the close of the Carboniferous and the beginning of the Lower Cretaceous (Wealden epoch), the Atlantic borders of the North American coast met the Atlantic Ocean far eastward of the present continental outline, and that this expansion of the land was at its maximum during the Jurassic period.[1] No marine formations of Atlantic origin representing the intervening periods of time between the Permian and Wealden Cretaceous have anywhere been found east of the Rocky Mountain front in the North American complex, south of the Black Hills, where boreal Jurassic forms are found, which probably came from the northwest.[2] From similar data it is also evident that the northern part of the South American continent likewise had eastward expansion in Jurassic time.

The distribution of fossiliferous marine Jurassic formations on the Pacific slope of North America also shows that the border of the Pacific Ocean at that time extended far eastward of its present position. It is probable that the continental mass as a whole, practically equivalent in area to the present one, occupied a position slightly east of its present locus. In my opinion, the submerged bench of the Atlantic coast of the United States represents approximately the eastern expansion of the North American Jurassic land. How and in what manner this theoretical eastern expansion of the Western Hemisphere affected the Antillean and Caribbean regions is a question of great importance, which can be only hypothetically answered.

That the waters of the two oceans were completely separated along the American Mediterranean region in Jurassic time by a narrow land area connecting North and South America is indicated by the entire dissimilarity of the Pacific and Atlantic faunas in the oldest Cretaceous sediments, as has been often shown. Furthermore, the Pacific faunas transgressed eastward in late Jurassic time far across the present site of the Mexican Plateau, having been found in the longitude of Cuba. This indicates that the continental bridge was then far east of its present location. If the Jurassic fossils in Western Cuba, as reported by Lea, should upon further study prove to be of a Pacific type, the Jurassic Isthmus must have been situated east of the longitude of Havana.

Another line of evidence indicates that the present isthmian region presented no barrier between the oceanic waters prior to late Cretaceous time, and that if a continental bridge then existed it must have been located towards the Windward side of the American Mediterranean. This is the testimony of the deep sea fauna of the Caribbean Sea. Ac-

---

[1] If the Wealden epoch is the top of the Jurassic instead of the base of the Cretaceous, as asserted by Marsh, it does not materially alter this proposition. The greater time of the preceding Jurassic is unrepresented so far as known by fossils or sediments on the Atlantic side of the continent.

[2] The Jurassic rocks of Mexico and Trans-Pecos, Texas, all occur, so far as known, to the westward of the east front ranges of the Cordilleras.

cording to A. Agassiz,[1] this is mostly of a Pacific type, which has existed in the Gulf and Caribbean since at least as far back as Cretaceous time. The minority of Atlantic forms from this fauna may also suggest that a partial barrier at least then existed to the eastward side of the Caribbean. From Florida to the northeast corner of South America we now have a chain of submerged banks, which constitute the rim of the Gulf and Caribbean basins and which may or may not represent elements of this ancient Jura-Cretaceous Isthmus, — the same which has been frequently used as data for constructing a hypothetical and impossible Windward bridge during later epochs. This is still covered by coatings of oceanic débris, or capped by volcanic ejecta, which rise at intervals as tips of land above it. The configuration of these submerged rims and islands is that of an old dissected land.

The submerged bench off the Floridian coast deflects southeastward towards and practically continuous with that of the Bahaman banks, where its continuity is broken by great western indentations extending along the north side of Eastern Cuba, Haiti, Porto Rico, and the Virgin Islands. Thence along the Windward Archipelago to the South American coast there are many banks which might be construed as such elements. The present outer rim of the American Mediterranean may indicate the former continuity of the Isthmian region of Jurassic time. If the Windward bridge did not exist at this period, it never existed, — certainly not since Eocene time, as will be shown later.

Hovey has described a series of specimens obtained from a well bored to a depth of 2,000 feet at Key West.[2] The Vicksburg formation was penetrated completely, the boring passing into the underlying Eocene between the depths of 1,450 and 1,875 feet. It is quite probable that the former is the base of the Vicksburg. There is indisputable geologic evidence in the land-derived material of the Eocene sedimentary rocks of the Antilles, the Virgin Islands, the Caribbees, and Barbados, that land areas from which they were derived existed in this general region in Cretaceous time.

Westward of this hypothetical bridge there could have stood but one or possibly two islets in the present Central American region south of the southern end of the Mexican Cordilleras. Rising east and west through the States of Oaxaca, Chiapas, and Guatemala, and probably in Cuba and Haiti, there are ancient ridges of Paleozoic sediments and igneous rocks, — short crescents curving to the northward and now

---

[1] Three Cruises of the Blake, Vol. I. p. 167.

[2] Bull. Mus. Comp. Zoöl., 1896, Vol. XXVIII. No. 3.

almost lost to sight by the overshadowing pre-eminence of the grander and later topographic features that surround them. These may then have been either islands in the Jurassic sea, the nucleal lands of modern Central America, the fundamental structure of which seems to have been since developed on lines parallel to these shadowy ancestors, or the southern margin of the North American continent itself. It is possible that during the Jurassic epoch the Caribbean Sea, into which the waters of the Pacific flowed freely from the west, was partially enclosed by an archipelago consisting of a Windward bridge on the east, the old Paleozoic ridges of northern Guatemala, and southernmost Mexico, Cuba, and Haiti on the north, and the South American land on the south. Panamic America, together with the submerged Mosquito and allied banks extending northwest to Jamaica, are regions concerning which we can attempt no restoration of their history in Jurassic and early Cretaceous time, as they nowhere exhibit rocks of Pre-Cretaceous age. Neither is it possible to interpret the history of the Bartlett, Yucatan, and Gulf basins in those days. They may or may not have existed as at present in Jurassic and Cretaceous times. If they did, no data are at hand for prognosticating whether they were connected or disconnected bodies of water or connected with either ocean. The Caribbean, however, most probably, and possibly the Gulf of Mexico, were Pacific indentations at this time.

It is a well known fact that the close of the Jurassic and beginning of the Cretaceous was a revolutionary period in American continental configuration. The gigantic Sierra Nevadan uplift, whose southern and eastward extents are not clear, elevated portions of the pre-existing Pacific borders of North America into land. Simultaneously with or just after this event in earliest Cretaceous time, the Atlantic side of the Cordilleran continent in the Mexican region underwent profound subsidence. The Gulf of Mexico was then as now an embayment of the Atlantic Ocean, which began to encroach upon the pre-existing margins of the Appalachian and Cordilleran regions. The interior shore of the Gulf migrated from the eastern part of Texas to southwestern Kansas, and degraded and buried the former southward extension of Appalachian lands then existing in the Coast Plains of northeastern Texas for a distance of 400 miles, while an embayment at its northwest corner near southwestern Kansas, indicated that the arterial Missourian-like drainage at that time was far westward of the present location. The Gulf also made a western transgression across Tropical Mexico from at least the present Gulf shore line to the present Pacific coast, and left thick deposits of chalky sediments over the areas, richly studded with remains of its animal life, but so different from similar life on the Pacific side that not a single fossil is common to the sediments of the two oceans.

The composition of these Lower Cretaceous beds clearly exhibits the fact that this subsidence deepened towards the southeast. Twenty-five thousand feet of limestones in eastern Mexico near the Tropic of Cancer, as seen by McGee and the writer, testify to the fact that it there equalled more than 6,000 fathoms, or as much as some of the greatest depressions yet discovered in the oceans, and yet there is no evidence in the Cretaceous faunas that the Pacific barrer was broken.

What happened in the Windward regions during Lower Cretaceous time can be only hypothetically conceived. Such a subsidence increasing southeastward may have been at least so far reaching in its effect as to affect and submerge the hypothetical Jurassic bridge of the Windward region. If so, the Windward barrier to the eastward was crossed by Atlantic waters, which probably came in across the north side of Southern Florida, which until very recent time has been West Indian in its relations. The absence of any known Lower Cretaceous fossils in the Antillean region suggests that a large land area may have existed during this epoch, composed of south Floridian, Bahaman, Antillean, and Windward lands.

The faunas of Trinidad and the northern regions of South America show that in Lower Cretaceous time the Atlantic waters were overcoming the southern end of the Jurassic Windward bridge, if it ever existed, and that the Atlantic littoral faunas were encroaching upon the present eastern Caribbean area, which had lost or was losing its connection with the Pacific.

In Middle Cretaceous time there was a considerable movement in the northern Gulf region, causing the land to emerge and the shore line to recede from southwestern Kansas to east central Texas. We have absolute record of the extent of this movement in the known migration of the line of the Dakota littoral. Inasmuch as all of the sedimental evidences in the littoral formations of our Coastal Plain are only the marginal phenomena of oscillations which probably had their greatest amplitude to the southward, the effects of this Mid-Cretaceous movement on the tropical regions must have been great. It was one of those oscillations which, had it occurred in later geologic time, would have been of considerable importance, but its effects and extent are completely obliterated by the grander changes which preceded and followed it. It is probable that a Central American land bridge connecting the continents via the

Isthmus of Panama was fully established at this epoch, as indicated by the stratigraphy of the succeeding Upper Cretaceous epoch, during which time events assume sufficient clearness to be more clearly interpretable in the Antillean and Caribbean regions.

In Upper Cretaceous time another subsidence ensued in North America. This produced the greatest known expansion of the Gulf of Mexico. The Dakota littoral of the Cretaceous Gulf of Mexico transgressed the Great Plains region from eastern Texas northward towards the British line, almost if not quite connecting with the waters of the Pacific and nearly separating the continent into Appalachian and Cordilleran Islands, and reaching westward towards the Sierra Nevada.

The Rocky Mountain or eastern area of the North American Cordilleran region, as far west as Utah, then became a submerged oceanic region, with ridges and islets of the older formations. The deepest deposits — the Niobrara chalks — could not be interpreted to indicate greater depths in the United States than a thousand fathoms, although the thickness of the sediments would indicate a subsidence of thirteen to fifteen thousand feet (not counting the Laramie) in the Rocky Mountain region, marked by deposition of littoral sands, carbonaceous shales, and the conspicuous Niobrara chalk horizon. All these strata, except the latter, indicated the degradation of a vast pre-existing land to the westward.

The known facts of paleontology indicate that a Central American bridge existed during the latest Cretaceous epoch. There is no evidence that the life of either ocean then passed that barrier, and old rhyolitic tuffs of Cretaceous age occur in Panama. Near the highest pass of Costa Rica, 5,000 feet above the sea, in the neighborhood of San José, there are Upper Cretaceous limestones, with fossils of Antillean facies, which show that the Caribbean Sea at that time had encroached at this locality far across the present Central American barrier. Similar limestones have also been reported from Guatemala by Sapper. These facts indicate Caribbean conditions in late Cretaceous time in portions of what are now the summit regions of Central America, and that the Cretaceous land barrier, if one existed, was then situated in a region now covered by the waters of the Pacific to the south of the present Central American land.

Vulcanism was active in the Coastal Plain and Cordilleras of western Texas, northern Mexico, along the southern end of the Mexican Plateau, in San Salvador, Panama, the Andes, and the Great Antilles. All these regions but the last were continental.

In the Antilles, instead of subsidence, volcanoes added vast accumulations of extruded débris to the pre-existing land masses, or built up islands in the sea like Jamaica, around which peculiar colonies of marine life separated from that of the continental borders by great depths were segregated.

The exact loci of the old Antillean volcanic outlets are now lost, but their débris constitutes the oldest known rocks of all the Antilles and Virgin Islands, with the exception of the few doubtful Paleozoic rocks of Cuba and Haiti previously mentioned. It is a possible hypothesis that these volcanoes were on the southern margin of an older Bahaman-Antillean land.

The close of the Cretaceous and initiation of the Tertiary was marked in both the North and South American continents by great orogenic revolutions in the Andean and Rocky Mountain regions. This is known to have affected the North American Cordilleras as far south as the south end of the Mexican Plateau, and elevated the Cretaceous sediments of the preceding northwestern extension of the Gulf of Mexico to heights of 15,000 feet or more.

In North America the material thus folded was the pre-existing Atlantic (Gulf) sediments, — and the land buttress was on the Pacific side. In South America the sea sediments folded were of Pacific origin, and the land buttress was the eastern or Atlantic side of South America. Somewhere between north latitudes 10° and 25° and longitudes 75° and 100°, including the Central American and West Indian regions, the axes of these two mighty uplifts passed each other *en echelon*. What physiographic changes occurred in the Mediterranean region between the termini of the stupendous orogenic uplifts acting upon it with tortional stress cannot readily be conceived, but changes of a most revolutionary nature undoubtedly took place.

Two of the principal events of Eocene time were faulting and vulcanism. According to Felix and Lenk, great faults of at least 12,000 feet downthrow to the southward, along which the present east and west series of living Mexican volcanoes are situated, developed along the south and east of the Mexican Cordilleras, at the great "Abfall" of the Plateau. Perhaps other faults, as described by these writers, extended in a complemental direction up the east side of the Plateau. Faulting of this epoch certainly influenced the southern part of Texas.

With the great elevation of this epoch, the shore line of the Gulf of Mexico receded with comparative rapidity from the eastern Rocky Mountain region to the interior margin of the present Coastal Plain, where it was located in Eocene time.

Vulcanism, which in the preceding Cretaceous epoch was largely dominant in the Antilles, was now active around the other borders of the Caribbean. The great accumulations of volcanic débris which now cover the southern ends of the North American Cordilleras, the northern end of the Andes, Tehuantepec, the Central American Plateau, the Isthmus of Panama, and along the Colombian coast and Windward Islands, are derived from volcanoes which had their greatest activity during early Eocene time, and are now quiescent in the Tehuantepec and Panama regions.

Stupendous masses of matter were extruded from the earth's interior, and piled upon its crust. The diastrophic effect upon the geography of these changes of mass and weight from the interior to the exterior of the earth's surface must have been appreciable. I can only say, for the present, that in my opinion that may have in some manner influenced the great series of oscillations of level which succeeded the following epochs of time from early Tertiary to the present, and which will presently be described.

Contemporaneous with and succeeding this tremendous volcanic revolution, the relative areas of land and sea were being readjusted. Degradation and deposition were shifting the load preparatory to a great subsidence soon to be initiated in the Atlantic, Gulf, and Antillean regions. Immediately after, or during the Cordilleran revolution in earliest Eocene time, an epoch of excessive littoral deposition set in, marked by great deposits of land-derived sediments, consisting of shallow water alternations of non-calcareous, ferruginous, plant-bearing clay, sands, and gravel. These were deposited around the perimeters of the Gulf and Caribbean, and on the site of the Great Antilles and Barbados. Of this nature is the Great Northern Lignite formation of the Gulf States, the Culebra formation of Panama and Central America, the Parian beds of the South American north coast and islands, the Scotland beds of Barbados, and the Richmond beds of the Great Antilles, — all essentially alike in thickness (± 1,500 feet), character, and arrangement, and evidently derived from near by lands during a great erosive epoch. In North and South America this material was derived from the interior bordering regions, but it cannot be said whence came these deposits in Central America, the Isthmus, the Antilles, and Barbados, unless there were pre-existing lands, such as I have suggested, and these must have been of large area to account for the vastness of the formations. In North Central America the old Guatemalan nucleus could have supplied only a fraction of the sediment. In Panama the source of these formations must have largely been either more extended lands than now exist, — probably in the region now covered by the Pacific waters in the south, or the regions of the submerged Mosquito and Roncador banks to the north. The lay of the formations indicates that the shore line was in the direction of the Pacific rather than the Caribbean, and this one fact, together with other considerations, may lead to the conclusion that land once existed off the Pacific side of Equatorial South America, and the submerged Mosquito banks did not then exist in their present geographic outlines.

But what was the source of these land derived sediments in the Antilles? At first it might be answered that the degradation of the Cretaceous volcanoes alone might account for this material; but, although the formation contains much volcanic material, it also has in it mica schists, quartz, and other débris foreign to the composition of the Antillean Cretaceous eruptions. Besides, the wide uniformity and assortment cannot entirely be satisfied by this hypothesis. On the other hand, the study of this material, considered from any point of view, suggests the hypothesis that the present Post-Cretaceous material was deposited upon the margin of pre-existing land areas lying to the northward, of which they were a part, including the south point of Florida, the Bahama banks, all of which may have been remnants of the northern part of the hypothetical Windward Jurassic bridge or Archipelago, and that these lands during this epoch were being base levelled and subsequently completely concealed by succeeding phenomena.

The presence of this land-derived material in the fundamental Scotland beds of the oceanic island of Barbados is indeed perplexing. The oldest formations of this little island, standing solitary and alone in the Atlantic Ocean, are clearly composed of the débris of a former land, of which there is now no track or trace unless it be the deep submerged ridge extending northward from South America. We search in vain the visible structure of the adjacent Windward Islands over a hundred miles to the westward, and separated by a deep submarine trough, for a solution, but can establish no connection between them. The only hypotheses entertainable are that they were either derived from a land now submerged, which constituted the eastern bank of the Windward platform, or from a peninsula which at that time may have extended out from the northeast corner of South America. If the latter conclusion is tenable, may we not also suppose that the Aves Island bank is also a relic of this old Cretaceous Windward land?

The early Eocene base-levelling was the beginning of initiation of a subsidence which took place in the latter part of the Eocene and early

Oligocene, which was of far reaching importance in the Gulf, Caribbean, and Antillean regions, although they but slightly affected our Coastal Plain. This profound subsidence is manifested by the nature and occurrence in the present upland structure of parts of the Antilles, Barbados, and Trinidad, of oceanic deposits composed largely of Globigerinæ and Radiolarians, such as are now known to occur at oceanic depths varying from 1,200 to 3,000 fathoms.

These beds are synchronous with the so called Jackson and Vicksburg formations of our southern coast, and their equivalents in Yucatan and Costa Rica. The exact geologic age and correlation of these beds have been ascertained by paleontologic data, and the extent and differential variations of this downward movement may be indicated in the composition of the synchronous deposits in different localities.

The effect of this subsidence upon our own Gulf coast east of the Mississippi was a slight northward transgression of the Gulf, as shown by the more mixed character of the formation around the American littoral in Mississippi and Alabama. Subsidence in that direction is distinctly recorded in the change of the Tertiary sediments from the impure land-derived character of the Lignitic and Claiborne beds into the 500 feet of limestones of the Jackson and Vicksburg epochs. The littoral nature of synchronous deposits in Costa Rica also indicates a shallower condition towards the continental shore line in that direction. In Cuba, near Havana and Santa Clara, the Vicksburg limestones contain small pebbles, probably indicative of persisting inequalities of bottom, as the land was being submerged there. Elsewhere in the Antilles and Barbados, the formation is of the deep oceanic nature described.

From the geographic occurrence of these beds I am inclined to believe that they were deposited in the troughs or deeper slopes of two great basins or depressions, separated by a ridge along the present site of the Caribbee Islands. One of these basins, the Barbadian, lay in the Atlantic proper, while the other was in the heart of the Caribbean, having an elliptical outline, whose longer and deeper axis extended through the Windward passage from Mississippi to Trinidad. This depression so largely drowned the Antilles that only the higher summits of Cuba, Haiti, and Jamaica remained above sea level as small islands. This basin shallowed rapidly towards its periphery, the Coastal Plain of the United States, the old lands of Costa Rica and Yucatan. The northern and eastern periphery of this basin during this subsidence could have been only the Bahaman, Floridian, and Windward banks, which must have been largely submerged.

The most important result of this subsidence was the fact that it submerged the Isthmus of Panama, and again permitted shallow connection between the great oceans, as I have shown in my report upon that region, — a passage which was temporarily closed shortly afterwards. All the known evidence, as presented in my recent report, tends to show that this passage was shallow and ephemeral. This is the only epoch in geologic history between the Cretaceous and the present in which there is evidence of this passage having been open.

Succeeding this Tertiary subsidence was the chief of the great orogenic movements which built up the east and west folds of the Antillean mountain systems as now occurring directly across the paths of the pre-existing Andean and Rocky Mountain trends. This undoubtedly was the most important relief producing event in all Antillean history; to it much of the present configuration of the land and sea bottom is due. The whole configuration of the Antillean lands, the western Caribbean floor, the northern shore of South America, and the Central American lands were revolutionized by the development of these corrugations, accompanied by igneous action, including great laccolithic intrusions of igneous rocks.

Seebach[1] long since pointed out the now accepted conclusion that the North American Cordilleras terminate with the "Abfall" of the Mexican Plateau, and showed the distinction between it and the entirely opposite orogenic trends in Central America and the Antilles. Suess, in his masterly compilation,[2] has still further demonstrated the existence of these trends, but owing to inaccuracies of the current geologic data he grouped the phenomena somewhat differently from the manner in which I would arrange them, having connected under the name of the Cordillera of the Antilles the true Antillean trends with those of the Caribbee chain. This, in my opinion, is not an harmonic arrangement. According to the elaborated strikes later platted by Sievers,[3] the Barbadian, Grenadan, and Aves Island ridges of the Windward bridge, at least in its southern half, are more in line with his "Carribischen" ranges of the north coast islands of South America than with the Antillean chain. These uplifts, collectively, now constitute a series of many chopped up, parallel east and west ridges, which have been greatly disconnected and partially submerged by subsequent events, but of which many distinct ranges may still be identified. The most northern of these are the Segovian trends of Oaxaca, Chiapas, Guatemala, and

---

[1] Epitomized by Dollfuss and Mont-Serrat.

[2] Das Antlitz der Erde, Chapter X. pp. 698–702.

[3] Petermann's Mitteilungen, Vol. XLII., 1896, Part 6.

western Cuba, presenting a curve singularly parallel with the Trans-Mississippian extension of the southern front of the Appalachians.

Next to the southward comes the true axial Antillean range of Porto Rico, Haiti, and the Santiago coast of Cuba, the Sierra Maestra of Cuba, and the Misterosa bank between the Caribbean and Yucatan Seas, to the Gulf of Honduras. From the centre of this a southern limb bifurcates and extends through the southwest peninsula of Haiti towards Jamaica, the Rosalind and Mosquito banks into northern Honduras, breaking up into numerous parallel ranges in Honduras, Nicaragua, and the submerged banks.

The continuity of the main Antillean axis of Haiti is through Porto Rico, the Virgin Islands, and St. Croix, breaking directly across the lines of the Bahaman and Caribbee trends, and not curving southward, continuously with the latter, as suggested by Suess.

A third line of Antillean trends is through the axis of the Isthmus of Panama, the Goajira peninsula of Colombia, and the islands of Curaçoa and Bonaire, pointing towards distant Barbados.

The fourth and most southern line of the group, closely related to and in echelon arrangement with the last, is the "Carribischen" system of the Venezuelan coast, embracing the Sierras Costano and Del Interior of Guaira, the peninsula of Paria, and the island of Trinidad.

I have given a general outline of the present arrangement of this system. During this epoch of mountain making, in my opinion, the land areas of the American Mediterranean received their greatest expansion and attained entirely new conformation. The Antilles were raised from submerged island peaks into a large continuous and connected land, which included most of the now submerged ridges and slopes, bringing up with them to a height of 3,000 feet above the sea the deep oceanic deposits (Globigerinal and Radiolarian earths) of the previous epoch. The Caribbean Coastal Plains of Honduras, Costa Rica, Panama, Colombia, and Venezuela were elevated above the sea and intensely folded into the present east and west ridges which occur in those regions.

The effect of this mountain making epoch is clearly and unmistakably exhibited in the geologic structure of Jamaica, Haiti, Cuba,[1] Porto

---

[1] The chief orogenic movements which gave to Cuba its most rugged relief took place in late Tertiary time, as is shown in two published cross sections of the island, the first of which, by the writer, is in the longitude of Havana, and the second across the east end from Guantanamo to Sagua la Grande, by Valentine Peleterro (Boletin de la Comision del Mapa Geologia de Espano, Tom. XX. pp. 89-98, Madrid, 1895).

Rico, Barbados, the Virgin Isiands, and the other regions mentioned, in all of which the Eocene strata are greatly elevated and intensely folded. For data showing the disturbance of this epoch see the various published geologic sections of the other islands.

It would be beyond all reason or interpretation of the known facts to conceive that the stupendous changes of this epoch did not affect the configuration of the adjacent sea bottoms. Neither the east and west trends of the mountain ridges, nor the mountainous configuration of the Great Antilles, cease with the margins of the water. The narrow trend of the Sierra Maestra range of Cuba, for instance, is traceable eastward by a shallow submerged ridge directly across to the northwest peninsula of Haiti, and westward by the Misterosa bank, a narrow mountainous submerged ridge lying between the Bartlett Deep and north Caribbean basin, and extending for hundreds of miles from the Sierra Maestra towards Guatemala. Furthermore, the slopes of the mountains are continued far beneath the waters. The steep declivity of the Sierra Maestra, which now projects 8,000 feet above sea level, continues downward beneath the water to a depth of 18,000 feet, showing indisputably that the present mountain phenomena of the islands are but the tips of submerged bases.

It is equally probable that the combined Mosquito, Rosalind, and Pedro banks constituted an extensive land in this mountain making epoch, connecting Jamaica with the Honduras-Nicaraguan coast. The Bahaman and south Floridian banks were also probably connected with northern Cuba, the Gulf Stream meanwhile flowing out across the northern part of Florida.

This east and west folding may have been instrumental in producing the wonderful Bartlett trough and its related depths adjacent to Cuba and Haiti, which constitute a narrow submerged furrow almost completely across the whole Mediterranean, as well as a parallel elongated submerged trough of the northwestern Caribbean lying south of the western end of Cuba and north of the Mosquito bank. These phenomena may have been initiated at a more remote epoch, but the known effects of the orogenic movements of this epoch, as now visible in the mountains of the Great Antilles, were amply sufficient to produce them.

This important Mid-Tertiary epoch of mountain making in America has not been fully appreciated, but its existence shows conclusively that in this country, as in the Pyrenees of Europe, there was a great east and west trending system at right angles to the trends of the main continental Cordilleras.

This orogenic elevation most probably united the Antillean lands, constructing bridges for the wide distribution of the ancestral forms of the wonderful land shell faunas of the Antilles from Central America to Guadeloupe, which are first found fossil in the succeeding Bowden formation. It also brought the submerged bottoms up to a height sufficient for the habitation of littoral Mollusca, and permitted them to migrate for the first time from the continental margins to the islands, and to attain wide West Indian distribution. The preceding marine faunas of Jamaica, at least of the Antilles, had been all insular and unlike that of the continental margins.

There are no geologic data to prove or disprove connection between the expanded mountainous Antillean lands with the main continent other than that a marine passage between the Gulf and the Atlantic continued across northern Florida. The absence in the Antilles of remains of continental vertebrates of this period, or living descendants thereof, would indicate that no such connection existed. Furthermore, the distribution of the land shells show that the Equatorial current was flowing into the Caribbean through breaks in the windward rims.

During this epoch the Caribbee volcanoes, persisting from the previous Eocene epoch, were in superb activity and undergoing their maximum development along the western border of the eastern limb of the submerged plateau which may have been the remnant of the probable bridge or Archipelago of Jurassic time.

The history of the western Gulf region during this epoch of Antillean uplift is obscure. Hilgard [1] has noted the absence, west of the Mississippi, of Tertiary deposits of later age than the Vicksburg, and concluded that the Gulf must have been closed on the eastern side. The probable absence from the surface west of Red River of marine deposits of late Oligocene and Miocene age,[2] and the presence of apparently fresh water formations in their place along the Texas coast, may seem favorable to this conclusion, but further study is much needed.

The evidence supporting a contrary hypothesis is of a few alleged old Miocene Gasteropods from a depth of some 3,000 feet, in the borings of a well at Galveston, which Harris alleges have Pacific affinities. No outcropping strata have as yet been discovered to support this purely paleontologic hypothesis.

However deficient may be our knowledge of the extent and details of

---

[1] Geological History of the Gulf of Mexico, pp. 6, 7.

[2] The late Tertiary and Pleistocene history of the Texas Coastal Plain has not as yet been fully studied or interpreted.

the lands produced by this Mid-Tertiary revolution, it was certainly one of the most marked and important events in Antillean history, and produced the major configuration of the islands and adjacent waters, which have persisted notwithstanding the modifications of later times. It is true that this configuration has suffered considerable alteration in subsequent epochs, through degradation and oscillations of level, but it has remained as a major mass out of, upon, and around which all later events have been carved.

The next events in Antillean and Central American history were the degradation, partial subsidence of the West Indian region, and dismemberment of this extended Mid-Tertiary Antillean land. The previously connected Antillean lands were severed and dismembered into almost their present outlines. The connections between the Antillean islands and the Bahaman and south Floridian lands were submerged; the waters of the Gulf Stream now flowed over the latter. The Misterosa and Rosalind peninsulas were submerged, and the littoral of the Caribbean migrated southward and westward and impinged upon what are now the land margins of Nicaragua, Costa Rica, Panama, Colombia, and Venezuela. During this epoch it is also probable that Trinidad, Tobago, and the adjacent islands were severed from the South American coast, and the disconnection of Barbados from the South American continent still further accentuated. No record has as yet been discovered showing that the Windward Archipelago participated in this downward movement. On the contrary, the formations recording it were not deposited in Barbados, and the volcanic piles of the Caribbean were more extended than at present.

The Andean, Central American, Mexican, and Windward volcanoes were as active as ever, piling up the vast eminences which from their superior magnitude have so obliterated the no less interesting minor topographic features. In this epoch ended, long before man had appeared upon the earth, all traces of Antillean land expansions upon which the least theory of an Atlantis could have been postulated, and all attempts at restoring connections between the islands, or the islands and the mainland, in subsequent epochs of late Tertiary and Pleistocene time belong to the realms of fancy.

The exact date of this late Tertiary dismemberment of the expanded Antillean lands cannot be stated with exactness. In my opinion, it was during late Miocene and Pliocene time, beginning with the Bowden epoch of the Jamaican sequence. Dr. Dall holds that the age of the Bowden beds is late Oligocene. It is my opinion that the stratigraphic relations of these beds in Jamaica indicate a later age. Deferring to Dall's opinion, I have tentatively accepted his conclusions, however, until more field work can be done.

This subsidence was the first of the group of oscillatory movements which succeeded the great Mid-Tertiary Antillean orogenic displacement, and which in succeeding cycles apparently became gradually more epeirogenic in character and successively of decreasing amplitude. While these movements in late Tertiary, Pleistocene, and recent time were far reaching and apparently of uniform character over wide fields of extent, they were rather of the nature of great swells or wide gentle folds, with movements of opposite direction in their ultimate extension, and of a nature which cannot as yet be completely harmonized with those of our Atlantic Coastal Plain. Furthermore, while in some epochs the records of these movements are most clear and unmistakable, there are others which it is exceedingly difficult to interpret, and hence their analysis as a whole is sometimes obscure.

Since the dismemberment of the Antillean lands through subsidence, the aggregate of the upward movement has not been sufficient to restore the islands to the heights they occupied during the orogenic expansion.

We have described with some care the various topographic levels which make great benches around the mountainous nucleus of Jamaica, and record phases in the physical history of the island. These levels practically belong to three great groups, the oldest of which are from 1,500 to 2,000 feet above the sea, and which may be called the Junki type; the next oldest, from 100 to 1,000, which may be called the Yumuri type; and the newest and most recent less than 100 feet. In a previous paper I have shown that these old levels are practically traceable around the island of Cuba, especially its eastern end. I can now add that they are also similarly developed on the island of Haiti. There can be but little doubt that these three series of terraces are characteristic of the Great Antilles adjacent to the Windward passage, while the two series are more widely identifiable. These stair-like terraces may record repeated intermittent upward movements, or such movements alternating with epochs of subsidence. I was unable to find in the geologic formations and structure any data to sustain the hypothesis of subsidence.

It is difficult to establish the chronology of Post-Bowden events because paleontology has given us no positive key by which we can distinguish with exactness the formations of the Pliocene, Pleistocene, and recent epochs. The calcareous Post-Tertiary material composing these islands resolves into two distinct types: coral reef rock, and white limestone and marls of shallow water origin. The limestones may be of the type of the Pliocene Manchioneal formation of eastern Jamaica, which is sparse in identifiable molluscan remains, although containing Pteropods and Brachiopods and a few thin beds of modern reef corals; or of the Falmouth type, largely composed of shells, in which the remains of a certain species of Bulla are specially abundant. I know of the occurrence of all these formations in stratigraphic juxtaposition only in Jamaica, although types of each have wide distribution throughout the Tropical region at altitudes nowhere exceeding 250 feet excepting in Barbados and the inner margin of the Caribbee Islands.

The oldest and highest group of these levels, composed of no later strata than the old Oligocene, may probably have been developed on the emerging land between the Montpelier and Bowden epochs of subsidence. They may present old levels engraved upon the margins of this Antillean land during the erosive epochs accompanying and following the culminating orogenic uplift. This is the level preserved on the summits of the Pan de Matanzas and Yunki of the north coast of Cuba, and the 2,000 foot limestone benches against the Sierra Maestra of the south side of the same island; also the John Crow and Yallahs Mountain levels of Jamaica.

The middle group may be of late Pliocene and early Pleistocene age, while the newer or coastal group, characterized by being largely composed of elevated reef rock, is the product of the late Pleistocene or recent emergence.

After the Bowden subsidence, there was further elevation, which added the Bowden formation to the Antillean margins. This was not so intense in amplitude as the preceding orogenic uplift, but far reaching in its effect and geographic importance. The Antilles were expanded to areas probably embraced by the present 100 fathom lines, enlarging the eastern and southern margins by narrow ribbons of restored land. This uplift was greatest on the continental mainland, the movement being less felt in the Antilles.

The whole of the Coastal Plain, with its Appalachian background and the Great Plains region of the United States, and probably the Cordilleran region also, participated in this upward movement. Southern Florida, heretofore West Indian in its relations, was united with the land to the north and became populated with North American mammals. The island could have had no Antillean or Bahaman connection at this time, for these mammals are not found in the latter regions. The elevation, however, was not sufficient to establish a united Antillean continent with great rivers which have since been submerged, as alleged by J. W. Spencer.[1] In the eastern and southern United States, Central America, Panama, and the Antilles, extensive degradation occurred, marked first by deep incisions of canyons on rapidly rising land and base-levelling of the borders, and next by deposition of the aggradational material over the recently formed plains. This epoch apparently corresponds with that which has been described as the Lafayette by McGee, the time of which was before the close of the Pliocene.

In the Antilles proper, and on both coasts of Costa Rica and Central America, this movement is recorded by a number of long continuous base and beach level terraces, the highest of which are 600 feet above sea level in the Antilles, as exemplified in the Yumuri terrace of eastern Cuba and about 200 feet in the Panama-Costa Rican region, as seen in the Monkey Hill and Naos benches of Panama. There are no bench marks in the Windward region by which this movement can be correlated there, the field of elevation probably not having reached so far to the eastward. If the Panama and Yumuri levels are synchronous, — and concerning their identity we are not yet fully satisfied, — there is evidence of a considerable difference in amplitude of uplift between the two points, the greatest movement having been in that portion of the Antilles adjacent to the Windward Islands, there exceeding that of the Panama coast by some 500 feet.

During this epoch vulcanism was continuously active in all the present regions of living volcanoes, as well as in the Cordilleran region of the United States, although expiring in the latter.

The margins of the present Antilles and Caribbean and Gulf mainlands were flooded by the seas in late Pliocene time, and subsidence may be presumed. The continental coastal plains of south Florida, Mexico, Yucatan, Costa Rica, and Trinidad, the lowlands of the pre-expanded Antilles, and the Atlantic margin of the Windward platform, were veneered during Pliocene time with a coating of oceanic débris composed of shells and calcareous muds. How the western Gulf region was affected during this epoch cannot be stated with clearness at present, but from the fact that the rivers of the back coast country of Texas were partially drowned and partially refilled with alluvial sediments, it is probable that that region was much lower than at present. In Tehuantepec and Costa Rica the Pliocene marine deposits indent the Gulf and Caribbean coasts for a considerable distance inland. During this

---

[1] Reconstruction of the Antillean Continent. Bull. Geol. Soc. Amer., Vol. VI. pp. 103–140, Rochester, 1895.

epoch the Antilles were restricted to a fraction less than their present dimensions.

This subsidence of late Pliocene or early Pleistocene time did not lower the Isthmian barriers sufficiently to permit the commingling of the two oceans across them, or to divert the Gulf Stream across it in Pleistocene time, as has been frequently asserted, nor is there a single fact in the geology or geomorphology of the Isthmus of Panama to warrant this conclusion. How long this subsidence persisted in the Tropical regions cannot be stated with accuracy.

There is one point in this history which seems to present a hiatus. There should be some record of a subsidence in early Pleistocene time corresponding with the great Columbian depression of the North American coast in the Glacial epoch. We must confess, however, that the structure of the islands affords no data whereby it can be exactly established in the islands, although the Isthmian and Texan coasts clearly record traces of such an episode.

Following this Pliocene expansion were a number of pseudo epeirogenic elevations which probably continued from Pleistocene time to the present, marked by a series of interrupted uplifts of a large portion of the West Indian region, bringing the pre-submerged plateaux, ridges, and benches to altitudes sufficiently near the surface (fifteen fathoms) to permit the growth of modern coral reefs, which as the elevation progressed were elevated above the water, while other slopes of the submerged lands were brought successively within the limits of the reef coral growth, by which they are now inhabited.

These later elevations of the West Indian region are recorded in the elevated reef and wave-cut bench and bluff topography or newer terraces of all the islands except the Leeward side of the Windward Islands. The topography, whether seen against the margins of the older mountainous islands of the Great Antilles, or in isolated islands like Barbuda, Desirade, Alta Viela, Navassa, or a dozen other examples that might be quoted, is the most striking modern feature of the West Indies, and consists of a series of two or more low benches and escarpments rising above the sea. In Jamaica, besides the higher benches of older origin, they comprise four benches, the oldest and highest of which is composed of elevated Pliocene marls, and the three lowest of elevated coral reef rock. Barbuda, Sombrero, Navassa, and others, show a double terrace, consisting of a low coastal bench surmounted by a higher mesa summit.

The newer group of terraces is traceable and recognizable throughout the islands and margins of the whole West Indies, with the exception of the Bahamas, the west side of the Caribbee volcanic chain, and perhaps the islands and coast of the north side of Venezuela, showing the wide extent of the recent epeirogenic uplifts. The elevated reefs of the West Indies, especially those forming the Great Antilles, are all manifestations of this event. On the mainland of Florida, Texas, Yucatan, and Panama, it is recorded in the elevated position of synchronous Post-Pliocene formations of diverse material above sea level. Many small isolated islets, like Barbuda, Desirade, Marie Galante, and Basse Terre of Guadeloupe, making the eastern limit of the Windward Islands, with their double benches, show their wide extent in that direction. Other isolated disconnected islets, like Navassa, southeast of Haiti and Alta Viela, show the same unmistakable record in their benched topography.

All these recently elevated benches are not reef rock, but many of them are wave-cut terraces. In Barbuda, for instance, they are composed of old beach and shallow littoral débris, now cemented into limestone, as are many of the Florida Keys described by A. Agassiz. It may be that the higher summits of the low benched islands of the Barbuda and Navassa type are remnants of the oldest Post-Pliocene elevation, and that the lower terraces record a later Pleistocene uplift.

Whether constructional benches of elevated reef rock or wave-cut cliffs and terraces, these phenomena are all manifestations of the same general uplift that has taken place in Tropical America since the Pliocene subsidence we have described.

The known data of the wide area of these Pleistocene and later uplifts, as uniform as they appear, present some interesting facts showing important differential movements. These are characterized by wide extent and small amplitude. The region of greatest uplift, excepting Barbados, is adjacent to the Windward passage, where a maximum of at least 600 feet is recorded. From this locality the amplitude decreases north, south, and west, the elevation being only a few feet at Colon and in southern Florida. To the south of east as far as Barbuda and Desirade east of Guadeloupe, the amplitude maintains an altitude of over 125 feet, indicating that the uplift was a very gentle oval swell, having an east and west axis. From Barbuda to Colon is about twenty degrees of longitude, or over 1,300 miles, and at the extremes and middle of this line there are stations by which the differentiation of the movement can be determined, and these show that considerable differences exist. At Barbuda the highest bench is 125 feet; at Navassa in the centre, 250 feet; at Colon on the west, five feet.

In the region of the Bahamas, according to A. Agassiz, subsidence has been progressing during epochs which correspond with these regional uplifts in the Antilles.

The uniformity of this epeirogenic movement is also broken at two places by synchronous orogenic deformation: on the Leeward side of the Windward Islands, where the modern reef rock is found 300 feet above the sea in disturbed patches, and at Port Limon, Costa Rica, where the Pleistocene beds are deformed. Furthermore, at the eastern extremity of the region, the island of Barbados, the Post-Pleistocene uplift is entirely discordant with that of all the rest of the region, the coral reefs of Barbados having risen to an altitude of 1,100 feet.

Synchronously with the rising of the reef, volcanic piling has continued on the mainland and in the Windward Islands, although the mass of ejecta during these later days is Lilliputian in comparison with the great heaps of débris piled up in preceding epochs. The present craters and vents of the Mexican, Costa Rican, and Windward summits are mere ant-hills capping the older mountains of ejecta. The last volcanic fires of the Cordilleran region of northern Mexico and the United States expired in Pleistocene time.

The differing altitudes of the synchronous elevated reefs teach some important lessons. On close analysis they show that the apparent uniformity of uplift does not persist, and resolves itself into a wide, swell-like movement, with different intensities in various parts of the field, gradually decreasing towards the United States, where hitherto Post-Pleistocene movements of the West Indies and the continent had been considered so uniformly continuous. These inequalities in the Post-Pleistocene uplifts of the West Indies also controvert the position maintained that the elevated terraces might be due to shrinkage of the sea rather than elevation of its bottom.

The data presented are insufficient to show enough expansion of the West Indian lands in Post-Oligocene times to have connected the islands with the mainland or with one another, or to have created a continuous Windward bridge, as has been alleged.

RÉSUMÉ.

With the data presented, we can now briefly review the major processes of diastrophism which have produced these great changes of level in the Tropical region in later Mesozoic and Cenozoic times, and their effects upon the configuration of the lands.

It is apparent that the borders of the region were indicated after the Appalachian revolution, at which time protean lands existed to the north and south in the then separate Americas. It is even possible that corrugations of Pre-Mesozoic rocks now concealed may have at that time underlain the North American Coastal Plain, and established the fundamental trends of the Floridian, Mexican, Central American, and Windward ridges, especially the long east and west Segovian ridge or ridges of Guatemala, and its possible extension into Cuba and Haiti, which constitute the most northern of the Tropical ranges.

The Sierra Nevadan revolution, at the close of the Jurassic time, undoubtedly played an important part in establishing the northwestern barrier of the Mediterranean region, and creating a permanent nucleus for the accumulation of subsequent lands against it. The present abrupt termination of the trend of the Sierra in southern California, and the absence of trends directly continuous therewith in northern Mexico, does not necessarily imply that related uplifts may not have occurred in the western Sierra Madre region of that republic concerning which we now know so little, except that its diminishing summits towards the American border, formulated by the later movements, are trending towards the Colorado Plateau. There may be nucleal lines of the older Nevadan trend in the Mexican region parallel to and *en echelon* with the Californian Sierra. No trace of this revolution can even be hypothecated elsewhere to the southward in the Tropical American region.

The Andean and Laramide (or Rocky Mountain) revolutions of late Cretaceous and Eocene time, although synchronous in age, have not thus far revealed continuity across the Tropical zone. As has been shown, no possible protraction of their trends can be connected across it. Neither can their trends anywhere be identified in Central America or the West Indies, where, on the other hand, the orogenic trends are directly across their paths and at right angles to them. The only visible effect of the Laramide movement upon Tropical America was to add another belt of land, the Mexican Plateau, to the previously existing continental mass northwest of the region.

The Antillean uplifts which occur in the West Indian region (Great Antilles and Virgin Islands), Central America, and the Isthmus of Panama and the ranges of the Colombian-Venezuelan coasts and islands, constitute the members of the latest and most important mountain movement, and one which produced the present configuration of the region mentioned.

On closer study this system presents several interesting minor trends, and its history reveals a complexity of movements. In Jamaica, for instance, and those islands around the Windward passage in the very heart of the region, two movements of different epochs and axial directions can be traced. The oldest of these produced the intense folds of higher summits of eastern Cuba, Jamaica, and western Haiti, composed of terrigenous and volcanic débris of Eocene and Cretaceous age. A subsequent subsidence destroyed the pre-existing continuity, and coated the lower slopes of these mountains with 3,000 feet of purely oceanic deposits. This was followed by another uplift of Mid-Tertiary time, which was produced or accompanied by the vast igneous intrusions. The trends produced by these two events are quite distinct. Those of the older uplift are northwest and southeast in Jamaica and Haiti, and continued with the Sierra Maestra of Cuba, and constitute an almost closed amphiteatre of summits, broken only in the west by the Bartlett Deep.

The trends of the later Miocene uplift, which added the present white limestone areas to the Antilles, are strictly east and west, and the structure is that of simple open anticlinal folds.

In the Panama and Honduras trends active vulcanism was in operation during the earliest of these mountain making epochs, the chief erupted material being augite-porphyrites. The second orogenic epoch in the Antilles was accompanied in the Panamic, Costa Rican, and Carribischen ranges by intrusions of a different nature.

The foregoing facts all lead to the conclusion that the orogenic growth of the cross ranges of the Tropical region was a series of intermittent processes. These were probably initiated back or before the early Mesozoic, as shown by the uplifts of the Segovian ranges which are concentric with the southern margin of the older Appalachian trends. This may have been followed by movements in the later Mesozoic not yet deciphered. The chief revolutionary movement effective in producing the present configuration occurred in the Miocene Tertiary. The Post-Eocene age of these uplifts is undoubtedly attested by the fact that in all the regions mentioned, including the Segovian, where older rocks also occur, the ranges are composed of intensely folded Eocene and Oligocene strata which have been cut through by granitoid and basic intrusives.

Concerning the origin and succession of volcanic events, the following facts can be stated. In late Cretaceous time vulcanism was active in the now quiescent regions of the North Mexican and Trans-Pecos Cordilleras, the Coastal Plain of Texas, the Isthmus of Panama, and the Great Antilles, Jamaica then being a volcanic island. The late Cretaceous limestones of Costa Rica contain angular specks of volcanic material intermixed with them, as also do the late Eocene sediments of Panama, which facts lead us to believe that the present Central American volcanic plateau has been an intermittent locus of volcanic activity from the Cretaceous to the present, as also has the volcanic region of Mexico.

The volcanoes of the Windward Islands, in my opinion, date back to at least the Eocene. In Mid-Tertiary time granitoid intrusions were pushed upward into the sediments of the Great Antilles, the Carribischen, Costa Rican, and Panamic regions. How extensively this remarkable event affected the Andean and Cordilleran regions we cannot say, except that we have fragmental data which lead us to conclude that it certainly extended to the Mexican Plateau, while Cross reports that the rocks of this epoch from Jamaica are singularly like the material of certain laccoliths of Mid-Tertiary age in Colorado.

After the Miocene vulcanism became quiescent in the Great Antilles, and the Coastal Plain of Texas, but has continued to the present in the four great loci of present activity, — Southern Mexico, the Northern Andes, Central America, and the Windward Islands. In the last two regions mentioned, the greater masses of the present volcanic heights were piled up before the Pliocene, and the present craters are merely secondary and expiring phenomena.

The wide occurrence of benches and terrace levels in the Tropical region is as conspicuous and important a topographic feature as the folded and volcanic mountains. Whether made by degradational or constructive processes, they record with unusual clearness the later regional movements, and in a manner corroborate the history recorded by sedimentary and paleontologic evidence. The three distinct groups of these phenomena of late Tertiary, Post-Pliocene, and Post-Pleistocene epochs respectively, having their typical development in the Antilles, around the Windward passage, are traceable, with local modifications on both sides of the Costa Rican divide. In the Windward Islands only those of the two later groups are positively defined as yet, while in Barbados only those of the last epoch occur under entirely anomalous conditions.

With the date presented we can summarize the known history of the Antillean region as follows: —

1. The geology and configuration present no evidence whatsoever whereby past land connections can be established between these islands and the North and South American lands in Post-Jurassic time, especially in the Tertiary, Pleistocene, or recent epochs.

2. The configuration and conditions of these islands in Pre-Jurassic time cannot even be surmised.

3. There are some hypothetical and biologic reasons for believing that the outer rim of the American Mediterranean constituted a partial or complete bridge between the continents in Jurassic time, and that the Panama bridge did not then exist.

4. The first definite evidence of Antillean lands is found in the eruptive rocks of late Cretaceous time, when it is probable that there were marine volcanoes.

5. The land débris constituting the Eocene strata throughout the islands testifies the pre-existence of extensive Cretaceous land areas.

6. There was a profound regional subsidence in late Eocene and early Oligocene time, which submerged all but the highest tips of the Antilles, and which extended to the margins of the surrounding continents.

7. In late Oligocene or Miocene time there was a tremendous orogenic movement which resulted in uplift, whereby many of the islands were connected with each other, and possibly an insular southern portion of Florida, but not establishing land connection with the North and South American continents.

8. In Miocene or early Pliocene time the islands were severed by submergence into their present outlines and membership, which they have since retained with only secondary modification.

9. In Pliocene and Pleistocene time there have been intermittent periods of elevation without serious deformation, but not sufficient to establish land connections or to restore the islands to the heights and areas of Mid-Tertiary time. The Pleistocene movements, while epeirogenic, were sufficiently differential to show that they were not uniform in all parts of the area, showing great differences in amplitude within the West Indian area, and were not harmonious with those of the North American coastal plain.

10. The irregularities of the submerged configuration of the West Indian region are orogenic, and not due to submerged continental drainage systems.

11. The elevated coral reefs of the West Indies were formed on rising lands.

PART VII.

APPENDICES.

I.

Additional Note on the Geology of Porto Rico and Santiago de Cuba.

Since the foregoing pages were placed in type I have made a geological reconnoissance of Porto Rico and Santiago de Cuba. In the former island I found the general Antillean sequence, but modified by certain features hitherto known only in the Caribbean chain: — 1. An older plexus of water-sorted hornblendic volcanic material, — tuffs and conglomerates with interbedded Cretaceous Rudistean limestone similar to that of Jamaica, composing the central mountains. 2. An Eocene system of impure lignitic sands and clays like the Richmond beds, occurring on the western side of the island near San Sebastian. 3. Fossiliferous marl beds overlapping the above, which at this writing have not been determined. 4. Miocene coral limestone, unlike anything hitherto recorded from the Great Antilles, but of the type occurring in Antigua. These constitute the hilly country north and northwest of Lares. 5. White limestones of probable Pliocene age, composing the hills of the south coast. 6. Elevated reefs, but feebly represented. 7. Alluvial plains of Pleistocene age. The terrace phenomena are less developed upon this island than in any of the other Great Antilles, although the Pleistocene base-levelling is well developed in stream valley phenomena. Dikes of syenitic-like porphyry, probably diorites, were also noted cutting the older hornblendic rocks.

Evidence was obtained indicating that the greater mountain movement culminated before the Miocene, and that there has been at least one thousand feet of vertical uplift since that epoch.

My researches at Santiago de Cuba, consisting of a section across the Sierra Maestra from the coast to the Rio Cauto, convinced me that the crystalline rocks of that region are Cretaceous and Post-Eocene Tertiary, and not Paleozoic, as asserted by Frazer; and I am more than ever inclined to doubt his conclusions and those of Bergt relative to Cuba and San Domingo. The descriptions of the region by Kimball are approximately correct and reliable.

II.

SOME CRETACEOUS AND EOCENE CORALS FROM JAMAICA. BY T. WAYLAND VAUGHAN.

Introductory.

Mr. Robert T. Hill has submitted to me for study the various fossil corals that he has collected in his visits, made for Professor Alexander Agassiz, to the West Indian Islands. The following paper has grown out of a study of a part of this material, i. e. the so called Cretaceous and the Eocene species.

Duncan is the only author who has contributed to the paleontologic literature on corals of these ages from Jamaica. His first paper, published jointly with Wall, "A Notice of the Geology of Jamaica, especially with reference to the District of Clarendon; with Descriptions of the Cretaceous, Eocene, and Miocene Corals of the Island,"[1] contains notices or descriptions of the following "Cretaceous" and Eocene species: —

Lower Cretaceous.

Diploria crassolamellosa, Edwards and Haime.
Heliastræa exsculpta, Reuss.
Heliastræa cyathiformis, sp. nov.
Cyathoseris haidingeri, Reuss.
Porites reussiana, sp. nov.

Five species in all, three of which are identified with European species and two described as new. As Duncan compares these species with the Gosau fauna, I took the opportunity while in Europe to visit the K. K. Naturhistorisches Hofmuseum in Vienna and study Reuss's types of the Gosau corals.[2] Later I went to London and studied in the collection of

---

[1] Quart. Jour. Geol Soc. London, 1865, Vol. XXI. pp. 1–15.

[2] I am deeply indebted to Prof. Theodore Fuchs, Director of the Geological Department of the Imperial Hofmuseum, and to Drs. Wähner and Kittl for giving me every facility possible in my studies. Prof. E. Suess gave me access to all the collections at the University of Vienna, and I express my hearty thanks to him.

the Geological Society of London the originals and types of Duncan.[1] The result of this study was somewhat as I anticipated, — all of Duncan's identifications with European species are wrong. The *Diploria crassolamellosa* (described in this paper as *D. conferticostata*) and *Cyathoseris haidingeri* of Duncan are both new species. Later I have described the former; the latter is still undescribed. Mr. Hill has collected no specimen of it in his travels, and I did not have time while in London to study the species properly and have figures drawn. Duncan's *Heliastræa exsculpta* is not only not the same as the *Heliastræa exsculpta* of Reuss, but does not belong to the same genus. It is a synonym of *Heliastræa* (= Multicolumnastræa, gen. nov.) *cyathiformis*, Duncan. This breaks down absolutely any comparison of the Jamaican corals with those from the Gosau. It might be added that the Gosau is not Lower Cretaceous, as Duncan states, but high in the Upper Cretaceous.

Eocene.

Paracyathus sp.
Stylophora contorta, Leymerie sp.
Stylophora contorta, var. nov.
Stylocœnia emarciata, var. Lamarck sp.

Duncan has published no descriptions or figures of these species, and only very scanty notes. I made the following notes on the original specimens in the collection of the Geological Society of London.

Paracyathus sp., which Duncan compares with *P. caryophyllus* (Lamarck).[2] The specimen is a fragment, so poorly preserved that one cannot determine any essential characters. Locality, "Black Shales, Grass Valley, Jamaica," according to label in collection of the Geological Society; "Yallahs Valley," according to Duncan.[3]

Stylophora contorta, Leymerie sp. (Duncan). I could see no reason for separating the specimens specifically from *Stylophora affinis*[4] of Duncan. The walls between the calices are usually not so thick. As the surface ornamentation has been eroded, the specimens cannot be accurately described.

Stylocœnia emarciata, Lamarck sp. (Duncan) from Port Maria. There are thickenings at the corners of some calices, and there appear to be

---

[1] For this privilege I am indebted to Mr. William Rupert Jones, Librarian, and Mr. L. L. Belinfante, Secretary of the Geological Society. Mr. C. Davies Sherborn, who was cataloguing and labelling the types in the Society's collections, did everything possible for me.

[2] *Op. cit.*, p. 8.

[3] *Op. cit.*, pp. 9, 13.

[4] Quart. Jour. Geol. Soc. London, 1863, Vol. XIX. p. 436, Pl. XVI. Fig. 4.

remains of some pillars, so the coral is pretty surely a *Stylocœnia.* The septa are apparently in two cycles of eight septa each, eight large septa, and eight small, making a total of sixteen. The walls are rather thin, .3 to .5 mm. thick. The calices are irregularly polygonal in outline, their diameters usually 2 mm. The calices are smaller than the measurements given by Edwards and Haime;[1] they give 2.5 mm. for *Stylocœnia emarciata.* The detailed characters of the pillars and of the upper surface of the wall cannot be made out. Later in the present paper I describe this as *Stylocœnia duerdeni.*

In a later paper,[2] Duncan describes another species, *Columnastræa eyeri*, sp. nov., from "Eocene shales, Jamaica." As he published a fair description and figures of this species, no further remarks are needed. In this same paper, in the table of West Indian fossil corals,[3] *Paracyathus crassus*, Edwards and Haime, is cited from "Jamaica, Eocene." The original specimen is indeterminable, and needs no consideration.

Duncan's last contribution to West Indian paleontology is "On the Older Tertiary Formations of the West Indian Islands."[4] This paper deals with a collection of corals, made by Mr. P. T. Cleve on the island of St. Bartholomew, and considered by Duncan as of Eocene age. Duncan lists or describes the following species:—

Flabellum appendiculatum, Brongniart sp.
Stylophora compressa, sp. nov.
S. distans, Leymerie sp.
S. conferta, Reuss.
S. tuberosa, Reuss.
Trochosmilia subcurvata, Reuss (figured).
T. subcurvata, var. nov.
T. insignis, sp. nov.
T. arguta, Reuss (figured).
Asterosmilia pourtalesi, sp. nov.
Stylocœnia emarciata, Lamarck.
Stephanocœnia incrustans sp. nov.
S. elegans, Leymerie sp.
Astrocœnia multigranosa, Reuss.
A. ramosa, Sowerby sp. var. 1 and 2.
A. d'achiardii, sp. nov.
Ulophyllia macrogyra, Reuss.
Plocophyllia caliculata, Catullo sp.
Manicina areolata, Linn. sp.
Leptoria profunda, sp. nov.
Circophyllia compressa, sp. nov.
C. clevei, sp. nov.
Goniastræa variabilis, sp. nov.
Solenastræa columnaris, Reuss.
Turbinoseris eocænica, sp. nov.
T. major, sp. nov.
T. grandis, sp. nov.
T. angulata, sp. nov.

---

[1] Hist. Nat. des Corall., Tom. II. pp. 251, 252.

[2] Quart. Jour. Geol. Soc. London, 1868, Vol. XXIV. pp. 17, 18, Pl. I. Figs. 1*a*, 1*b*.

[3] *Op. cit.*, p. 23.

[4] Quart. Jour. Geol. Soc. London, 1873, Vol. XXIX. pp. 548–565.

Turbinoseris antillarum, sp. nov.
T. clevei, sp. nov.
T. cyclolites, sp. nov.
Astræopora panicea, Pictet.
Actinacis rollei, Reuss.
Porites ramosa, Catullo.

The originals and types of these species are partly in Stockholm and partly in the collection of the University of Upsala. I have not been able to make the journey necessary for seeing them. I am confident that the collection needs very careful revision, after having studied, with Duncan's work in hand, the types of all of the species of Reuss with which he identified West Indian species. I have studied also specimens of all the other European species considered by Duncan in his paper. The corals from St. Bartholomew have an undoubted Eocene or Oligocene facies.

Résumé of the Hill and Jamaica Institute Collections by Localities.

Solomon Mountain, west of Mint, Westmoreland Parish: Cladocora jamaicaensis, sp. nov.; Leptophyllia agassizi, sp. nov.

Craigie, Parish of Hanover: Stiboriopsis jamaicaensis, gen. et sp. nov.

Pennants, District of Clarendon, Parish of Clarendon: Diploria conferticostata, sp. nov.

Mount Hindmost, District of Clarendon, Parish of Clarendon: Multicolumnastræa cyathiformis (Duncan).

Point Haldane, Port Maria, District of St. Mary, Parish of St. Mary: Stylocœnia duerdeni, sp. nov.

Catadupa: Trochosmilia hilli, sp. nov.; Multicolumnastræa cyathiformis (Duncan); Diploria conferticostata, sp. nov.; Diploria conferticostata, var. columnaris, var. nov.; Trochoseris catadupensis, sp. nov.; Mesomorpha catadupensis, sp. nov.

Near Cambridge Station, south of Montpelier, St. James Parish: Turbinoseris jamaicaensis, sp. nov.; T. cantabrigiensis, sp. nov.; Dendracis cantabrigiensis, sp. nov.

The Faunal Relations of the Jamaican Pre-Bowden Corals.

Because of insufficient description or the undeterminable character of the original specimens of Duncan we must eliminate Cyathoseris haidingeri, Duncan (non Reuss); Paracyathus sp., cf. caryophyllus, Lamarck; Paracyathus crassus, Edwards and Haime.

Arranging the other species according to Hill's stratigraphic succession, we have:—

Cretaceous.

Blue Mountain Series. Cladocora jamaicaensis, sp. nov.; Leptophyllia agassizi, sp. nov.; Solomon Mountain. Stiboriopsis jamaicaensis, sp. nov., Craigie, Parish of Hanover. Multicolumnastræa cyathiformis (Duncan), Mount Hindmost, Trout Hall, and Cupius. Diploria conferticostata, sp. nov.; Trout Hall and Upper Clarendon District, Pennants in Upper Clarendon District. Porites reussiana, Duncan, Upper Clarendon District.

Eocene.

Richmond Beds. Stylophora contorta, Leymerie sp. (fide Duncan), Port Maria. Astrocœnia duerdeni, sp. nov., Port Maria and Point Haldane, St. Mary Parish. ? Columnastræa eyeri, Duncan, Locality?

Cambridge Beds: Turbinoseris jamaicaensis, sp. nov.; Turbinoseris cantabrigiensis, sp. nov.; Dendracis cantabrigiensis, sp. nov.; near Cambridge Station.

Catadupa Beds. Trochosmilia hilli, sp. nov.; Multicolumnastræa cyathiformis (Duncan); Diploria conferticostata, sp. nov.; Diploria conferticostata, var. columnaris, var. nov.; Trochoseris catadupensis, sp. nov.; Mesomorpha catadupensis, sp. nov.; Catadupa.

We appear to have in these corals the unusual condition of several Cretaceous species ranging far up into the Eocene. Mr. Hill has a lengthy discussion of this subject in his report on Jamaica.

There are six species from the Blue Mountain Series. As two of them belong to new genera, any evidence for geologic age must be drawn from the remaining four. The genus *Cladocora* ranges from Jurassic to present time, so the first species is indefinite in its evidence. *Leptophyllia* is Jurassic, Cretaceous, and Eocene, but the Jamaican species, *L. agassizi*, seems more closely related to the Cretaceous forms. The range of *Diploria* is from Cretaceous to the present. The nearest species to *D. conferticostata* is an Italian Eocene species. The genus *Porites* is a Tertiary genus, and if Duncan's generic diagnosis is correct, the *Porites reussiana* would argue for the age of the beds in the Upper Clarendon District being at least not older than Eocene. If the genus of the species should be *Litharæa*, as I suspect to be the case, it might be Cretaceous, but it seems more closely related to some of the Eocene species. It seems to me that there are two faunas in the Blue Mountain

Series, one from Solomon Mountain and most probably Cretaceous; the other from the Clarendon District, practically identical with the Catadupa fauna, might be Eocene in age.

The Richmond beds are undoubtedly Tertiary, and from the similarity between *Stylocœnia duerdeni* and *Stylocœnia emarciata*, I believe Duncan was correct in referring the beds whence they were derived to the Eocene.

The Cambridge beds can be referred to the Eocene (or possibly Oligocene) on the strength of their containing abundant specimens of *Dendracis*. This genus is not known from rocks older than Eocene or younger than Oligocene. Both specimens and species are abundant in Southern Europe and Northern Africa in strata of these ages.

The Catadupa beds also can probably be referred to the Eocene on the evidence of the *Trochosmilia*, which has a near European relation in *T. acutimargo*, Reuss. The *Diploria* also has a European relation. *Trochoseris* is a doubtfully Cretaceous genus; it occurs in the Eocene, and there is a recent species. The occurrence of the species of *Diploria* and *Multicolumnastrœa* in the Blue Mountain Series has been noted.

The faunas from the Richmond, Cambridge, and Catadupa beds seem quite different from the St. Bartholomew fauna, described by Duncan. Apparently they possess only one species in common, viz. the *Stylocœnia*, identified by Duncan as *emarciata*. The stratigraphic affinities of the Jamaican species for European species are the same as those of the St. Bartholomew corals, and I believe more extensive study and collecting will show considerable resemblance, — especially after a revision of Duncan's types from St. Bartholomew.

A very interesting fact is the great difference between the Eocene corals of Jamaica and those from the United States. I am very familiar with the Eocene corals from the latter, having just prepared an extensive monograph on them. So far not a single species common to both has been found. Eocene corals are very abundant in the United States, but they are mostly simple species belonging in large part to the genera *Flabellum*, *Turbinolia*, *Sphenotrochus*, *Caryophyllia*, *Trochocyathus*, *Paracyathus*, *Discotrochus*, *Platytrochus*, *Parasmilia*, *Eupsammia*, *Balanophyllia*, *Endopachys*, and *Stephanophyllia*. *Oculina*, *Madracis*, and *Dendrophyllia* are well represented. In the Oligocene deposits of Mississippi, Alabama, and Florida, there are many compound forms. A species of *Mesomorpha* occurs in the Lower Eocene (Midway beds) of Alabama.

DESCRIPTION OF SPECIES.

TROCHOSMILIA, Edwards and Haime.

Trochosmilia hilli, sp. nov.

Plate XXXVI. Figs. 1-4.

Form irregularly cyathiform, with a stout thick pedicel about one half the length of the corallum. Height of corallum about 22 mm. The calice oval, with a slightly sinuous outline. Greater diameter 23.5 mm.; diameter at right angles to the greater, in the plane containing the vertical axis, 15.5 mm. The costæ are very fine, alternating in size, with beaded margins, as shown in Figure 3, Plate XXXVI. The crowded, very fine, beaded costæ appear to be splendid specific characters. Septa very numerous, thin and crowded. One hundred and ninety septa were counted in the type. The systems and cycles, probably due to the irregular transverse outline of the calice, are not distinctly differentiated, but there appear to be six complete cycles. The total number of septa for a calice with six cycles is 192. The septal margins are not dentate, but there are striations extending across them perpendicular to the flat planes of the septa. The calicular fossa is rather shallow, the calice being wide open, with a small depression in the centre. No columella; the edges of the principal septa meet in the axial space.

Locality. Catadupa, Jamaica (collected by R. T. Hill).

Type. Museum of Comparative Zoölogy.

Remarks. This species bears considerable resemblance to the *Trochosmilia acutimargo* of Reuss, from the Eocene of Monte Grumi, near Castel Gomberto, and Monte Carlotta,[1] Northern Italy. I would call especial attention to the specimen figured in Vol. XXVII. of the Denkschriften of the Vienna Academy of Sciences.[2]

I had the opportunity to study the original figured specimen of this form in the University of Vienna geological collections. The chief difference between the two species seems to consist in the difference in the character of the costæ. The costæ of *acutimargo* are acute or moderately rounded, while in *hilli* the sides of the costæ are perpendicular to the wall of the corallum.

---

[1] Denkschrift d. Wiener Akad. d. Wissenschaft Mat. Naturhist. Cl., 1868, Bd. XXVIII, Plate I. Fig. 1. Denkschrift d. Wiener Akad. d. Wissenschaft Mat. Naturhist. Cl., 1874, Bd. XXXIII., pp. 26, 27, Plate XLIII. Figs. 3-7.

[2] In this volume, page 139, Reuss calls this species *Trochosmilia profunda*, but later, in Vol. XXXIII. of the same series of publications, he shows that he had at first confused two species under the name *profunda*, and separates the forms into *T. profunda* and *T. acutimargo*, Plate I. Fig. 1, Vol. XXVIII., taking the latter designation.

By comparing the description given above of *hilli*, with Reuss's excellent description of *acutimargo*,[1] the close relationship of the two species will be very apparent.

CLADOCORA, Ehrenberg.

Cladocora jamaicaensis, sp. nov.

Plate XXXVI. Figs. 5–7.

One specimen has been submitted to me. It consists of many branches of *Cladocora* firmly embedded in an indurated matrix of dark colored calcareous sand and clay, or argillaceous limestone. In places the matrix is stained yellow by oxide of iron.

The greatest length of the branches could not be made out, but one piece measured at least 65 mm., and another 50 mm. The following will show the size, in millimeters, of the corallites in cross section. The numbers marked by asterisks are young.

	1	2	3	4	5*	6*
Greater diameter . .	7.5	6.5	8	7	5	4
Lesser " . .	6.	5.	6.5	5	4	3.5

The distance apart of the branches in the colony is variable, but they are not much crowded, the usual distance being from 3.5 to 7 mm. To be sure, in some instances the branches may be closer together or farther apart. No epitheca was observed. The outside of the corallites is marked by low acute costæ, corresponding to all septa. In size they may vary according to the cycles of septa to which they respectively belong, or may be subequal. The septa are in four complete cycles, and there may occasionally be some members of the fifth. The larger septa show thickenings on their inner ends, probably pali. There are not many dissepiments, those present are thin and belly inward toward the centre of the corallite. The columella is variable in its development: in one young calice there is no columella, the axial space being vacant; in other corallites there are a few processes from the septal ends forming a very insignificant false columella, while in others the septal processes have formed a distinct well developed false columella. Reproduction by lateral gemmation, two buds may stand opposite each other, as in Figure 6, Plate XXXVI.

Locality. Solomon Mountain, west of Mint, Westmoreland Parish (R. T. Hill, collector).

Type. Collection of Museum of Comparative Zoölogy.

---

[1] *Op. cit.*, Vol. XXXIII. pp. 26, 27.

STYLOCŒNIA, Edwards and Haime.

Stylocœnia duerdeni, sp. nov.

Plate XXXVII. Figs. 1-4.

1865. *Stylocœnia emarciata,* Duncan (non Lamarck), Quart. Jour. Geol. Soc. London, Vol. XXI. pp. 7, 8, 13.

1868. *Stylocœnia emarciata,* Duncan, Quart. Jour. Geol. Soc. London, Vol. XXIV. p. 23.

Form of corallum, a convex mass; type specimen, 28 mm. in diameter on the base and 24 mm. high. The specimen is broken off from a larger piece, as Fig. 2, Plate XXXVII. shows; therefore the above measurements do not represent the original size of the corallum. Calices shallow, hexagonal, subequal in size, 1.5 mm. to 2 mm. in diameter, close together, separated by a simple wall which is from a quarter to a half millimeter thick; often there are thickenings at the corners of the calices, and remnants of what appear to have been pillars. Septa sixteen, eight large, which fuse to the columella, and eight small shorter ones. Dissepiments present, apparently numerous, very thin, in places may be close together, .5 mm. apart. The columella is styliform.

Locality. District of St. Mary, Parish of St. Mary, Point Haldane (Institute of Jamaica); Port Maria (Geological Society of London).

Type. Collection of Institute of Jamaica.

The specimen that has come under my observation does not permit a more detailed description. The description and figures seem sufficient to make the species recognizable. This is undoubtedly the same as Duncan's *Stylocœnia emarciata,* as a comparison of the above description with the notes already given on his original specimen will show. The *Stylocœnia duerdeni* seems to me distinct from *Stylocœnia emarciata,* both from the descriptions of the latter and after a comparison with specimens of the latter in the U. S. National Museum. The calices of *emarciata* are much larger, the maximum diameter being 3 mm. The usual diameter is 2.5 mm. or a little more, while in *duerdeni* the usual diameter is between 1.5 and 2 mm., with 2 mm. as a maximum. This makes a difference in size of almost a millimeter. Although the specimen of *duerdeni* is worn, in places the surface does not appear to have lost much from attrition, so one can determine the depth of the calices. They are much shallower than in *emarciata.*

MULTICOLUMNASTRÆA, gen. nov.

This genus is closely related to both *Orbicella,* Dana, and *Columnastræa,* d'Orbigny. In the description of the only known species of the genus much detail is given, so here only the more general characters will be pointed out.

Corallum, compound, one of the *Astræidæ agglomeratæ gemmantes* according to Duncan's classification. Reproduction by budding between the calices. The form ramous, or in small heads (see Duncan's *M. cyathiformis*). Corallites rather small, joined by costæ. The surface of the extra corallite area granulate, the granules placed along the costæ, which become plainly visible only in sections. Septa, in type species in three cycles, with very obscurely dentate, almost entire margins, sides granulate. Pali before the first and second cycles. The pali are small and delicate, and are not arranged in two distinct crowns, although sometimes those before the second cycle are a little nearer the wall than those of the first cycle. Endotheca present. Columella usually of several stout pillars, each having a rounded knob-like upper surface. The number of pillars varies from one to four. When there are one or two large pillars a small one or two may often be seen. In section, the pillars are joined by processes to each other and to the inner ends of the septa, so the columella in sections appears spongy, but by careful examination the pillars can be distinguished.

This genus, although it groups with *Orbicella* and *Columnastræa*, is very distinct. The surface between the corallite is very different from that of the former, and a further distinction is in the columella. *Orbicella* has a false spongy columella. In Münich, through the courtesy of Geheimerath Prof. von Zittel, I had the opportunity of studying a fine suite of *Columnastræa striata* (Goldfuss), the type species of the genus.[1] The columella in *Columnastræa striata* is a simple style. There is a single crown of six pali surrounding it, standing before only one cycle of septa. In neither of these essential generic characters does the Jamaican coral agree with *Columnastræa*; the columella of the former, as already stated, is not a single style, but consists usually of several pillars; there are not six, but twelve pali. It seems impossible to include the two in the same genus; therefore I have suggested a new generic designation for Duncan's *Heliastræa cyathiformis*.

In the following specific description there is some repetition of the descriptions of characters given in the above.

Multicolumnastræa cyathiformis (Duncan).

Plate XXXVII. Figs. 5-7, and Plate III. Fig. 1.

1865. *Heliastræa exsculpta*, Duncan (non Reuss), Quart. Jour. Geol. Soc. London, Vol. XXI. pp. 7, 8, 11.

1865. *Heliastræa cyathiformis*, Duncan, Quart. Jour. Geol. Soc. London, Vol. XXI. pp. 7, 8, Plate I. Figs. 1 *a*, 1 *b*.

1868. *Heliastræa exsculpta*, Duncan, Quart. Jour. Geol. Soc. London, Vol. XXIV. p. 24.

1868. *Heliastræa cyathiformis*, Duncan, Quart. Jour. Geol. Soc. London, Vol. XXIV. p. 24.

---

[1] Edwards and Haime, Hist. Nat. des Coral., 1857, Tom. II. pp. 262, 263.

Corallum usually branched; the branches make a very acute angle with one another at place of bifurcation, rounded or compressed; the diameter ranges from 1 to 3 cm. One compressed branch has a greater diameter of 25 mm., and a lesser of 13 mm. The ends. of the branches are rounded, sometimes swollen. An aberrant and unusual form is that of the specimen figured by Duncan as the type of *Heliastræa cyathiformis.* This specimen is expanded above and excavated in the central portion so that it has some resemblance to a cup. The calices project very slightly or not at all above the extra corallite areas. Their diameter is 2 mm., and the distance apart 1 to 1.5 mm. The extra corallite portion of the corallum densely granulate, the granules rounded or elongate and arranged along the summits of flexuous costæ, which are not distinct on the unworn surfaces. Corallites joined by costæ. Calicular fossa shallow. The septa are crowded, and the upper margins form a little rim that contrasts strongly with surrounding granulate area. There are three complete cycles. The first and second cycles are usually indistinguishable in size, both reach far into the corallite cavity and have pali on the inner terminations. The margins are slightly dentate. The columella is variable. It consists of one, two, three, or four stout pillars, each with a rounded upper surface. Endotheca well developed, the dissepiments are fine and close together.

Localities. Catadupa, Jamaica (R. T. Hill, collector); Mount Hindmost, District of Clarendon, Parish of Clarendon (Jamaica Institute collection).

Notes. The results of the study of the type of Reuss's *Heliastræa exsculpta,* of the original specimens of Duncan's "*H. exsculpta,*" and of the type of Duncan's *Heliastræa cyathiformis,* have already been given in the Introductory remarks.[1] Duncan's specimens of "*Heliastræa exsculpta*" are of the same form as Plate (so called) are not the species of Reuss at all, but are branches of his own XXXVII. Fig. 5 of this paper. His *Heliastræa cyathiformis* is only an abnormal form (i. e. it possesses an abnormal shape) of the same thing. The calices, etc. are identical in the two. Duncan's figure of the calices of *Heliastræa cyathiformis* is extremely misleading.

Additional Localities. Duncan had specimens from Trout Hall, Mount Hindmost, and Cupuis identified as *Heliastræa exsculpta.* The specimens from the first two places are without any doubt *Multicolumnastræa cyathiformis.* The specimen from Cupuis is worn, and I could not identify it positively without sections, but it seems to be the same species as the other specimens.

The type of *Heliastræa cyathiformis* is from Trout Hall.

STIBORIOPSIS, gen. nov.

Corallum massive, heavy, subplane above. Septa solid, imperforate, dentate, pali or paliform lobes before the principal septa. Endothecal dissepiments abundant. Wall formed by the fusion of the distal ends of septa. Columella

---

[1] Vide *ante,* p. 228.

spongy, with a papillary upper termination. Reproduction by septal budding and fission. The calices form short series, with two to four distinct calicinal centres. In many places on the upper surface of the corallum the walls of neighboring series seem fused together, but in more eroded places the walls appear distinct. In the section represented in Plate XXXVIII. Fig. 4, it is distinctly shown that the walls of the series are not fused, but that the corallites are joined to each other by their costæ. There appears to be some exotheca.

Three other genera seem closely related to the one here characterized. The first is *Stiboria* of Étallon. The following is the original description:[1] "Polypier massif, étroitement fixé, en lames peu épaisses; les séries d'assez faible longueur; calices doubles, plus ou moins tortueux, séparés par un sillon assez étroit, au fond duquel on aperçoit plusieurs séries de granulations; tissu peu compacte. Centres complètement indistincts, pas de columelle. Les cloisons dentées seulement près du centre; une épithèque." The points of difference are, 1st, the series in *Stiboriopsis* are not separated by a furrow; 2d, the calcinal centres are distinct; 3d, there is a spongy columella, with a papillary upper surface, as stated in the description.

The genus is also closely related to *Symphyllia*, Edwards and Haime, and *Isophyllia* of the same authors; but both of the genera have the septa strongly spined, whereas *Stiboriopsis* has simply dentate septa.

Stiboriopsis jamaicaensis, sp. nov.

Plate XXXVIII. Figs. 2-4.

The details already presented need not be repeated. The specimen upon which the genus and species are based is a mass 89 mm. long, 63 mm. wide, and about 45 mm. thick. As the specimen has been subjected to some rolling, it originally was larger. The upper surface is subplane, slightly convex. Solitary calices have a diameter of 7 to 9 mm. One series of three calices measures 15 mm. long and about 5 mm. wide; another of four calices is 20 mm. long and 5 to 7 mm. wide. The thickness of the walls, with interspace between the series, is from 1 to 2 mm. The series are rather straight, very slightly flexuous. The valleys are not very deep, and are widely open. The septa are only moderately stout and are not greatly crowded. A solitary calice about 8 mm. in diameter has about thirty-six septa, alternately large and small. This would be three complete cycles, with twelve members of the fourth. This septal arrangement is common. The various systems and cycles are not distinctly differentiated. The teeth on the septal margins could be seen on only a few septa, but they are not coarse. The inner terminations of the large septa are swollen, and bear paliform teeth. The swollen ends and paliform lobes make a sort of

---

[1] Lethea Bruntrutana, 1863, p. 386; see Plate LVII. Fig. 1. The date of this work is a little uncertain. The Geological Society of London Catalogue gives it as 1861.

crown surrounding the columellar termination. The upper end of the columella is in a depression surrounded above by the crown. These swollen ends of the septa sometimes fuse laterally with one another. The sides of the septa are beset with crowded pointed granules. Endothecal dissepiments very abundant; in the cross section of one interseptal loculus seven were counted; usually at least three are present in each cross section of the loculi. The dissepiments are thin.

Locality. Craigie, Parish of Hanover.

Type. Collection of Institute of Jamaica, Kingston, Jamaica.

DIPLORIA, Edwards and Haime.

In examining the literature on *Diploria* I find that certain of its features are so vaguely described that one is likely to fail to recognize the genus. In characterizing the genus Edwards and Haime state, "la columelle est spongieuse, essentielle et bien développée."[1] Duncan's description of the columella in his "Revision of the Families and Genera of the Madreporaria,"[2] is merely a translation of the original French. In examining specimens of the species of *Diploria* herein described, of *D. crassolamellosa*, Edwards and Haime, and from figures of *D. flexuosissima*, d'Achiardi, the persistent presence of a lamellar columella was noticed.

In the first characterization of *Diploria*,[3] only the *Mœandrina cerebriformis* of Lamarck is mentioned, so this species, the common *Diploria cerebriformis* of the West Indies, is the type of the genus. A study of this species has shown that it possesses a lamellar columella, which is given a spongy appearance in places by the inner termini of some septa fusing to it and sending out some processes in the axial space. The columella is not continuous throughout the whole length of a series, but is broken here and there by what probably are calicinal centres. A section of one series parallel to the septal planes showed a perfectly distinct lamellar columella through a vertical distance of 1 cm. This was the length of the section.

The usual definition of *Diploria* must be modified so as to include the observations above noted.

Diploria conferticostata, sp. nov.

Plate XXXIX. Figs. 1-3.

1865. *Diploria crassolamellosa*, Duncan (non Edwards and Haime) Quart. Jour. Geol. Soc. London, Vol. XXI. pp. 7, 12.

1868. *Diploria crassolamellosa*, Duncan, Quart. Jour. Geol. Soc. London, Vol. XXIV. p. 24.

---

[1] Hist. Naturelle des Coralliaires, 1857, Tom. II. p. 401.

[2] Journ. of the Linn. Soc. (Zoöl.), 1884, Vol. XVIII. p. 88.

[3] Comptes Rendus de l'Acad. des Sc. (Paris), 1848, Tom. XXVII. p. 493.

An examination of the original specimens of Duncan in the collection of the Geological Society of London proved that the specimens collected by Mr. Hill at Catadupa are identical with the *Diploria crassolamellosa* of Duncan, which a study of *Diploria crassolamellosa,* Edwards and Haime, showed to be an entirely different species.

Form, flat, lobed, or subglobose masses. The largest specimen examined (from the Institute of Jamaica collection) is 80 mm. long, 64 mm. wide, and 51 mm thick. The series are very long, narrow, and flexuous; one series may wind around over nearly the entire upper surface of the specimen. The valleys are elevated above the collines, — i. e. the depression between the series is quite deep, sometimes as much as 2 mm. The width of the series is from .5 to 1.5 mm.; 1 mm. is a fair average; the distance between the series is from 1.5 to 3 mm. The whole upper extraserial surface of the corallum is covered with very fine, low, acute equal costæ, with granulations on the edges. There are 45 to 48 costæ to the centimeter. The septa correspond to the costæ in position and number; they are very crowded, are of the same size, or are alternately slightly larger and smaller. Their upper edges but little elevated, falling in a convex curve to the bottom of the calicular furrow, which is very narrow. Dissepiments are quite numerous. The columella is lamellar, broken here and there by calicinal centres. In longitudinal section it can be seen that the inner edges of the septa fuse by processes placed one above the other to the columella.

Localities. According to Duncan, Trout Hall and Upper Clarendon. R. T. Hill's collection, Catadupa. A specimen from the Institute of Jamaica is from the District of Clarendon, Parish of Clarendon.

Types. Museum of Comparative Zoölogy, Harvard University, and Institute of Jamaica; specimens in collection of the Geological Society of London.

Remarks. It is difficult to see how Duncan ever identified this species with *D. crassolamellosa*, as Edwards and Haime state: "Largeur des vallées, 3 millim. On compte environ 18 cloisons dans la longeur d'un centimètre." [1] As already noted, the width of the valleys in *D. conferticostata* is .5 to 1.5 mm., and there are 45 to 48 septa to the centimeter. The species are only generically related. But the Jamaican form is extremely closely related to *Diploria flexuosissima*, d'Achiardi,[2] from the Eocene of San Giovanni Ilarione, Italy. In fact they are so near each other that I thought at first the Jamaican form must be considered identical with the Italian form. Reuss[3] has published a good figure of *D. flexuossissima,* and made some critical notes. For purposes of comparison the greater part of Reuss's description is quoted: "Die Oberfläche ist mit schmalen und seichten, sehr langen, vielfach gewunde-

---

[1] Hist. Nat. des Corall., Tom. II. p. 405, 1857.

[2] Corallarj Fossili del Terreno Nummulitico dell' Alpi Venete, Mem. della Soc. Ital. di Sc. Nat., Tom. IV. No. 1, 1868, p. 26, Plate XI. Fig. 4.

[3] Denksch. d. Wiener Akad. der Wissensch. (Math.-Wiss.), Bd. XXXIII. p. 11, Plate XXXIX. Fig. 1, 1874.

nen Sternreihen bedeckt, die einen Querdurchmesser von 2–3 Millim. besitzen. Sie werden durch wenig tiefe Zwischenfelder getrennt, die in der Regel eben so breit sind als die Thäler und nur stellenweise, besonders an Punkten stärkerer Krümmung, sich mehr ausbreiten oder im Gegentheile verengern. Sie sind mit gedrängten, wenig ungleichen Rippchen besetzt."

The columella is practically the same as in *D. conferticostata*, sometimes appearing somewhat spongy. "Die Septallamellen sind gedrängt und dünn, an Dicke wenig ungleich. Zwischen zwei längere findet man jedoch fast regelmässig eine viel kürzere eingeschoben. Die längeren verdicken sich in der Nähe der Axe zu einem starken Knötchen, das sich mit den benachbarten verbindet. Die dadurch entstehende Knötchenreihe wird von der Axenlamelle durch eine ziemlich tiefe Furche geschieden. In der Lange eines Centimeters zählt man etwa 44 Septallamellen."

From this description three points of difference become apparent: 1st, the valleys in *D. conferticostata* are only about half as wide as in the species from San Giovanni Ilarione; 2d, in the former there is not that alternation of longer and shorter septa characteristic of the latter; 3d, in the Jamaican species there is no series of fused knobs, corresponding to the inner termini of the larger septa, on either side of the columella, and separated from it by a rather deep furrow. After having made this comparison, it will be easily seen that the two species are very distinct; but the features that they have in common show them to be closely related.

Diploria conferticostata, var. columnaris, var. nov.

Plate XXXIX. Fig. 4.

In the preceding discussion, I have purposely omitted the consideration of a specimen that seems to me to be a young one of *D. conferticostata*, with a different mode of growth. The form is a short ascending column, about 38 mm. high, with the following dimensions. 28 mm. below the top: greater diameter, 18 mm.; lesser, 12.5 mm. At the top the specimen is compressed and has begun to bifurcate. Here the greater breadth is 22 mm.; the lesser varies from 2.5 to approximately 10 mm. The 10 mm. is the thickness of the thicker branch. The series are very long and much wound. The distance across the valleys is 1 to 1.5 mm.; across the collines about .5 mm. There are about 30 costæ or septa to 5 mm., — 60 to the centimeter. The depression on the summit of the colline is usually very obscurely or not at all marked; in some places it is moderately distinct. These are the points of difference. The specimen is evidently immature, and I am confident that it is only a young, somewhat peculiar variety of the *D. conferticostata*.

Locality. Catadupa, R. T. Hill, collector.

Type of Variety. Museum of Comparative Zoölogy, Harvard University.

TROCHOSERIS, Edwards and Haime.

Trochoseris catadupensis, sp. nov.

Plate XXXIX. Figs. 5, 6.

Corallum short cornute, attached by a pedicel, calice flaring out. Height of corallum 13 mm. Diameters 3 mm. below calicular margin: longer, 12 mm.; shorter, 10 mm. Diameters of calice: greater 16 mm.; lesser 15.5 mm. The outer surface marked by low subacute costæ, alternately larger and smaller in size, with granulated or dentate margins. The wall, where it could be cleaned, showed no perforations. The exact number of septa could not be made out with absolute certainty; by counting costæ and septa where not broken off, 140 seemed to be the number, — i. e. there are five complete cycles with about half the members of the sixth. To be sure, the septa are much crowded together. The members of the first, second, and some of the third cycles reach the columella; those of the higher anastomose to the lower after the type of junction in *Trochoseris distorta* (Michelin). The septa are solid, their sides are granulate, and their margins appear to be dentate. Synapticulæ present in the interseptal loculi. The interseptal loculi filled up with calcareous deposit. The calicular fossette in the axial region is narrow and moderately deep. The columella is small, rather deep seated. It appears to be composed of several trabeculæ. The characters of the columella could not be made out as fully as was desired, but one is present, though it is small.

Locality. Catadupa (R. T. Hill, collector).

Type. Museum of Comparative Zoölogy, Harvard University.

Remarks. The specimen on which this species is based is apparently well preserved, but on account of the calcareous filling of the lower portion and the indurated condition of the matrix, calcareous sand and clay, many hours of study were necessary before the features embodied in the above description could be discovered. The description is not so full as is desirable, but in every essential feature the species coincides generically with *Trochoseris*, as a very careful comparison with *T. distorta* showed, and as it is peculiar for the West Indies, it should be easy to recognize it hereafter.

LEPTOPHYLLIA, Reuss.

Leptophyllia agassizi, sp. nov.

Plate XL. Figs. 1-4.

Form of corallum: only one piece, with a few attached very young individuals, has been submitted to me. This piece is 27 mm. long; on the lower end the greater diameter is 14 mm., the lesser 12.5; on the upper end the cross section is practically circular, and is about 17 mm. in diameter. The base of one attached young individual measured, greater diameter, 7 mm.; lesser, 5 mm.; height, 3.5 mm. The base may be larger or smaller, judging from other imperfect young. From these data, the corallum is tall, subclavate, gradually enlarging upward, attached by a moderately large base, with a slightly elliptical cross section. Strictly speaking, there is no wall, the septa joined in their distal portions by numerous synapticulæ. Externally the corallum is ornamented by very many very fine costæ (the peripheral ends of the septa). The costæ show sometimes a faint, sometimes a distinct, alternation in size; the edges are granulate. Between the costæ are numerous delicate synapticulæ. There is no epitheca. Septa very crowded, numerous; 144 were counted on the smaller end of the type; some small ones may have been overlooked. There are five complete cycles, and many members of the sixth. There is some anastomosing among the septa, the 1st, 2d, and 3d cycles reaching the axial space. The septa are very thin, very perforate, and synapticulæ are very abundant in the peripheral portion of the corallum, making a good substitute for a wall. Dissepiments may be present. I was unable to deter mine this. On the sides of the septa, pointed granulations are quite frequent. There is no true columella, but a few processes from the larger septa form a very lax and very insignificant false one. The calice in the specimen has been destroyed, but it can be seen that the fossa was moderately deep.

Locality. Solomon Mountain, west of Mint, Westmoreland Parish (R. T. Hill).

Type. Museum of Comparative Zoölogy, Harvard University.

Remarks. Every character of the coral seemed to agree with those of *Leptophyllia.* For a description of the detailed characters of the genus, Pratz's "Ueber den Aufbau des Septalapparates einiger charakteristischer Gattungen" should be consulted.[1]

TURBINOSERIS, Duncan.

Much difficulty has been experienced in trying to place generically the two corals next to be described. This difficulty has arisen from the insufficiency of the original characterization of the genus. Duncan proposed the genus[2] for a new species called by him *Turbinoseris de-fromenteli* from the Lower Greensand, giving the following generic diagnosis: "The corallum is simple, more or less turbinate, or constricted midway between the base and calice. The base is either broad and adherent, or small and free.

"There is no epitheca, and the costæ are distinct.

"There is no columella, and the septa unite literally [*sic*, laterally], and are very numerous."

---

[1] Palaeontographica, 1882, Bd. XXIX. pp. 90–92.

[2] Monograph Brit. Foss. Corals, 2d series, Palæontog. Soc., Vol. for 1869 (1870), pp. 42, 43, Plate XV. Figs. 13–18.

In describing the species, two additional characters of importance are stated: "The synapticulæ are well developed," and "The costæ are well developed, and often not continuous with the septal ends." No discussion of the character of the wall is given, but both Figures 13 and 14, Plate XV., represent a perforate or synapticulate composition. Figure 18 of the same plate illustrates the noteworthy condition of the costæ alternating with the septa. Figure 16, representing a calice natural size, shows an apparently imperforate wall, though not of uniform thickness, and the septa in the majority of cases corresponding in position to the costæ. The type species needs a new study, and we cannot have a clear conception of its characters until this is made.

Duncan, in his paper on the St. Bartholomew corals,[1] described six species that he referred to *Turbinoseris,* but no additional data on the generic characters are given. He speaks of the wall being "thick" in most of the species, and both mentions and figures synapticulæ between the costæ.

He considers the genus again in his Revision of the Genera of the Madreporaria,[2] but, excepting the statement that the septa are solid and the wall stout, no additional information is given. The genus is classed in the "*Lophoseridæ*," "Funginæ in which the wall is neither perforate nor echinulate," etc.[3]

From a comparison of the figures of the two species herein described with those of the species of *Turbinoseris* from St. Bartholomew, given by Duncan in Volume XXIX. of the Geological Society of London, the generic identity of the forms is most apparent. The only possible opportunity for error would be in the wall of the St. Bartholomew corals being imperforate, but I cannot believe this with Duncan's figures before me. Therefore I have referred the two Jamaican corals to *Turbinoseris* on the strength of their resemblance to the species from St. Bartholomew, but whether Duncan was correct in referring the latter corals to that genus must be left to future work.

Especial attention should be called to *Turbinoseris jamaicaensis*, as, besides the synapticulæ between the distal ends of the septa, quite often the septal ends are solidly united by a thecal or pseudo-thecal thickening.

The similarity in the general structural features of these two species to that of *Leptophyllia* deserves a note. The septal structure (i. e. the septa are composed of ascending trabeculæ) is the same, except that in the species of *Leptophyllia* the trabeculæ are not fused together to a great extent, whereas in *Turbinoseris* the fusion is so complete or so nearly complete and septal perforations are so rare that the septa can best be considered solid. The character of the columella and that of the wall (or absence of wall) in both are respectively of the same type, the latter structure in *Turbinoseris* is not so loose as in *Leptophyllia*, and, as already stated, in *Turbinoseris* there is in places theca or pseudo-theca. The typical species of *Leptophyllia* are attached by broad bases.

---

[1] Quart. Jour. Geol. Soc. London, 1873, Vol. XXIX. pp. 558–561.

[2] Jour. of the Linn. Soc. (Zoölogy), 1884, Vol. XVIII. p. 148.

[3] *Op. cit.*, p. 146.

Turbinoseris cantabrigiensis, sp. nov.

Plate XL. Figs. 5–7.

Form compressed, conical, attached by a very small pedicel. Measurements of two specimens give the following: —

	Height of Corallum.	Greater Diameter of Calice.	Lesser Diameter of Calice.
a (figured type)	18.5 mm.	10.0 mm.	6 mm.
b	15.0 mm.	11.5 mm.	8 mm.

The costæ are very fine, crowded, not prominent and acute, alternating in size. The wall is synapticulate. There is no wall properly speaking, but the many synapticulæ near the peripheral ends of the septa serve as one. Of course, perforations between the distal ends of the septa are frequent. The septa are composed of ascending trabeculæ; the fusion between them seems sometimes, but very rarely, incomplete, leaving pits or occasional perforations. The septa are very numerous, extremely thin, and very much crowded; not thickening at the centre. The type has between 80 and 90 septa; the other specimen, whose measurements are given above, has five complete cycles, apparently 99 septa. Some septa of the higher cycles fuse by their edges to the sides of the members of the lower cycles. Calice rather shallow. Strictly speaking, there is no columella, a few septa fuse loosely in the axial space.

Locality. Near Cambridge, south of Montpelier, St. James Parish, Jamaica (R. T. Hill, collector).

Remarks. The species above described is very close to Duncan's *Turbinoseris eocænica*,[1] from the limestone of St. Bartholomew. I have been unable to see the types of the species from St. Bartholomew, as they are in Stockholm and Upsala, therefore the following comparison is based on the original description. There are two points of difference. *The first* is one of size. Duncan gives the size of *T. eocænica*, "Height of full grown specimen 1 inch (= 25 mm.). Length of calice $\frac{7}{10}$ inch (= 18 mm.). Breadth $\frac{4}{10}$–$\frac{5}{10}$ inch (= 10 to 12.5 mm."[2] *T. eocænica* is a much larger species. Duncan states that there are five cycles of septa with some members of the sixth in the species; therefore the septa in *T. cantabrigiensis* are necessarily more crowded. *The second* difference concerns the inner terminations of the septa. Duncan says that in *T. eocænica* the ends of the larger septa are swollen, and bound the axial space. As stated above in its description, *T. cantabrigiensis* does not have the ends of the larger septa so swollen. The two species are close, but appear distinct. Duncan's Figure 12, Plate XXI., of the costal synapticulæ in *T. eocænica* would apply equally well to *T. cantabrigiensis*.

---

[1] Quart. Jour. Geol. Soc. London, 1873, Vol. XXIX. p. 558, Pl. XXI. Fig. 12.

[2] I have inserted the approximate equivalents in millimeters.

Turbinoseris jamaicaensis, sp. nov.

Plate XL. Figs. 8-10.

Corallum subconical, tip of base a small nipple-like pedicel. Height of corallum, 19.5 mm.; greater diameter, 15 mm.; lesser, 13.5 mm. The external surface covered with small, densely crowded granulate costæ, alternately larger and smaller in size ; synapticulæ abundant between them. The wall is for the greater part synapticulate and perforate, but in places it is solid to a greater or less extent. Septa very numerous and very much crowded; there are over 100, so there are more than five cycles, but the sixth is not complete; their margins apparently finely dentate; the septa of the lower cycles are thicker around the axial space than peripherally. The calicular fossa is narrow and deep. There is no columella, but some of the principal septa meet in the axial space.

Locality. Near Cambridge Station, south of Montpelier, St. James Parish (R. T. Hill, collector).

Type. Museum of Comparative Zoölogy, Harvard University.

Remarks. This species differs from the preceding, *T. cantabrigiensis*, by its more robust form, and the inner thickening of the larger septa. The calicular fossa is deeper and narrower. It is closer to *T. eocænica*, Duncan, from which it differs in its form. The axial ratio for *T. eocænica* is $\frac{10\text{-}12.5\text{ mm.}}{18\text{ mm.}}$; for *T. jamaicaensis*, $\frac{13.5\text{ mm.}}{15\text{ mm.}}$; the former is much more compressed laterally.

It is evident that *T. cantabrigiensis* and *T. jamaicaensis* are very close to each other, and both are extremely near to *T. eocænica*, but as differences of considerable importance exist between all three of the forms, it is best to regard them as specifically distinct.

MESOMORPHA, Pratz.

Mesomorpha catadupensis, sp. nov.

Plate XLI. Figs. 1-3.

Corallum depressed, flat above, transverse outline, subelliptical. Measurements: height (thickness), 7 mm.; greater distance across, 26 mm.; lesser distance across, 24 mm. The base of the corallum has on it some concentric folds, and there is an incomplete epitheca. The costæ are low, equal, and have synapticulæ between them. The outer or common wall probably is synapticulate, i. e. probably there is none, strictly speaking. The calices are concentrically arranged. In the centre is a larger calice, outside of it are two concentric rings, and near the edge of the corallum some small calices belonging to a third one. From the central calice to the calices of the first ring is 5.25 mm. The calices in the first ring are usually 4 mm. apart. There is a slight variation above and below this number. The distance between the first ring and the second ring of calices is from 3 to 5 mm. The distance between calices in the second ring is usually 3 mm. The septo-costæ are directly continuous from one calice to the other, and there is no indication of any sort of bounding wall between the calices. The septa are thick, very close together, the number in the larger calices is twenty-nine to thirty. There is considerable anastomosing between them. The margins are formed by series of roundish or squarish knots. The septa are composed of ascending moniliform trabeculæ, which are slightly inclined inward. The upper terminations of the trabeculæ make the knots on the septal margins. The fusion of adjoining trabeculæ is apparently complete, so the septa are solid except occasionally just below their upper margins. Synapticulæ are abundant. No dissepiments were seen. Calices wide open, not very deep. In the columella space are a few papillæ.

Locality. Catadupa (R. T. Hill, collector).

Type. Museum of Comparative Zoölogy, Harvard University.

Remarks. The generic determination of this species, and also one already mentioned as coming from the Midway (basal Eocene) beds of Alabama, has given me enormous trouble. There is no way of distinguishing from the literature the difference between *Mesomorpha* and *Thamnastræa*, because no thorough study of the type of the latter genus, *Thamnastræa dendroidea* (Lamouroux), has been made. Pratz in his memoir, "Ueber den Aufbau des Septalapparates einiger charakteristischer Gattungen,"[1] does not even mention the type species. So, although Pratz has added some interesting observations on the septal structure of some corals, he has not informed us what *Thamnastræa* really is. He has not given the name of the species on which he based his figures and studies, therefore we do not know that he studied *Thamnastræa* at all.

According to Pratz's figure of *Mesomorpha*,[2] apparently the species under consideration must belong to that genus, but it is impossible to decide whether it is a *Thamnastræa*. The following is Pratz's definition of *Mesomorpha*:[3] "Polypar massiv, knollig, höckrig oder ästig, zuweilen incrustirend. Kelche niedrig, nicht durch scharfe Grate umschrieben, sondern durch Septocostalradien untereinander verbunden. Eine mauer fehlt oder ist höchtens rudimentär und von den Septocostalradien versteckt. Septa compact, an den Seitenflächen mit Körnern versehen. Die benachbarten Septalflächen sind durch starke, echte Synaptikeln mit einander verbunden. Letztere verleihen dem zwischen den Kelchcentren befindlichen Sclerenchym bei unregelmässigem Verlaufe des Septocostalradien zuweilen ein Coenenchym-artiges Aussehen. Der Septalrand ist regelmässig gekörnelt und deutet auf einen trabeculären Aufbau hin. Säulchen papillär häufig mit mehreren Sternleisten verschmolzen." There

---

[1] Ueber die verwandschaftlichen Beziehungen einiger Korallen Gattungen. Palaeontographica, 1882, Bd. XXIX. pp. 92–98.

[2] Eocäne Korallen aus der Libyschen Wüste und Aegypten, Palaeontographica, Bd. XXX., 1883, Pal. Theil, pp. 226–227, Pl. XXV. Figs. 45, 45*a*.

[3] Eoc. Korall. aus der Lib. Wüste, etc., *loc. cit.*

might be two reasons for questioning my generic reference: the first is, I have not stated whether the synapticulæ are true or false. As no thin section was made, this point of structure could not be determined. But I do not believe in the systematic value of dividing synapticulæ[1] into true and false. Whether the synapticulæ are true or false depends largely upon spacial relations, as do many other microscopic features of the coral skeleton. If the septa are crowded the synapticulæ are apt to be false, while if they are more remote from each other the synapticulæ are apt to be true. Figure 71, in Miss Ogilvie's "Microscopic and Systematic Study of Madreporarian Types of Corals,"[2] is a good illustration of this. This figure represents two adjoining septa of *Siderastræa.* Near the peripheral ends of the septa the synapticulæ are true, i. e. there are new calcification centers introduced to effect the junction of the opposing septal granulations; whereas, near the inner ends of the septa, where the opposing septal surfaces are close together, no additional centers of calcification are needed to make the junction of the granulations, so they fuse directly and form a pseudo-synapticula.

Probably another note should be added on the septal structure. The trabecular composition has already been noted. In the lower part of the calices the trabecular fusion seems perfect, but near the septal margins the fusion apparently may quite often be incomplete. Here pits are very distinct on the flat surfaces of the septa, should the septa be not completely perforated. This might be a second reason for the removal of the species from *Mesomorpha.*

It was not determined whether dissepiments are present or not.

Species of *Mesomorpha* occur in the Gosau Cretaceous and in the Eocene of the Arabian Desert. Pratz is of the opinion that *Thamnastræa ferojuliensis*, d'Achiardi, from the Italian Eocene, and *Thamnastræa balli*, Duncan, from the lower Eocene of India, also belong to this genus.

DENDRACIS, Edwards and Haime.

Dendracis cantabrigiensis, sp. nov.

Plate XLI. Figs. 4-6.

The corallum is composed of small slender branches from 3.5 to 8.5 mm. in diameter. The branch 3.5 mm. in diameter is 26 mm. long. There is no means of knowing to what length the thicker branches will attain. The calices are distributed in rather regular spirals; the usual diameter is 1 mm, and the distance apart also usually 1 mm. On very small branches some calices may have a diameter very slightly less than a millimeter, and may be a

---

[1] Consult G. von Koch: "Das Skelett der Steinkorallen," Festschrift für Carl Gegenbauer, 1896, p. 260.

[2] Phil. Trans. Roy. Society, 1896, Vol. 187, p. 244.

little more than a millimeter apart, but the average is as first stated. The calices on the upper side are not at all elevated above the cœnenchyma, but on the lower side they stand about 1 mm. above it. The outside of the projecting part of the corallite has distinct equal costæ corresponding to each septum. I observed no perforations between the costæ. The cœnenchymal surface is densely and minutely granulate; when the outer surface is worn away its porous nature is revealed. Septa : there are six septa larger and more prominent than the others; in each well preserved calice examined, *between each pair of larger septa is a pair of smaller septa.* The septa are stout, so far as could be made out solid, imperforate, and have entire margins. There is no columella.

Locality. Near Cambridge Station, south of Montpelier, St. James Parish, Jamaica (R. T. Hill, collector).

Types. Museum of Comparative Zoölogy, Harvard University.

Remarks. This species has considerable resemblance to *Dendracis haidingeri*, Reuss, from Oberburg, Steiermark,[1] also found at Castel Gomberto, Monte Grumi and Monte Viale, Italy. Felix[2] reports it from Gebel Auwēbet, Egypt. The following notes made on specimens in the Vienna Hofmuseum show the differences. The calices of *D. haidingeri* tend to be constricted above. There are two complete cycles of septa, with members of the third cycle sometimes present. On the lower side of the projecting part of a corallite there are two or more costæ for each septum.

PORITES, Lamarck.

Porites reussiana, Duncan.

1865. *Porites reussiana*, Duncan, Quart. Jour. Geol. Soc. London, Vol. XXI. p. 8 (original description), Pl. I. Fig. 2. Another reference, p. 7.

1868. *Porites reussiana*, Duncan, Quart. Jour. Geol. Soc. London, Vol. XXIV. p. 25.

Original Description. "The corallum is in more or less cylindrical branches, which leave the stem at an acute angle, and are often flattened, and always rugged and gibbous. The calices are large, irregular in size, and shallow. The columella is small, and there are sometimes more than six distinct pali. The septa are from eight to twenty-four in number. Diameter of calices often $\frac{1}{10}$ inch; that of the branches from $\frac{6}{10}$ to $\frac{13}{10}$ inch.

"*Locality.* Upper Clarendon District, Jamaica."

I saw the type in the collection of the Geological Society of London, and add a few notes to the above description. The usual number of cycles of septa is

---

[1] Denkschrift d. Wiener Akad. d. Wissenschaft. (Mat. Natur.), Bd. XXIII. 1st Abtheil, 1863, p. 27, Pl. VIII. Figs. 2–5.

[2] Felix, Zeitschrift d. deutsch. geolog. Gesellschaft, 1884, Bd. XXXVI. p. 424, Pl. III. Fig. 12.

three ; the arrangement into cycles does not appear perfectly regular and uniform, so Duncan's figures must be used with a qualification. In the best preserved portions there is no granulate area on the summit of the wall between the ends of the septa. Apparently the upper edge of the wall is acute in perfect material. Diameter of the calices 2.5 to 4 mm. ; the usual diameter is slightly less than 3 mm. The specimen does not permit the details of the pali (?) to be made out. It seems quite probable that the species is a *Litharœa*, and not a *Porites*.

LIST OF TEXT FIGURES.

EXPLANATION OF THE PLATES.

PLATE I.

Contour Map showing the Physiography of Jamaica.

PLATE II.

Geologic Map of Jamaica.

PLATE III.

Typical Blue Mountain Scenery, Blue Mountain Ridge. Road to Castleton.

PLATE IV.

Types of Blue Mountain Scenery.

Fig. 1. St. Catherine's Peak, Blue Mountain Ridge.
Fig. 2. Ascent of Blue Mountain.

PLATE V.

Blue Mountain Scenery near Newcastle Barracks.

PLATE VI.

Blue Mountains, Liguanea Plain, and Palisades near Kingston.

PLATE VII.

Bull Head Mountain, Clarendon Valley.

PLATE VIII.

Coast Border opposite Port Royal.

PLATE IX.

Types of Erosion.

Fig. 1. A central Basin near Catadupa.
Fig. 2. Sink Hole Topography in White Limestone.

PLATE X.

Canyon of Cobre River, Bog Walk.

PLATE XI.

Types of Cockpit Erosion in White Limestone.

Fig. 1. Cockpit Topography, St. James Parish.
Fig. 2. Remnantal conical Limestone Hill, Westmoreland.
Fig. 3. Remnantal Hills, Westmoreland; Limestone almost destroyed.

PLATE XII.

Survivals of Limestone Erosion.

Fig. 1. Remnantal Hill, Montpelier Formation. Morgan's Gut.
Fig. 2. Limestone Hills near Montpelier.

PLATE XIII.

Types of Coast Topography.

Fig. 1. Cabaritta Island and adjacent Mainland, Port Maria.
Fig. 2. South Coast near Yallahs, showing Coast Lowland, Manchioneal Level, Yallah's high Level, and White Horse Bluff.

PLATE XIV.

Types of Old Levels.

Fig. 1. Back Coast Border and Coast Plain, Falmouth.
Fig. 2. High Level back of Porus, about 1,000 Feet.
Fig. 3. Profile of Plateau overlooking St. Thomas, about 3,000 Feet.

PLATE XV.

White Horse Bluff and Bench, South Coast.

PLATE XVI.

Remnant of 100 Foot Coast Bench near Northeast Point.

PLATE XVII.

Manchioneal Bench, East End.

PLATE XVIII.

Indented Coastal Plain between Mulatto Bay and Manchioneal.

PLATE XIX.

Liguanea Plain, Palisades, and Port Royal Hill, Kingston.

PLATE XX.

Mangrove Hills (Pseudo Atolls) and Terraced Back Coast Border, Montego Bay.

PLATE XXI.

Type Outcrops of Formations.

Fig. 1. Folded Structure, Blue Mountain Ridge.
Fig. 2. Surface Weathering of Moneague Limestone, Moneague.

PLATE XXII.

Overthrown Folds of Eocene Richmond Beds, south of Montego Bay.

PLATE XXIII.

Richmond Conglomerates, Galinas Point. Sea Wall of Reef Rock.

PLATE XXIV.

Outcrop of Formations.

Fig. 1. Clays of Blue Mountain Series, St. Thomas-in-the-Vale.
Fig. 2. Montpelier Beds near Port Antonio.

PLATE XXV.

Outcrop of Older White Limestone near Ipswich.

PLATE XXVI.

Upper Part of Older White Limestones, Montego Bay Railway.

PLATE XXVII.

Buff Bay (Bowden) Formation.

PLATE XXVIII.

Lowest Elevated Reef, Northeast Coast. Detail of Surface in Foreground.

PLATE XXIX.

Elevated Reef Rock showing Large Coral Head.

PLATE XXX.

Elevated Reef Rock, Port Maria.

PLATE XXXI.

Elevated Reef Rock near Port Maria.

PLATE XXXII.

Old Elevated Reef Rock in Contact with Folded Eocene Strata near Barbican.

PLATE XXXIII.

Altered Structure of Old Elevated Reef Rock.

PLATE XXXIV.

Upland Topography of Jamaica, Montpelier Valley.

PLATE XXXV.

Topographic Evolution of Jamaica.

Fig. 1. Hypothetical Old Land, Pre-Tertiary.
Fig. 2. Restricted Land during early Tertiary Subsidence.
Fig. 3. Mid-Tertiary Expansion.
Fig. 4. Axes of old Tertiary Uplift, Dotted Lines. Axes of Mid-Tertiary Uplift, Solid Lines.
Fig. 5. Late Tertiary Degradation.
Fig. 6. Drainage of Jamaica.

PLATE XXXVI.

Figs. 1–4. Trochosmilia hilli, sp. nov. Fig. 1, natural size; Fig. 2, calice from above, about 1½ natural size; Fig. 3, costæ magnified; Fig. 4, view looking toward the septal margins, magnified, to show striæ crossing the septal margins and on the sides of the septa.

Figs. 5–7. Cladocora jamaicaensis, sp. nov. Fig. 5, section across colony, ⅚ natural size; Fig. 6, two branches, one showing lateral buds, natural size; Fig. 7, cross-section of corallite, to show septal arrangement, magnified 2½ times.

PLATE XXXVII.

Figs. 1–4. Stylocœnia duerdeni, sp. nov. Figs. 1, 2, general views of specimen, natural size; Fig. 3, portions of calices magnified to show pillars at their corners; Fig. 4, sections of corallites, magnified about 6⅔ times, to show septal arrangement.

Figs. 5–7. Multicolumnastræa cyathiformis (Duncan), gen. nov. Fig. 5, general view of a specimen, natural size; Fig. 6, several calices, enlarged 4⅙ times; Fig. 7, a calice more magnified, and made slightly diagrammatic to show the relations of pali to septa, etc.

PLATE XXXVIII.

Fig. 1. Multicolumnastræa cyathiformis (Duncan), gen. nov. Cross-sections of several corallites, magnified about 6⅔ times.

Figs. 2–4. Stiboriopsis jamaicaensis, gen. et sp. nov. Fig. 2, view of corallum from above, natural size; Fig. 3, a calice magnified 3 times, shows the paliform teeth on the inner edges of the large septa; all the septa are not distinct; Fig. 4, cross-section of several corallites, magnified about 4½ times, shows the abundant dissepiments and series joined by their costæ.

PLATE XXXIX.

Figs. 1–3. Diploria conferticostata, sp. nov. Figs. 1 and 2, views of two different coralla, natural size; Fig. 3, 1 cm. of a series on specimen represented by Fig. 1, enlarged.

Fig. 4. Diploria conferticostata, var. columnaris, var. nov., natural size.

Figs. 5, 6. Trochoseris catadupensis, sp. nov. Fig. 5, view from side; Fig. 6, view of calice; both natural size.

PLATE XL.

Figs. 1–4. Leptophyllia agassizi, sp. nov. Fig. 1, general view of specimen; Fig. 2, costæ enlarged, shows their trabecular nature and some synapticulæ between them; in many instances at the surface the trabeculæ are not fused together, in others they are; synapticulæ are more abundant than is represented; Fig. 3, a portion of a cross section magnified $3\frac{1}{3}$ times; Fig. 4, several septa more highly magnified, to show the synapticulæ. It is doubtful if there are any dissepiments, though some may be present.

Figs. 5–7. Turbinoseris cantabrigiensis, sp. nov. Fig. 5, view from side, natural size; Fig. 6, costæ (peripheral ends of the septa) enlarged, to show the synapticulæ between them; Fig. 7, portion of a section of a corallum to show synapticulæ between septa, magnified about 8 times. There also appear to be occasional perforations near the inner terminations of the septa.

Figs. 8–10. Turbinoseris jamaicaensis, sp. nov. Fig. 8, view of specimen from side, natural size; Fig. 9, view of calice from above, $1\frac{2}{3}$ natural size; Fig. 10, costæ (peripheral ends of septa) magnified to show synapticulæ between them.

PLATE XLI.

Figs. 1–3. Mesomorpha catadupensis, sp. nov. Fig. 1, view from above; Fig. 2, view of corallum in profile, both natural size; Fig. 3, several calices, magnified nearly 3 times.

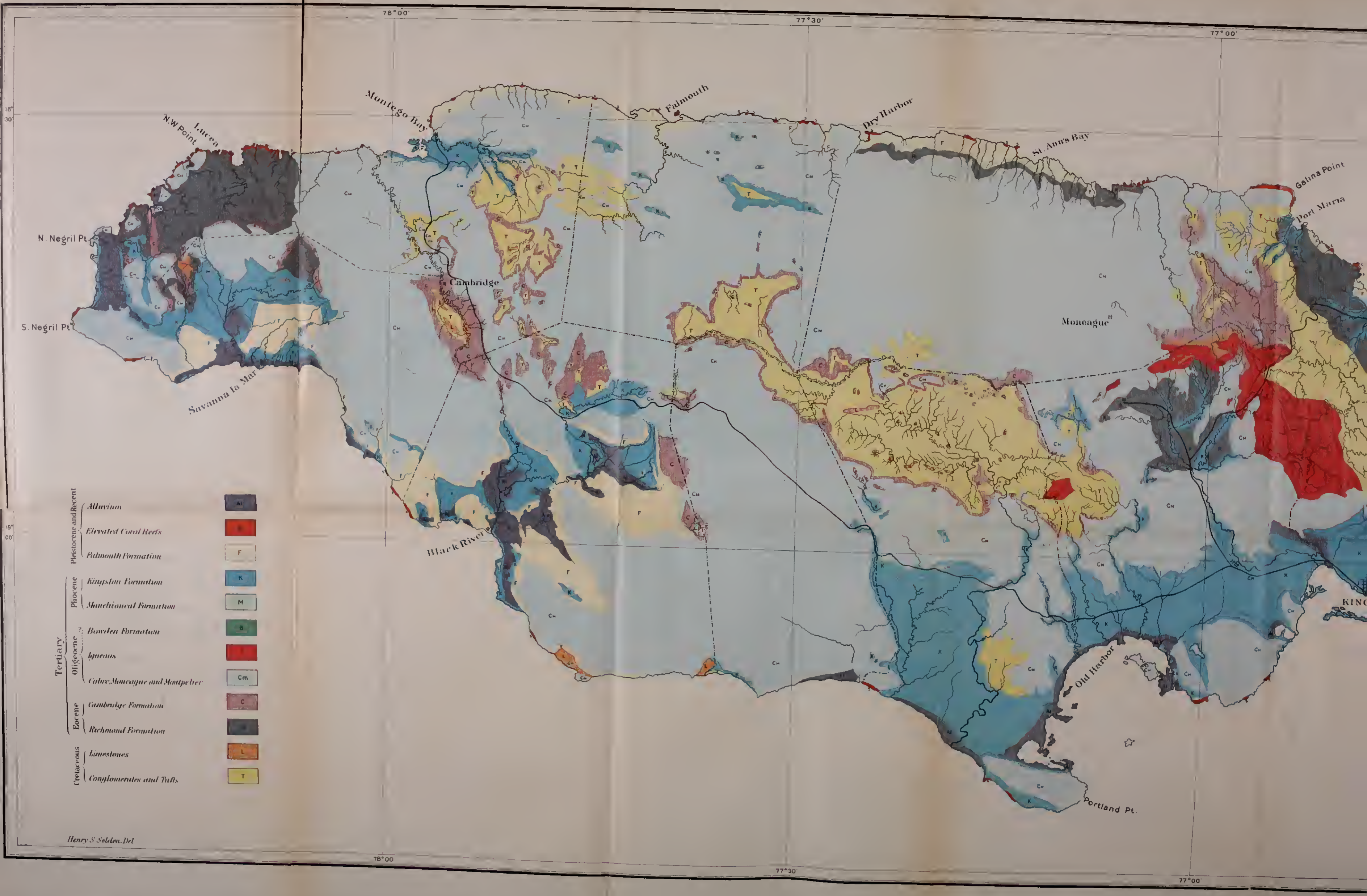
Figs. 4–6. Dendracis cantabrigiensis, sp. nov. Fig. 4, a fragment of a rather thick branch; Fig. 5, a young slender branchlet; both natural size; Fig. 6, several corallites and surface magnified.

PLATE. 1

CONFIGURATION OF JAMAICA


77°00'
76°30'
18° 30'
18° 00'
Dry Harbor
St. Ann's Bay
Galina Point
Port Maria
Browns Town
AMPSHIRE VALLEY
E G I O N
S T A N N
Moneague
Annotto Bay
Buff Bay
Port Antonio
ST. MARY
R I D G E
MT. DIABLO
Ewarton
N D O N
BULL HEAD
LUIDAS VALE
ST. THOMAS VALLEY
P O R T L A N D
B L U E M O U N T A I N S
JOHN CROW PLATEAU
Bog Walk
Chapelton
ST. ANDREW
CLARENDON
ST. CATHERINE
Manchioneal
Rio Cobre
Spanish Town
L I G U A N E A P L A I N
KINGSTON
S T. T H O M A S
Yallahs R.
Plantain Garden R.
Morant R.
S.E. Point
Bowden
Yallahs Bay
HEALTHSHIRE HILLS
Old Harbor
BRAZILETTO HILLS
Rio Minho
PORTLAND RIDGE
Portland Pt
77°00'
76°30'

JAMAICA


78°00'
77°30'
77°00'
18° 30'
18° 00'
N.W. Point
Lucea
Montego Bay
Falmouth
Dry Harbor
St. Ann's Bay
Galina Point
Port Maria
N. Negril Pt.
S. Negril Pt.
Cambridge
Moneague
Savanna la Mar
Black River
Old Harbor
Portland Pt.
KING
Pleistocene and Recent
Alluvium
Al
Elevated Coral Reefs
Falmouth Formation
F
Tertiary
Pliocene
Kingston Formation
K
Manchioneal Formation
M
Oligocene
Bowden Formation
B
Igneous
Cabre, Moneague and Montpelier
Cm
Eocene
Cambridge Formation
C
Richmond Formation
Cretaceous
Limestones
L
Conglomerates and Tuffs
T
Henry S. Selden, Del.

GEOLOGIC MAP
OF
JAMAICA

Compiled from Map of Sawkins and Brown
with additional data
by
Robert T. Hill.

SCALE
1 0 5 10 15 MILES
1898

B. Meisel lith. Boston

THE HELIOTYPE PRINTING CO BOSTON

TYPICAL BLUE MOUNTAIN SCENERY, ROAD TO CASTLETON.

1

St. Catherine Peak.

2

Up the Blue Mountains.

THE HELIOTYPE PRINTING CO. BOSTON

PLATE V.

THE HELIOTYPE PRINTING CO. BOSTON

BLUE MOUNTAIN SCENERY, NEWCASTLE BARRACKS.

THE HELIOTYPE PRINTING CO. BOSTON

BLUE MOUNTAINS, LIGUANEA PLAIN AND PALISADES NEAR KINGSTON.

THE HELIOTYPE PRINTING CO., BOSTON

BULL HEAD MOUNTAIN, CLARENDON VALLEY

THE HELIOTYPE PRINTING CO. BOSTON

COAST BORDER OPPOSITE PORT ROYAL.

Fig. 2. Sink Hole Topography in White Limestone, St. Ann Parish.

Fig. 1. A Central Basin near Catadupa.

THE HELIOTYPE PRINTING CO. BOSTON

PLATE X.

THE HELIOTYPE PRINTING CO. BOSTON

CANYON OF COBRE RIVER, BOG WALK.

1

Cockpit Topography.

2

Remnental Conical Limestone Hills.

3

Remnental Hills, Westmoreland Limestone.

THE HELIOTYPE PRINTING CO. BOSTON

Fig. 1. Remnental Hill of Montpelier Formation. Morgan's Gut.

Fig. 2. Limestone Hills near Montpelier.

THE HELIOTYPE PRINTING CO. BOSTON

Fig. 1. Cabaritta Island and adjacent Mainland. Port Maria.

Fig. 2. South Coast near Yallahs Point, showing Lowland, Manchioneal Level, Yallahs Level, and White Horse Bluff.

THE HELIOTYPE PRINTING CO. BOSTON

1

Back Coast Border and Coast Plain.

2

High Level Back of Porus.

3

Profile of Plateau Summit of St. Thomas Valley.

THE HELIOTYPE PRINTING CO. BOSTON.

THE HELIOTYPE PRINTING CO. BOSTON

WHITE HORSE BLUFF AND BENCH, SOUTH COAST.

THE HELIOTYPE PRINTING CO. BOSTON

REMNANT OF 100 FOOT COAST BENCH NEAR NORTHEAST POINT.

PLATE XVII.

THE HELIOTYPE PRINTING CO. BOSTON

MANCHIONEAL BEACH, EAST END.

THE HELIOTYPE PRINTING CO., BOSTON

INDENTED COSTAL PLAIN BETWEEN MULATTO BAY AND MANCHIONEAL.

THE HELIOTYPE PRINTING CO. BOSTON

LIGUANEA PLAIN, PALISADES AND PORT ROYAL HILL.

THE HELIOTYPE PRINTING CO. BOSTON

MANGROVE ISLANDS PSEUDO ATOLLS. MONTEGO BAY.

1

Folded Structure. Blue Mountain Ridge.

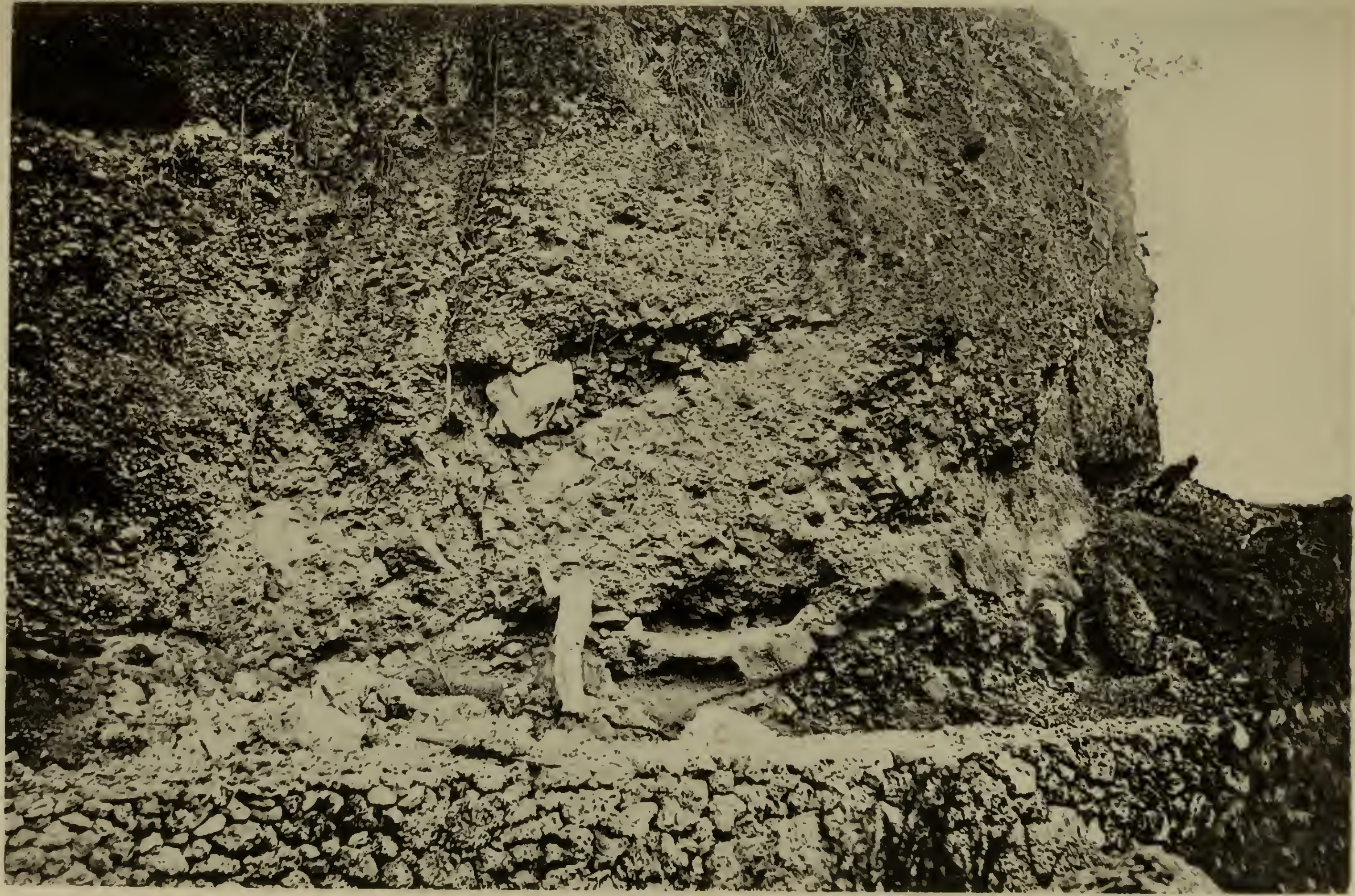
2

Surface Weathering. Moneague Limestone.

THE HELIOTYPE PRINTING CO. BOSTON

THE HELIOTYPE PRINTING CO., BOSTON.

OVERTHROWN FOLDS OF EOCENE RICHMOND BEDS.



THE HELIOTYPE PRINTING CO., BOSTON

RICHMOND CONGLOMERATES, GALINAS POINT.

Fig. 1. Clays of Blue Mountain Series. St. Thomas-in-the-Vale.

THE HELIOTYPE PRINTING CO. BOSTON

Fig. 2 Montpelier Beds near Port Antonio.

THE HELIOTYPE PRINTING CO. BOSTON

OUTCROP OF OLDER WHITE LIMESTONE NEAR IPSWICH.

PLATE XXVI.

THE HELIOTYPE PRINTING CO. BOSTON

UPPER PART OF OLDER WHITE LIMESTONES, MONTEGO BAY RAILROAD.

PLATE XXVII.

THE HELIOTYPE PRINTING CO., BOSTON

BUFF BAY (BOWDEN) FORMATION.

THE HELIOTYPE PRINTING CO., BOSTON.

LOWEST ELEVATED REEF, NORTHEAST COAST.

THE HELIOTYPE PRINTING CO., BOSTON.

ELEVATED REEF ROCK, SHOWING LARGE CORAL HEADS.

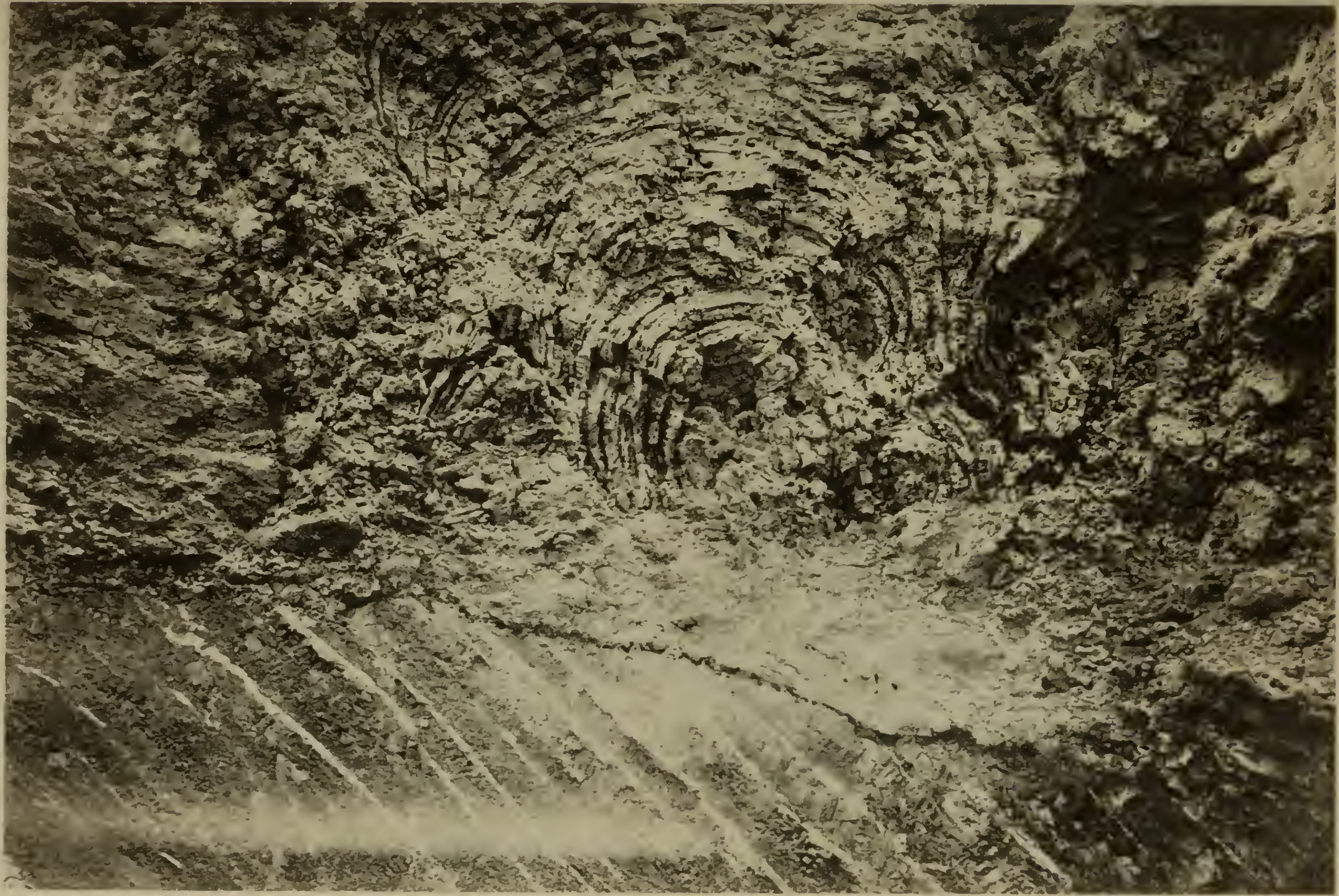
PLATE XXX.

THE HELIOTYPE PRINTING CO. BOSTON

ELEVATED REEF ROCK, PORT MARIA.

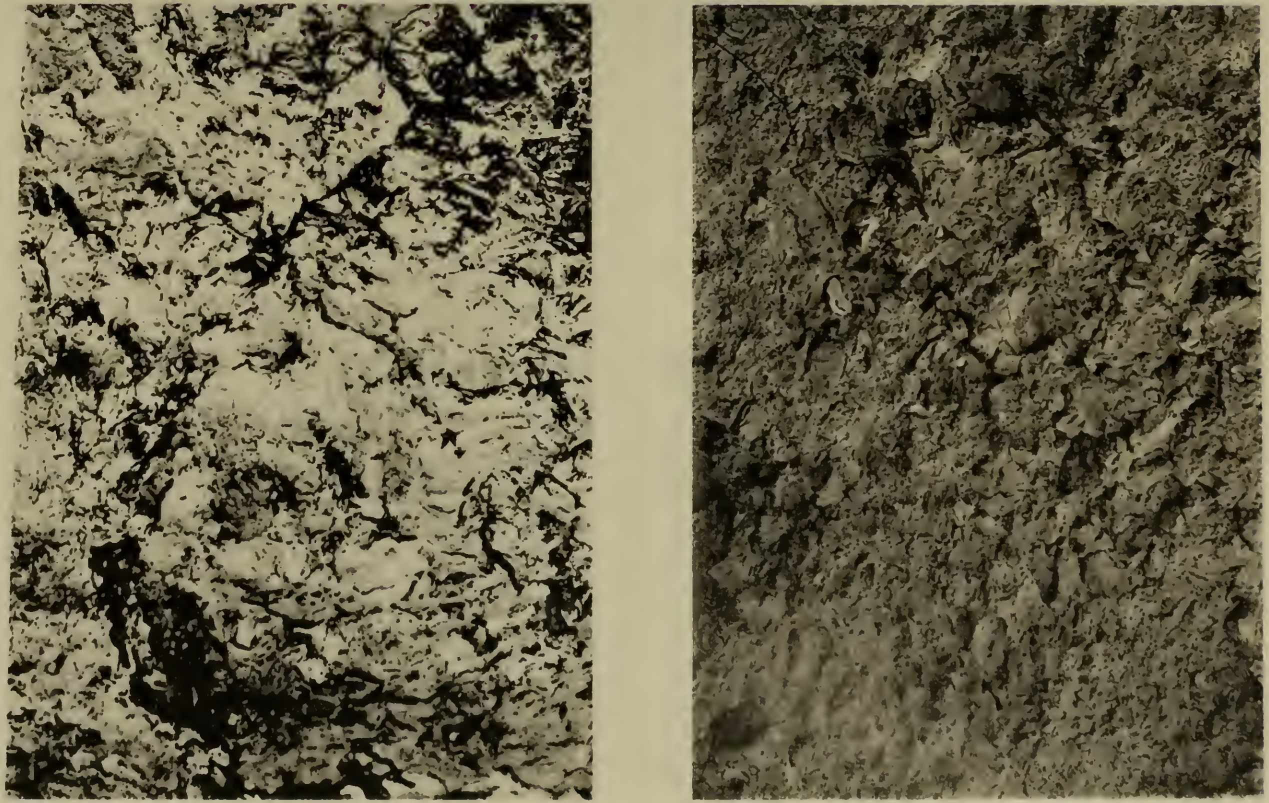
THE HELIOTYPE PRINTING CO., BOSTON

ELEVATED REEF NEAR PORT MARIA.



THE HELIOTYPE PRINTING CO., BOSTON

ELEVATED REEF IN CONTACT WITH FOLDED EOCENE STRATA.



THE HELIOTYPE PRINTING CO. BOSTON

ALTERED STRUCTURE OF OLD ELEVATED REEF ROCK.

PLATE XXXIV.

THE HELIOTYPE PRINTING CO. BOSTON

TOPOC

UPLAND TOPOGRAPHY OF JAMAICA. LIMESTONE HILLS OF MONTPELIER VALLEY.

THE HELIOTYPE PRINTING CO. BOSTON

UPLAND TOPOGRAPHY OF JAMAICA. LIMESTONE HILLS OF MONTPELIER VALLEY.

Hill. Jamaica.

(1)

Hypothetical Old Land. Pre-Tertiary.

ig 3.

(2)

Restricted Land during early Tertiary Subsidence.

(3)

Mid-Tertiary Expansion.

TOPOGRAPHIC E

THE HELIOTY

PLATE XXXV.

(4)
Axes of old Tertiary Uplift, Dotted Lines. Axes of Mid-Tertiary Uplift. Solid Lines.

(5)

Late Tertiary Degradation.

(6)

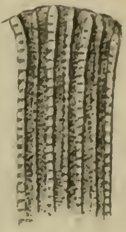
Drainage of Jamaica.

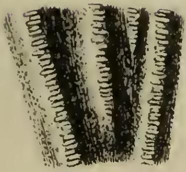
UTION OF JAMAICA.

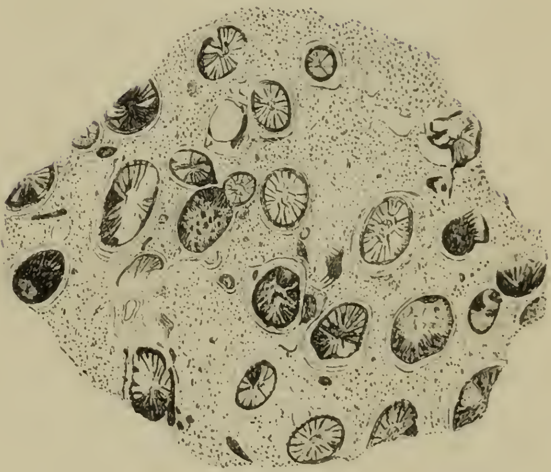
TING CO., BOSTON


1.

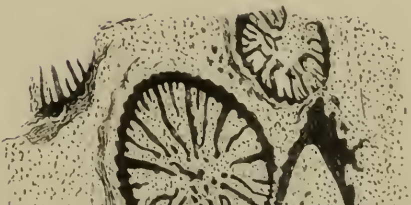

2.


3.

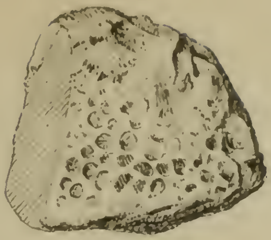

4.


5.


6.

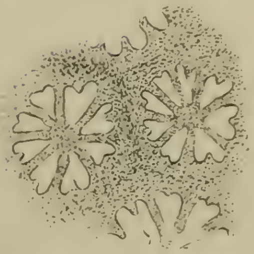

7.

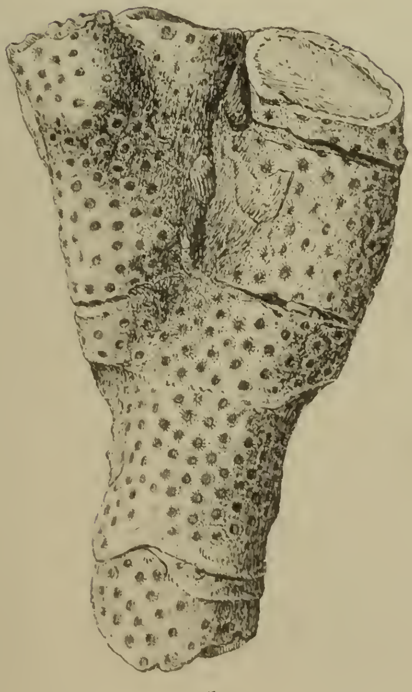
THE HELIOTYPE PRINTING CO., BOSTON

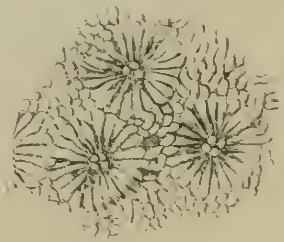

1.

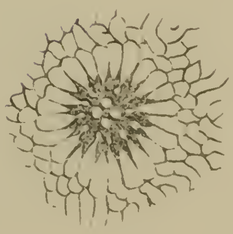

2.


3.


4.


5.


6.


7.

THE HELIOTYPE PRINTING CO., BOSTON

1.

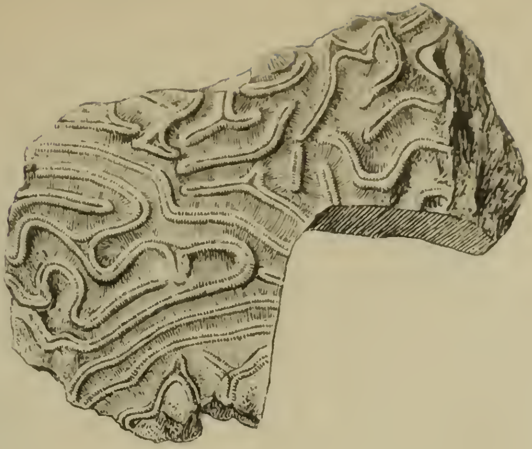
2.

3.

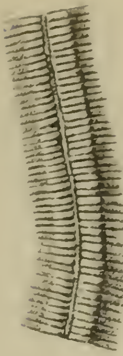
4.

THE HELIOTYPE PRINTING CO., BOSTON

Hill. Jamaica. Plate XXXIX.



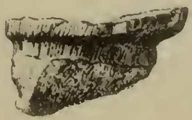
1.



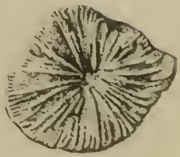
3.

2.

4.



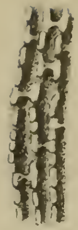
5.



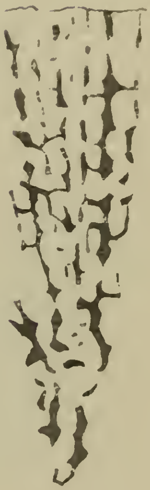
6.

THE HELIOTYPE PRINTING CO., BOSTON


1.

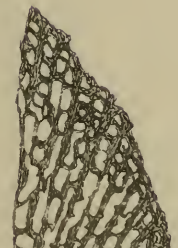

2.


3.


4.


5.


6.


7.


8.


9.


10.

THE HELIOTYPE PRINTING CO., BOSTON

BULLETIN

OF THE

MUSEUM OF COMPARATIVE ZOÖLOGY

AT

HARVARD COLLEGE, IN CAMBRIDGE.

VOL. XXXV.

CAMBRIDGE, MASS., U. S. A.
1899–1900.

University Press:
John Wilson and Son, Cambridge, U. S. A.

CONTENTS.

No. 1. — *Preliminary Account of Planktonemertes Agassizii, a new Pelagic Nemertean.* By W. McM. Woodworth.

Since the final report on the Nemerteans taken by the "Albatross" expedition cannot be ready for publication in the near future, owing to absences of the writer from Cambridge, the following brief preliminary account of a new pelagic Nemertean in the Albatross collections is now presented. No free swimming Nemertean has been described since the appearance of Moseley's[1] accounts of the two specimens of Pelagonemertes taken by the "Challenger." The Challenger material was afterward reported on in detail by Hubrecht,[2] and more recently Bürger,[3] in his great monograph, has made two distinct species out of the two specimens taken by the Challenger merely upon an examination of Moseley's sketches, basing his distinction upon the differences in the number of lateral diverticula of the intestine in the two specimens.

The form to be considered here, like Pelagonemertes, was taken in the Pacific Ocean, and in trawls from considerable depths. While the Challenger specimens came from latitudes well outside of the tropics, and from the western part of the Pacific, the specimens taken by the Albatross came from near the equator in the eastern part of the ocean. There are many points of resemblance between the two forms, resemblances in form, color, and even finer structure, which will not be discussed here, but a careful comparison with the detailed description by Hubrecht shows differences in structure of such fundamental importance that it has been necessary to establish a new genus in Moseley's family Pelagonemertidæ.

---

[1] Moseley, H. N. On Pelagonemertes Rollestoni, Ann. Mag. Nat. Hist., Vol. XV. p. 165, 1875. A Young Specimen of Pelagonemertes Rollestoni. Ibid., Vol. XVI. p. 377, 1875.

[2] Hubrecht, A. W. W. Report on the Nemertea collected by H. M. S. Challenger. Challenger Report, Zoölogy, Vol. XX., 1887.

[3] Bürger, O. Nemertinen. Fauna u. Flora Golfes von Neapel, Monographie XX., 1895.

Family PELAGONEMERTIDÆ Moseley.

Pelagic Nemerteans with a broad, flattened, leaf-like, gelatinous, very hyaline body. Rhynchocœlome extending nearly the entire length of the body. Proboscis unarmed. No cephalic grooves or organs of special sense. Intestinal tract dendrocœlous.

Genus PELAGONEMERTES Moseley.

Mouth and proboscis openings separate and distinct. Supraœsophageal ganglia larger than subœsophageal. Median dorsal vessel lacking. Lateral diverticula of the intestine comparatively few in number.

Genus PLANKTONEMERTES, nov.

A common external opening for the mouth and proboscis. Supraœsophageal ganglia smaller than subœsophageal. Median dorsal vessel present. Lateral diverticula of the intestine very numerous.

Planktonemertes agassizii sp. nov.

Five specimens were taken as follows: —

1. Station 3383, Lat. 7° 21′ 0″ N., Long. 79° 2′ 0″ W., 1832 fms. 6.51 A. M., March 8, 1891. Length 47 mm., greatest breadth 13.5 mm., greatest thickness 3 mm., color "orange." Figure 1.

2. Station 3361, Lat. 6° 10′ 0″ N., Long. 83° 6′ 0″ W., 1471 fms. 7.33 A. M., February 25, 1891. Length of body 24 mm., length of everted proboscis 28 mm., greatest breadth 9 mm., greatest thickness 2.5 mm., color "orange." Figure 2.

3. Station 3388, Lat. 7° 6′ 0″ N., Long. 79° 48′ 0″ W., 1168 fms. 6. 41 A. M., March 9, 1891. Length 14 mm., greatest breadth 5.5 mm., greatest thickness 1 mm., color "orange."

4. Same station as No. 3. Length 38 mm., greatest breadth 16 mm., greatest thickness 1 mm., color "orange." Figure 3.

5. Station 3406, Lat. 0° 16′ 0″ N., Long. 90° 21′ 30″ W., 551 fms. 6.47 A. M., April 3, 1891. Length 37 mm., greatest breadth 16 mm., greatest thickness 2 mm., color "pink." Figure 4.

The soundings given above indicate the depth at which the dredgings were made with an open trawl. The colors given in quotation marks are from notes taken by Alexander Agassiz on board the Albatross, and refer to the living animal. A water color drawing made by Mr. Agassiz of the living animal represented in Figure 4 shows the color as light brilliant scarlet, the intestinal diverticula and proboscis showing as bands of deeper color. The shape of the living animal as indicated by the sketch was like that of many of the larger marine Turbellaria, with parallel undular sides, and bluntly rounded at both ends.

All of the specimens except No. 2 (Fig. 2), which was not sectioned, proved to be females. In specimen No. 4 (Fig. 3) the ovaries were slightly developed, and could be seen only in sections. In the other three specimens the ovaries were prominent even before the specimens were subjected to a clearing reagent. Both specimens of Pelagonemertes taken by the Challenger were also females.

The chief differences between Pelagonemertes and Planktonemertes may be summarized as follows. In Pelagonemertes there are distinct openings for the mouth and proboscis, the former being ventral, the latter terminal; the dorsal cerebral ganglia are much larger than the ventral pair; the vascular system does not include a median dorsal vessel; the intestinal tract is comparatively simple, i. e. with few lateral diverticula, five and thirteen in the two specimens so far known. In Planktonemertes there is a common external opening for mouth and proboscis, slightly subterminal in position; the dorsal pair of brain ganglia are much smaller than the ventral pair; the vascular system includes a dorsal median vessel, which extends in the posterior portion of the ventral wall of the rhynchocœlom, and unites with the lateral vessels at the posterior end (this is seen in Figure 3); the intestine bears a great many (more than 50) lateral diverticula, and so profuse is the dendritic branching of these that in a transverse section the body appears to be honeycombed with cavities of varying size and outline, the gelatinous mesenchyma being but slightly developed.

A detailed study of this interesting form has already been made, but will be delayed in publication until the completion of the report upon the other Nemerteans taken by the expedition.

Museum of Comparative Zoölogy, Cambridge, Mass.,
May 10th, 1899.

EXPLANATION OF PLATE.

All Figures are of Planktonemertes agassizii.

The Figures were all of them drawn from unstained specimens cleared in oil of cloves.

All Figures magnified about $1\frac{3}{4}$ times.

1.

2.

3.

4.

W. McM. W. Del.

Boston Eng. Co.

Bulletin of the Museum of Comparative Zoölogy
AT HARVARD COLLEGE.
VOL. XXXV. NO. 2.

THE ANATOMY AND PHYSIOLOGY OF THE MOUTH-PARTS OF THE COLLEMBOLAN, ORCHESELLA CINCTA L.

BY JUSTUS WATSON FOLSOM.

WITH FOUR PLATES.

CAMBRIDGE, MASS., U.S.A.:
PRINTED FOR THE MUSEUM.
JULY, 1899.

No. 2. — *The Anatomy and Physiology of the Mouth-Parts of the Collembolan, Orchesella cincta L.*[1] By Justus Watson Folsom.

INTRODUCTION.

The group Apterygogenea (Apterygota) of Brauer comprises two distinct groups, termed the orders Collembola (Lubbock) and Thysanura (Latreille). The Collembola, to which Orchesella belongs, have been comparatively little studied by naturalists, owing in part, no doubt, to their being small, unobtrusive, and delicate insects. It is not surprising, in view of the small size of the Collembola, that entomologists have described their mouth-parts imperfectly and very diversely; on the other hand, it is remarkable that so much good work has already been accomplished by dissection, unaided by the improved modern methods of technique.

An excellent résumé of preceding descriptions of the mouth-parts has been given by Lubbock ('73), to whose account, however, I shall make certain additions.

Fabricius (1777) briefly mentions the palpi, mandibles, maxillæ, and bifid labium of Podura, the genus in which all Collembola were originally placed. His description, especially inapplicable as regards the palpi, has been commented upon by Latreille and Lubbock.

Latreille ('32), who noticed the labrum, was hardly more successful than his predecessor. His account, quoted in full by Lubbock ('73), is characterized by the latter as being "vague as well as inaccurate."

Bourlet ('39), in a brief paragraph, also quoted by Lubbock ('73), adds "une languette large, saillante, ciliée, à deux divisions, chaque division quadrifide." Like Fabricius, he erroneously supposed that there were two pairs of palpi, to which he gave names.

Nicolet ('41), in his classical memoir, gives an extended and careful description of the most salient characteristics of the mouth-parts, recog-

---

[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College, under the Direction of E. L. Mark, No. XCVI.

nizing the anomalous condition found in Achorutes. Although a few of his interpretations are inaccurate and his drawings rather imaginative, Nicolet decidedly improved upon preceding authors, and his work is of great historical importance.

Lubbock ('62, '73) enumerates and figures the mouth-parts of Smynthurus, Papirius, and Tomocerus, recognizing "second maxillæ," which "are closely attached to the ligula." His clear descriptions are quite accurate, as far as they go, and have never been disputed. His elaborate elucidation of the body-muscles of Tomocerus and Smynthurus, which no subsequent worker has attempted to repeat, leads one to wish that Lubbock had extended his patient researches to the muscles of the head.

De Olfers ('62) describes the coarse anatomy of the mouth-parts; his account agrees in the main with Lubbock's. De Olfers notices a "lingua" and "organa cochleariformia," the confluent margins of the latter forming a tube, as expressed in the following passage: "Margines organorum cochleariformium confluentes ut supra diximus tubulum formant, quem œsophagum appellamus." He is mistaken, however, in terming this tube the œsophagus.

For the sake of completenesss, I allude to the work of Laboulbène ('65) upon the general anatomy of Anurida maritima, the mouth-parts of which differ widely from the type prevailing among Collembola.

Meinert ('65), in his noted paper upon Campodea and Japyx, gives important generalizations upon the mouth-parts of insects.

Packard ('71) offers several suggestions upon the homologies of the mouth-parts of Collembola.

Tullberg ('72), in an especially important contribution to the study of Collembola, describes and figures the skeletal portions of the mouth-parts of Tomocerus vulgaris in some detail, showing the general structure and more evident relations of the parts, and adding much to the meagre accounts of other authors. This author discovered and figured salivary glands in Tomocerus flavescens.

Sommer ('84) describes the muscles of the pharynx and œsophagus.

Oudemans ('87), in a valuable anatomical work, gives a convenient summary of the results of preceding investigators of the anatomy of Collembola.

Nassonow ('87) figures the salivary glands of Lipura [Aphorura] ambulans.

Von Stummer-Traunfels ('91), in the only article devoted exclusively to this subject, discusses the mouth-parts of Collembola and Cinura with reference rather to their systematic value than to their anatomical detail. His accurate description, relating mainly to skeletal structures, is of great value.

Fernald ('90, '90^a) maintained that the so called "salivary glands" of Anurida maritima opened into what Tullberg named the linea ventralis, a median ventral groove terminating in the ventral tube.

Willem and Sabbe ('97) accept the results of Fernald, and infer that the well known exudation from the ventral tube is secreted by the large cephalic glands, which had been regarded as salivary in nature.

Upon the whole, our present knowledge of the mouth-parts of Collembola is fragmentary and far from complete; it is indeed insignificant, compared with what is known of the mouth-parts of most other orders of insects. The physiological side of the subject is practically untouched.

METHODS.

The mouth-parts of Orchesella cincta[1] were studied from dissections supplemented by serial sections. Dissections were necessarily made with needle-knives under dissecting or compound microscopes. First, the chitinous skeletons were prepared from alcoholic or fresh material by separating the mouth-parts in water and treating them with potassic hydrate. The immediate muscular attachments were then studied from dissections in water, weak alcohol, or glycerine, permanent preparations being made in glycerine. The normal relations of the mouth-parts were ascertained by rendering the entire head gradually transparent by weak potassic hydrate. At a certain stage in the process, the mouth-parts become prominent, owing to the pink or purple color they acquire from the solution and diffusion of the ectodermal pigment they contain. The stain thus obtained is permanent in glycerine or balsam dissolved in xylol.

For killing and fixing, preparatory to sectioning, the principal agents used were either hot water, hot alcohol, hot corrosive sublimate, or picro-sulphuric acid. Hot water or hot alcohol was as good as anything, causing a well relaxed condition; some of my best preparations were killed in hot alcohol of seventy per cent. Embedding was most conveniently per-

---

[1] The species used in this research has hitherto been called Orchesella flavopicta Pack.; it is, however, synonymous with the European O. cincta L., as I have ascertained by comparing Packard's types, which are preserved in the Museum of Comparative Zoölogy, with examples of the latter species given to me by Dr. C. Schäffer of Hamburg, by whom they were identified.

formed in watch-glasses. Serial sections of the head, from $3\frac{1}{3}\ \mu$ to $10\ \mu$ thick, were cut with a Minot-Zimmermann microtome, not only in the three principal planes, but also obliquely. All sections were affixed to the slide with Mayer's albumen mixture, stained on the slide and preserved in xylol balsam. The most satisfactory of many staining methods tried was Kleinenberg's hæmatoxylin followed by safranin. Victoria green, like safranin, is a good stain for chitin. For differentiating nervous structures, good results followed the use of Vom Rath's picric-osmic-acetic mixture. For elucidating the structure of the glossa and paraglossæ, the useful device of reconstruction in wax from sections was used.

Mouth, Pharynx, and Œsophagus.

The external appearance of the mouth has already been described by previous authors, beginning with Nicolet; indeed, the figures of Tullberg and von Stummer-Traunfels are so accurate that my own figure (Plate **1**, Fig. 1) is unnecessary, except for completeness. The mouth in repose is tightly closed by the labrum, labium, and palpi, the palpi fitting snugly into apertures on either side of the labrum. When the insect is eating, the tips of the mandibles and maxillæ may be seen projecting a little from the mouth to grasp the food, but at other times they are concealed within the capacious pharynx. In no other order of insects is this curious protrusion and retraction of the jaws found.

The pharynx is evaginated to form four deep pockets, two on either side. In the dorsal and ventral pair of pockets are situated respectively the mandibles and maxillæ (Fig. 2). The glossa and paraglossæ are median in relation to the other mouth-parts (Fig. 3). The lower wall, or floor, of the pharynx is the dorsal surface of the labium, and its upper or anterior wall is formed by the labrum.

The œsophagus ascends abruptly from the antero-dorsal part of the pharynx (Figs. 2 and 3), but quickly bends directly backward to the middle of the mesothorax, where it terminates in a valve. The œsophagus is a slender tube of uniform calibre, except that the lumen of its anterior portion gradually enlarges from behind forwards.

The anatomy of the fore-gut has already been studied, especially by Sommer ('85), whose excellent account of Tomocerus applies also to Orchesella in most respects. There is a distinct intima of uniform thickness (Fig. 4, *i.*), which I have shown by chemical tests to be chitinous, and in some individuals this is furnished with numerous small and irregular teeth, as mentioned by Sommer. In other specimens, however, no such structures are observed, and, if they are not artificially produced, their presence may possibly depend upon the interval which has elapsed since the last moult, the intima being shed and replaced at every moult. The epithelial wall consists of a single, well developed layer of pigmented cells (Figs. 3 and 4, *e'th.*). The boundaries of the individual cells are not well indicated, but the arrangement of their large round or oval nuclei is an indication of their size. These cells, being doubtless of ectodermic origin, are, like the permanent "hypodermal" cells, pigmented; the pigmentation extends back through the whole length of the œsophagus to the stomach. The epithelium is thrown into four or five prominent longitudinal ridges (Fig. 4). A delicate hyaline and homogeneous basement membrane (*mb. ba.*) is distinguishable, surrounding which is a single layer of circular or constricting muscles (Figs. 3 and 4, *c'stt.*). Around the anterior portion of the œsophagus, which Sommer designates as pharynx, the muscle fibres are quite stout, but farther backward they gradually decrease in size, as do their nuclei also, and finally disappear near the base of the head. As there is but one nucleus to each circular fibre, the statement of Sommer ('85, p. 696) that "Jeder Ring entspräche hiernach vielleicht je einer Muskelzelle" is unnecessarily cautious. The nuclei of the circular muscles lie, as others have observed, in a single (median dorsal) line (Fig. 3, *nl.*), and each nucleus is contained in a loose sheath which is external to the muscle proper. The condition in Orchesella is so nearly identical with that of Macrotoma [Tomocerus] that I can apply Sommer's ('85, p. 691) description without change to the former species: "Die Muskeln zeigen eine zarte feinkörnige Aussenschicht, Perimysium, in welcher in ziemlicher Anzahl kleine runde Kerne eingelagert sind. Dieses Perimysium ist besonders mächtig an den Muskelbündeln des Kopfes entwickelt." There are no longitudinal muscles enclosing the constrictors. All the muscles in the head are conspicuously striated, and, in Sommer's ('85, p. 691) words, "Die im Körper sich findenden Muskelbündel sind von verschiedener Dicke, die einfachsten bestehen wohl aus einer einzigen Muskelfaser, während die stärkeren aus einer Anzahl von Primitivbündeln zusammengesetzt sind, wie man an Querschnitten leicht sehen kann. Die Insertion der Muskelbündel an die Chitincuticula erfolgt nicht unmittelbar, sondern mittelst einer Sehne."

The pharynx and œsophagus are dilated by means of thirteen pairs of muscles (Fig. 3, *dil.*), situated as follows. Four short muscles (Fig. 3, *dil. phy.*) originate on the clypeus in paramedian positions, and immediately above the depressors of the labrum. The more dorsal pair pass directly backward, and are inserted side by side on the anterior wall of the pharynx (Plate **4**, Fig. 29, *dil. phy.*). The other pair are similar, but longer, and are inserted considerably below the preceding. These four muscles evidently pull upon the toothed epipharynx, and serve to withdraw it from the teeth of the paraglossæ. On the dorsal side of the anterior part of the œsophagus are seven pairs of long slender muscles which originate on the front, and are affixed to the chitinous intima of the œsophagus (Fig. 3, *dil. œ.*). The members of each pair are widely separated in origin, but converge as they approach the œsophagus, penetrate between the circular muscles and epithelial cells, and are inserted dorso-laterally on the intima of the œsophagus by means of short spreading tendons. The posterior three muscles of either side unite to form a single head. Opposed to these dorsal muscles are four pairs on the ventral side of the œsophagus, which have a common tendinous origin on the anterior margin of the tentorium, and run forward under the œsophagus, to which they are affixed ventro-laterally in the same manner as the dorsal muscles. The function of these dorsal and ventral muscles is manifestly to enlarge the gullet; thus they are antagonistic to the circular muscles previously described.

Before describing the mouth-parts, it is best to consider an endoskeletal structure which is intimately concerned with them.

Tentorium.

The tentorium of Collembola has never been described; to dissect it out is extremely difficult; in potash preparations it is partially destroyed, and it is not easy, owing to its form, to make serial sections of it which will permit of accurate reconstruction. The failure to recognize the tentorium of Collembola as being the place of origin of the principal cephalic muscles, and homologous with the same structure in Orthoptera and other mandibulate insects, has led students to assign an altogether undue importance to the "Stützapparat" of the ligula, which has erroneously been regarded as a sort of substitute for a tentorium. Partly as a result of this error, systematists have acquired an exaggerated opinion of the differences which separate Collembola and Thysanura from insects of other orders.

The tentorium (Figs. 5 and 6) is a chitinized structure in the middle of the head, underlying the œsophagus, extending upward on either side of it, and held in place by three pairs of arms diverging from the median plane. The ventral portion of the tentorium consists of a thin frontal plate (Figs. 5 and 7, *la. f.*), to the anterior margin of which are attached the ventral dilators of the pharynx (Figs. 3, 6, and 7), and under which may be seen certain of the muscles which adduct the mandibles (Fig. 7, *add. md.*). From the frontal plate diverge two anterior arms (Figs. 5 and 6, Plate **2**, Fig. 10, *br. a.*), which pass forward and downward, and become united with the paraglossæ (Plate **3**, Fig. 22, *br. a.*). The anterior arms bow outwards, and serve for the origin of the protrusors of the mandibles (Plate **2**, Fig. 14, *pr't.*). A second, or dorsal, pair of arms (Fig. 5, *br. d.*) diverge from the tentorium, and extend upwards on either side of the supra-œsophageal ganglion to the skull. Each dorsal arm is differentiated into two parts: a short proximal projection, which is part of the tentorium proper, and a long distal strand, less chitinized than the tentorium proper and distinctly fibrous in nature. As the strand shows no trace of cross striation and is chitinous, it can hardly be regarded as a muscle, but may be called a ligament. The third pair of arms project behind the tentorium (Figs. 5 and 6, *br. p.*). Each posterior arm curves downward, as well as outward, and consists distally of a ligament such as just described for the dorsal arms. The ligaments not only become continuous with the body of the tentorium, but also are securely attached to the heels (*cx.*) of the chitinous legs which support the ligula (Fig. 6).

The responses of the tentorium to stains and to potash prove it to possess three degrees of chitinization, the ligaments being least chitinous, the anterior arms strongly so, and the body of the tentorium intermediate in this respect. In preparations rendered transparent with potassic hydrate, whether subsequently stained with safranin or not, no trace of the tentorium is to be seen, except the anterior arms (Plate **2**, Fig. 10, *br. a.*) attached to the paraglossæ. When the tentorium is intact, the union of these arms with the rest of the endoskeleton is distinctly indicated by two curving sutures (Fig. 6, *sut.*).

The mass of muscles originating in the tentorium is at first bewildering; it is, nevertheless, possible to trace each muscle to its insertion, or, better, *vice versa*, and to infer its function. Having done this, I find no muscles which might protrude or retract the tentorium as Meinert ('65) claims for Japyx. This author (Meinert, '67, p. 367) says, "The opposite ends of the flexors of the mandibles, as well as of their tensors, in Japyx are attached to a chitinous plate situated between the mandibles, and steadied by a double set of muscles." The author figures the muscles referred to, and describes them as steadying, protruding, and retracting the chitinous plate. The homologous muscles of Orchesella, however, and probably of other Collembola, I believe serve severally, not to move the tentorium, but to dilate the œsophagus (Fig. 6, *dil. œ.*), to move the antennæ, and to effect certain movements of the entire head (Fig. 6, *mu.*). The tentorium appears to be immovably fixed in place by means of the chitinous arms and ligaments already described. As I shall show, contrary to the views of other authors, the protrusion and retraction of the mandibles and maxillæ are accomplished, not by corresponding movements of either the tentorium or the "Stützapparat," but in both cases by special muscles.

I shall now describe the mouth-parts in the order of their position, passing from the dorsal toward the ventral side of the head.

Labrum.

The labrum is trapezoidal in external aspect (Plate **1**, Fig. 1, *lbr.*) and wedge-shaped in sagittal section (Plate **1**, Fig. 3). The external surface bears three transverse rows of stout bristles. Between the labrum and clypeus is a deep transverse suture, formed by the infolding of the chitinous cuticula, which becomes thin to form a hinge (Fig. 3). At either end of the hinge, however, the cuticula is swollen into a conspicuous chitinous lobe, which projects into the pharynx to fit against a corresponding prominence of the mandible. This relation between labrum and mandibles was expressed by de Olfers ('62, p. 12) in the following passage, which has been overlooked by subsequent writers: "Margo posterior [labri] incrassatus et formam literæ C imitans deorsum inflexus, qua re fit, ut duo apices in cavum oris promineant, qui mandibulas sustinent." The mandibles, when at rest, are held in place by these protuberances, and the surfaces against which the mandibles are applied show stout parallel ridges, which perhaps hold the mandibles effectively. Immediately behind the distal margin of the labrum are minute teeth projecting into the mouth in a transverse row, which becomes interrupted in the middle (Plate **2**, Fig. 9, *de.*). Between these submarginal teeth and the margin itself is a transverse groove, in which I have found the apex of the glossa locked by means of a corresponding transverse ridge (Plate **1**, Fig. 3).

Tullberg ('72, p. 20) discovered an epipharynx in Tomocerus vulgaris, and briefly described it in a sentence which I translate: "The pharynx is bounded above [anteriorly] by a palate, or epipharynx, which consists of a chitinous membrane furnished with several toothed elevations." The same structure also occurs in Orchesella (Plate **2**, Fig. 9, *e'phy.*). The teeth of the epipharynx are directed towards those of the paraglossæ, in conjunction with which they appear to hold the food (Plate 4, Fig. 30).

The only muscles within the labrum are dilators of the pharynx (already described) and depressors of the labrum. The latter consist of a pair of muscles (Plate 1, Fig. 3, *dep.*), which originate on the lower margin of the clypeus in paramedian positions and converge downward toward the place of insertion, which is a chitinous ledge or shelf projecting inward from the anterior wall of the labrum. The contraction of these muscles doubtless closes the upper lip. I find no muscles which could conceivably elevate the labrum in opening the mouth. This being the case, the most satisfactory alternative which suggests itself is to assume that the external cuticula, which is bent like the letter S at the clypeo-labral suture (Plate 1, Fig. 3), possesses an elasticity sufficient to raise the labrum when the depressors are relaxed.

The labrum is supplied by a pair of short nerves, which originate from the œsophageal commissures where the latter merge into the supra-œsophageal ganglion. The nerves soon ramify and become distributed between the hypodermal cells of the epipharynx and other regions. The labrum is lined with a single layer of deeply pigmented hypodermis cells with moderately large round nuclei (Plate 1, Fig. 8, *h'drm.*). Near the base of the labrum and surrounding its central lumen, or body cavity, are grouped large oval nuclei (Fig. 8); each nucleus occupies the base of a filiform cell, which may often be traced directly to the base of one of the stout setæ (*set. sns.*) which cover the exterior of the upper lip. Sommer ('85, p. 703) regarded these in Tomocerus as sensory bristles, and the large oval nuclei as belonging to ganglion cells, although he gave little attention to the subject: "Was die Sinnesorgane betrifft, so muss ich mich darauf beschränken, dass sich eigenthümlich gestaltete Borsten, welche ich als Sinnesborsten bezeichne, an den Beinen, den Palpen, so wie der Ober- und Unterlippe vorfinden . . . sie stehen, wie ich das an denjenigen der Oberlippe direkt nachweisen konnte, mit Nervenfäden in Verbindung, welche aus einen Haufen von Nervenzellen hervortreten."

The so called "nerve-cells" have no direct connection with the central nervous system, however; they do adjoin a network of connective tissue (Fig. 8). I am disposed to consider the filiform cells as glandular in function, since they probably serve to produce the chitin of the sensory bristles. Deeper than the zone of large oval nuclei may be seen true ganglion cells, the nuclei of which are small and round, and in every respect like those in the periphery of the brain, within the mandibles (Plate **2**, Fig. 17) and elsewhere. A delicate nerve fibre from each ganglion cell penetrates between the glandular cells and appears to accompany the filiform processes of the latter as far as the cuticula.

MANDIBLES.

In general form, the chitinous skeleton of either mandible (Plate **2**, Fig. 10, *md.*) is a modified, elongated hollow cone, a cross section of the least modified part being almost circular (Plate **4**, Fig. 31, *md.*). The specialized regions consist of an anterior or dental portion, and a posterior portion, named by Tullberg the fulcrum, for articulation and muscular insertions. The apex of the mandible bears several sharp, incisive teeth on its median side (Plate **2**, Figs. 10, 11), invariably five on the right mandible and four on the left in the many cases I have observed. Behind the apex, also on the median side, is an extensive convex molar surface (Figs. 10, 12) composed of minute raised teeth arranged in quincunx. This denticulated molar surface is bounded ventrally by a row of several large rounded conical teeth (*de. v.*). On the posterior end of the molar face is a single blunt tooth at right angles to the median plane of the head. At the base of the mandible is a conspicuous triangular medioventral opening (Fig. 15, *of.*) through which the large adductor muscles enter. Near the anterior angle of this aperture, on the median dorsal side is a conical projection (Fig. 10, *pr'j. con.*), serving for the insertion of a rotating muscle. Other muscles are inserted on the mesal face of a dorsal and oblique *basal ridge* (Fig. 10, *crs. ba.*). The extreme base of the mandible, a prolongation of its dorsal wall, is formed into a blunt pivot (Fig. 13, *cdx.*), upon which the mandible turns. This pivot is peculiar in that it does not form part of an ordinary articulation ; it simply rests freely in a chitinous pocket or stirrup (Fig. 13, *sta.*), from which it is withdrawn when the mandible is protruded. The chitinous stirrup is formed from the cuticular lining of the cavity in which the mandible lies. The end of the stirrup against which the pivot bears when in motion is thickened, thus offering better resistance (Fig. 13, *cht.*). The pocket of the stirrup is fashioned from one extremity of an elongated, trough-shaped strap, the other end of which passes through the hypodermis and is continuous with the external cuticula of the head. I at first thought that the stirrup was free to swing forward and backward, carrying the mandible with it, but am now convinced that it is fixed in place and supports the mandible only when the latter is retracted.

Immediately behind the stirrup is a gland (to be described later) which may, as a secondary function, lubricate the pivot of the mandible.

The mandibles are situated in finger-like evaginations of the pharynx, and, except for muscular and nervous attachments, are unconnected with the pockets in which they lie, as is easily demonstrated in transverse sections of the mouth-parts. As von Stummer-Traunfels ('91, p. 220) observes, "Die mandibeln sind ganz frei in der Kopfkapsel gelegen, mit dem Stützapparate nur durch jener starken Muskel verbunden, und verdanken die Stellung, die sie einnehmen, nur noch dem Zuge der Kaumuskeln und einem Chitinvorsprunge an der Innenseite der Kopfkapsel, auf dem sie mit ihren hinteren Enden pivotiren und der diesem entgegenwirkt." It is evident that this arrangement facilitates the protrusion of the mandibles, which lie obliquely in the head (Plate **1**, Fig. 2, Plate **2**, Fig. 10), their bases close beside the skull on either side, while their apices converge, so that the opposing incisive teeth and molar surfaces meet in the sagittal plane. On account of the oblique position of the mandibles (Fig. 2), which in this agree with the maxillæ and tongue, it happens that microtome sections frontal or transverse in relation to the œsophagus are oblique in relation to these organs, and *vice versa.* Throughout this paper, when I refer to frontal and transverse sections, I shall use those terms with reference to the internal mouth-parts, conceiving the axial line between the mouth-parts to be their long axis, unless otherwise specified.

From the abundance of muscles in the head I have studied out the surprising number of ten distinct pairs which are concerned in moving the mandibles alone. This has been done by the study of serial sections in different directions and of dissections. The diverse directions taken by the muscles render them difficult to follow on sections in any single direction. On the whole, however, most may be learned from sections which are frontal, i. e. parallel with the plane in which the mandibles lie, and I shall describe the muscles as studied in successive frontal planes, beginning on the dorsal side. The order in which the muscles are numbered is necessarily somewhat arbitrary, but is chosen as being that in which they may with least difficulty be identified by any one who may wish to study the subject hereafter.

1. *Lateral Rotator.* This muscle (Plate **2**, Fig. 14, *1. rot. l.*) arises on the skull at the side of the head, passes forward and downward, crossing obliquely the dorsal surface of the mandible, and is inserted on the conical, medio-dorsal projection of the mandible. The same muscle is also represented as it appears in a transverse section of the mouth-parts

in Figure 16, *1. rot. l.* Its function evidently is to rotate the mandible in such a way as to raise the molar surface. The opposing muscle is designated as *3. ret. rot.*

2. *Abductor.* An extensive muscle (Fig. 14, *2. abd.*), which arises at the side of and anterior to the lateral rotator, passes obliquely forward and downward, and is inserted obliquely on the lateral surface of the mandible, which is excavated to receive the belly of the muscle. This is the only muscle which can act in opposition to the adductor (*9. add.*), and may also assist in the process of retraction.

3. *Retractor* and *rotator.* A slender muscle (Fig. 14, *3. ret. rot.*), which originates near the base of the skull in a dorso-lateral position, passes forward and downward, and is attached to the inner side of the basal ridge of the mandible described above.

4. *Retractor.* Although distinct from the preceding retractor, it follows nearly the same course (Fig. 14, *4. ret.*), but is more ventral; it originates nearer the median plane, and is inserted on the basal ridge immediately behind its companion. Both these muscles are adapted to withdraw the mandible into its socket after it has been protruded by muscles 5 and 6; No. 3, however, appears in addition to be the only muscle which is capable of rotating the mandible in opposition to Nos. 1, 7, 8, and 10, that is, so as to lower the molar surface.

5. *Lateral Protrusor.* The contraction of the outer of two slender cylindrical muscles (Fig. 14, *5. pr't. l.*) which originate on the anterior arm of the tentorium results in protruding the mandibles. It passes upward and backward from the tentorium along the mesal surface of the mandible, and is inserted immediately under the insertion of No. 3. Its function is doubtless to protrude the mandible by pulling its base forward.

6. *Mesal Protrusor.* This muscle accompanies No. 5 (Fig. 14, *6. pr't. ms.*), at the side of which it originates, but its course is more ventral, and its insertion is on the basal ridge just behind that of No. 5. The last two muscles are distinct, but have the same function, that of protruding the mandibles in opposition to muscles 3 and 4.

7. *Rotator.* A long stout muscle (Fig. 14, *7. rot.*), which begins on the side of a median dorsal chitinous projection near the base of the head. The muscle runs forward, outward, and downward, and terminates in a tapering pigmented tendon, which crosses under the base of the mandible (Fig. 15, *7. rot.*) and is inserted in the outer angle of the large triangular opening.

8. *Rotator.* A long, powerful muscle, which originates near the base

of the skull, being behind the preceding muscle and crossing the median plane (Fig. 14, *8. rot.*). It also ends (Fig. 15, *8. rot.*) in a tapering pigmented tendon, which is inserted close in front of the tendon of the last described muscle. Both muscles must act as rotators, twisting the mandible so that its molar surface moves upward and outward.

9. *Adductor.* This muscle, the only one hitherto mentioned by writers, is the most powerful muscle in the head. It originates principally on the tentorium (Fig. 14, *9. add.*), passes directly outward, penetrates the large triangular orifice of the base of the fulcrum (Fig. 15, *9. add.*), and is inserted on the inside of the lateral wall of the mandible. In addition, several of its fibres pass under the tentorium (Plate 1, Fig. 7, *9. add. md.*) and become continuous with similar fibres from the opposite mandible. Thus, these fibres must pull against each other with the effect of closing the jaws, but with this exception the adductors are attached to the tentorium. These strong muscles are counteracted by muscle No. 2.

10. *Rotator.* A long, slender muscle, beginning at the median dorsal line, passing forward, outward, and downward, and inserted by a pigmented tendon along with Nos. 7 and 8. To avoid confusion I have omitted this muscle from Figure 14, but the figures of No. 7 (Figs. 14 and 15, *7. rot.*) will serve perfectly well for No. 10, if it be remembered that the latter muscle lies under the former. It will be observed that I have described as many as four muscles (Nos. 1, 7, 8, and 10) which appear to rotate the mandible in the same direction; I see no other function for these muscles, however. The rotation in the opposite direction seems to be comparatively unimportant, being accomplished by a single slender muscle (No. 3), the primary function of which is perhaps retraction. Among the mass of antennal muscles originating on the tentorium there is one which might easily be mistaken for a rotator of the mandible, in function similar to No. 3. This muscle (Fig. 16, *mu. at.*) in some sections is moulded against the mesal surface of the conical projection to which is inserted rotator No. 1. In other preparations, however, in which the mandible happens to have been rotated so as to remove the projection from its proximity to the antennal muscles, it may be seen that the apparent rotator is really unattached to the chitinous projection.

The nerves to the mandibles are the first pair of the infra-œsophageal ganglion; they arise from either side of the anterior part of the ganglion, pass directly outwards, enter the mandible at the anterior angle of its large lumen and extend the length of the mandible and into fine canals in the chitinized apex. Each nerve fibre, soon after penetrating the mandible, becomes enlarged to contain a small round nucleus (Figs. 16 and 17, *cl. gn.*). The mandible is lined with a thick layer of deeply pigmented hypodermis (*h'drm.*), the confluent cells of which contain large oval nuclei (shown in cross section in Fig. 16), strongly contrasting in size with the nerve nuclei of the core of the mandible.

MAXILLÆ.

The maxillæ (Plate 3, Fig. 18) are about as long as the mandibles, and composed of two specialized regions: first, an anterior terminal movable lobe (Fig. 18, *cpt.*), which is subdivided into several smaller lobes and teeth; secondly, a posterior framework bearing muscles and supporting the terminal lobe and the palpus. The dorsal and outer portion of the terminal lobe is wholly chitinous and bears three stout, incurving claws (Fig. 19, *ga.*). This portion de Olfers ('62) compares with the galea of Orthoptera, and Packard ('71, p. 100), referring to the mouth-parts of Tomocerus plumbeus, writes, "The middle lobe, or galea, is nearly obsolete, though I think I have seen it in Smynthurus, where it forms a lobe on the outside of the lacinia." Von Stummer-Traunfels ('91, pp. 221, 223), however, says, "Es ist mir darum sehr zweifelhaft, ob dieser Theil des Kieferapparates die Deutung als äussere Lade wirklich verdient. . . . Bei Japyx noch zweifach gegliedert, ist er bei Campodea schon mehr reducirt und fehlt bei den Collembolen gänzlich." The careful comparative studies of the last mentioned author give much weight to his opinion. Underlying the tridentate lobe, or so called galea, are four chitinous lobes, or lamellæ, each of which bears on its inner margin a comb of fine teeth. Three of these lobes are falcate in form, and the fourth or inmost lobe (Fig. 19, *lcn.*) bears a prominent hook on its upper surface. These four fringed lobes probably represent the lacinia, or inner lobe, of other insects. The seven lobes and claws described appear to be firmly united basally, and, if so, cannot move separately, but must all move together by means of the articulation (Fig. 19, *atc.*) at the apex of the stipes. The movement is lateral only, and the adduction is accomplished by muscles which terminate in a slender chitinous rod (Figs. 18, 19, and 20, *bac.*) having the function of a tendon, and so named by von Stummer-Traunfels. This tendon is attached to the base of the inmost lobe of the lacinia.

Considering now the framework of the maxilla, the stipes (Figs. 18–20, *stp.*) is a stout chitinous structure, the form of which I may roughly compare to a long, shallow boat, pointed at both ends and somewhat crescentic in transverse section (Plate **4**, Figs. 29–32, *stp.*). The two thickened margins of the stipes are not parallel, however; the anterior portion of the dorsal margin is twisted toward the median plane of the head, as shown in Fig. 18. The ventral margin, moreover, is sharply incurved, as may be seen in transverse sections of the stipes (Plate **4**, Figs. 31, 32). The anterior end of the stipes is rounded where it articulates (Fig. 19, *atc.*) with the movable head (*cpt.*) of the maxilla. The stipes is strengthened by a somewhat oblique cross rib connecting the two margins; the rib is prolonged beyond the dorsal margin as a free projection (Fig. 18, *pr'j.*), the function of which I am unable to state; I find no attachment of muscles or other structures upon it. The base of the stipes is immovably fixed to the cardo, the junction being indicated by a distinct suture (Fig. 18, *sut.*). The cardo (Fig. 18, *car.*) is shaped like a shoe, the toe of which is attenuated to form a chitinous ligament (Figs. 18 and 20, *lig.′*), which is continuous with a ligament from the foot of the glossa, a suture showing that the now single ligament originated from the union of two. By means of this peculiar articulation — already noticed by de Olfers, Tullberg, and von Stummer-Traunfels — and the ligament from the glossa to be next described are permitted the movements of the maxilla as a whole. The toe of the glossa, namely, is extended into a long flexible chitinous ligament (Fig. 10, *lig.*), which is fastened to the outside of the base of the stipes. The length of this outer ligament evidently determines the extent to which the maxilla may be protruded, the supporting stalks of the glossa being stationary.

The rod of chitin previously mentioned as assisting in the adduction of the head of the maxilla is crescentic in cross section (Plate **4**, Figs. 29 and 30, *bac.*). Articulating with the base of the rod is a chitinous expansion (Fig. 18, *exp.*) for the insertion of four muscles. This expansion is nearly λ-shaped in cross section (Plate **4**, Fig. 31, *exp.*), there being a dorsal longitudinal ridge with a sloping wing on either side. In the angle between the ridge and the lateral wing is inserted muscle No. 7 of the maxilla. The opposite or mesal wing is prolonged backward in line with the rod (Figs. 18 and 20), and serves for the insertion of muscles Nos. 2 and 3. The base of the rod itself is prolonged into a short ligament (Fig. 18, *lig.*), by means of which the rod is connected with the adjacent corner of the base of the paraglossa (Fig. 18, *pa'gls.*). In order to show the ligament in Figure 18, I have represented the maxilla as withdrawn from the paraglossa. Normally, however, the rod (*bac.*) is situated in a lateral concavity of the ligula (Plate **4**, Figs. 29, 30, *gls.*), and consequently underlies the lateral margin of the paraglossa. The significance of the chitinized rod, or tendon, and its ligament, I shall presently show when describing how the head of the maxilla is abducted.

There are ten separate muscles which belong to each maxilla, excluding those of the palpi; like the muscles of the mandibles, they are most conveniently studied in frontal sections, although these must be supplemented by sections in other planes, as well as by dissections. The maxillæ are more complicated than the mandibles, and are correspondingly more difficult to understand; after long study, however, I have but little doubt as to their structure and movements.

1. *Retractor* and *abductor*. A long, slender muscle (Fig. 20, *1. ret. abd.*), which arises immediately beneath the origin of mandibular muscle No. 7 (Fig. 14) on the same median dorsal projection, and passes forward, outward, and downward to be inserted on the anterior concavity of the cardo (cf. Fig. 18). This muscle appears to retract and slightly abduct the entire maxilla by pulling the cardo backward. The retraction must be of slight amount, however, as the two ligaments which attach the cardo to the foot of the glossa prevent any extensive retraction or protrusion.

2 and 3. *Adductors*. Two cylindrical muscles, distinct from each other but lying side by side (Fig. 20, *2. 3. add.*, Plate **4**, Fig. 32), which arise on the dorso-lateral part of the skull, pass forward and downward under the adductors of the mandible, and by means of several slender tendons fuse with the posterior elongation of the chitinous expansion just described (Fig. 20, *exp.*). I believe their function is, in co-operation with muscles Nos. 4 and 7, to adduct the head of the maxilla. In Figure 20, muscles 2 and 3 are represented as interrupted, in order to show certain underlying muscles.

4. *Adductor*. A stout muscle (Fig. 20, *4. add.*), which arises on the most anterior surface of the cardo, passes forward and is inserted on the ventral surface of the chitinous expansion.

5. *Protrusor* and *adductor*. A slender muscle (Fig. 20, *5. pr't. add.*), which begins on the side of the tentorium, goes outward and somewhat backward, and is attached to the anterior concavity of the cardo, just beneath the insertion of muscle No. 1.

6. *Protrusor* and *adductor*. Similar to the last in origin and direction, but more ventral and anterior in position (Fig. 20, *6. prt. add.*) and inserted on the most anterior surface of the cardo, just under the insertion

of No. 4. Muscles Nos. 5 and 6 both appear to have the same function, i. e. to protrude and adduct the entire maxilla by pulling upon the cardo. Protrusion may evidently take place until the outer ligament (Plate **2**, Fig. 10, *lig.*) has become tense, whereupon additional contraction would produce adduction of the maxilla.

7. *Adductor.* A stout mass of muscle fibres within the maxilla (Fig. 20, *7. add.*) arising along the base of the stipes and inserted on the lateral aspect of the chitinous expansion (Plate **4**, Fig. 31, *7. add.*). This large muscle passes under the free dorsal projection of the stipes, to which it does not appear to be fixed. The four muscles numbered 2, 3, 4, and 7, which are all attached to the chitinous expansion, which in turn is articulated with the chitinous tendon (*bac.*) from the head of the maxilla, probably adduct the head of the maxilla by retracting the rod, so that the claws of the head are rotated in a frontal plane toward the claws of the opposite maxilla, in order to meet them and grasp food; this function of the maxillæ seems to be the most important one, judging from the number and size of the muscles which close the claws.

8. *Retractor* and *adductor.* A short muscle on the ventral side of the maxilla (Fig. 21, *8. ret. add.*), its course also shown faintly in Figure 20, arising on the stalk of the glossa, passing obliquely forward and outward, and inserted on the inflexed lower margin of the stipes. This muscle must retract the stipes and draw it toward the median plane.

9. *Protrusor* and *adductor.* A broad, oblique muscle (Fig. 21, *9. pr't. add.*) beneath and running at right angles to the last, also arising on the stalk of the glossa and inserted on the upturned border of the stipes. By this muscle the stipes is protruded and also drawn towards the glossa.

10. *Adductor.* A short, stout muscle (Fig. 21, *10. add.*, Plate **4**, Fig. 31) passing directly outward from the stalk of the glossa to the inflexed margin of the stipes. The function of this muscle is clearly to pull the stipes towards the glossa, i. e. to adduct it.

I believe that the three muscles last described have the important function of abducting the head of the maxilla, or separating the claws of the maxillæ preparatory to grasping food. The head of the maxilla is adducted by muscles numbered 2, 3, 4, and 7, which, by retracting the rod, cause the head to rotate upon the end of the stipes. The reverse movement, the opening, appears to be accomplished by the successive retraction and adduction of the stipes by means of muscles Nos. 8, 1, and 10, during which the head rotates upon the end of the chitinous rod until in the position shown in Figures 18 and 19. In this condition the rod has evidently been pulled back, as far as its ligament (Fig. 18 *lig.*) allowed, by the action of the adductors of the head, and must manifestly be thrust forward before it can again be withdrawn. This protrusion of the rod appears to be a necessary result of the simple protrusion of the stipes, by muscles Nos. 9, 5, and 6; the advancing stipes pushes forward both the head and the attached chitinous rod until the ligament of the latter has become tense in the opposite direction.

The above explanation of the movements of the terminal portion of the maxilla is the only one I can offer, after long study. It appears reasonable to me, and accounts for the presence of the peculiar chitinized tendon or rod of the maxilla, as well as the unique ligamentous connection between the maxilla and paraglossa. I shall again refer to this connection when describing the palpi.

The maxillæ are supplied by the second pair of nerves from the infraœsophageal ganglion; each nerve begins at the side of the ganglion, a little behind the mandibular nerve, goes directly outwards for a short distance and enters the maxilla at the posterior end of the chitinous expansion; a branch is soon given off to the palpus. The anterior portion of the maxilla is occupied by a core (Fig. 19, *gl. et n.*) of filamentous cells which penetrate into the lobes of the lacinia through an orifice in the base of the head of the maxilla; these filamentous cells are of two kinds and precisely similar to those already described for the labrum, the base of certain cells containing a large oval nucleus (Fig. 19), while intervening cells are ganglionic, with small round nuclei. The maxilla is lined with a single layer of confluent hypodermis cells, deeply pigmented and containing round nuclei of moderate size.

PALPI.

The palpi, consisting of but one pair, are of special interest because von Stummer-Traunfels considered them quite anomalous in position, having described and figured them as separated from the maxillæ and joined to the paraglossæ. This author ('91, p. 226) emphasizes, "Die grosse Unwahrscheinlichkeit, dass der sogenannte Maxillartaster der Collembolen wirklich zur Maxille gehört, indem diese von jenem vollständig getrennt ist und derselbe vielmehr in innigem Verbande mit der Paraglossen steht." This view originated, however, with Tullberg, as his description and figure show. I believe that this view is erroneous, and that the palpi unquestionably belong to the maxillæ; I shall show how the mistake mentioned might easily be made.

Each palpus (Fig. 18, *plp.*) is finger-shaped and composed of but a single segment. The extremity is provided with five bristles, each seated upon a tubercle, the proximal bristle and its tubercle being much the largest. The palpus lies dorsal to its maxilla and its base is attached to the chitinous expansion of the maxilla, as represented in Figure 18. It will be noticed that the palpus joins the expansion close to the ligament which unites the chitinous rod (*bac.*) and the paraglossa (Fig. 18, *pa'gls.*), so that the ligament might readily be mistaken for a prolongation of the palpus. Careful study shows, however, that the ligament is directly continuous with the rod, and not with the palpus. If the palpus is connected with the paraglossa at all, the attachment is only of the most incidental nature.

The palpus contains at least two longitudinal muscles, which arise from the chitinous supporting structure at its base and extend to its free extremity. The palpus is lined with confluent, deeply pigmented hypodermis cells; beneath the setæ are filiform cells, each with an enlarged base which contains a large oval nucleus; a condition also found in the labrum and labium.

GLOSSA AND PARAGLOSSÆ.

These structures have been briefly mentioned and differently named by several authors. By de Olfers ('62) they were called respectively *lingua* and *organa cochleariformia;* by Lubbock ('62), *ligula* and *second maxillæ;* by Meinert ('65), *lingua* and *paraglossæ;* by Tullberg ('72), *lamina hypopharyngis inferior* and *laminæ hypopharyngis superiores*; finally, by Grassi, Oudemans, and von Stummer-Traunfels, *ligula* and *paraglossæ.* Careful comparison has led me to believe that the ligula and paraglossæ of Thysanura are the equivalents, respectively, of the glossa and paraglossæ of other mandibulate insects; the Thysanura, however, exhibit the more primitive or generalized condition of tongue, which is not consolidated with the labium. The term ligula, at present, is properly applied to the glossa and paraglossæ taken together, rather than to the glossa alone.

The *paraglossæ* (Plate **3**, Fig. 22, *pa'gls.*) are two membranous, transparent, chitinous appendages attached to the dorsal surface of the glossa. The basal half of either appendage is firmly united to the glossa, and therefore can have no power of independent movement. The apical half is a free lobe, oval in cross section (Plate **4**, Fig. 28, *pa'gls.*). A paraglossa viewed from above presents somewhat the form of an isosceles triangle with a rounded apex and nearly equalling the glossa in length. The lateral surfaces are strengthened by being thicker and more rigid (Fig. 22, *cht.*). The inner margins of the two appendages approximate each other, leaving an elliptical aperture however (Fig. 22, *lu.*), beneath which may be seen a single median row of fine teeth belonging to the dorsal surface of the glossa (Fig. 22). The inner edge of either paraglossa is furnished with teeth along its posterior half. Considering the teeth successively, the most anterior are blunt and lie in a frontal plane; as we pass backward the teeth are not only longer and more slender, but, as they approach the median plane, also become gradually erect, so that at length the posterior teeth project in a parasagittal plane. This change in direction is brought about by a curvature of the edge of the paraglossa, the dorsal surface of which, in passing backward, gradually becomes more concave, causing the inner margin to curve upward, or forward, as the parts naturally lie. The concavity of the paraglossa matches the convexity of the molar surface of the mandible on the same side of the head, and the sagittal teeth of the paraglossæ normally intervene between the grinding faces of the mandibles (Plate **4**, Fig. 30, *md.*).

I find no well marked bundle of nerve fibres for the glossa and paraglossæ, but many separate fibres, each from a ganglion cell, are given off directly from the infra-œsophageal ganglion and penetrate between the hypodermal cells of the tongue, which are for the most part attenuated like the filamentous chitin-forming cells of the labrum.

The *glossa* (Plate **3**, Fig. 23), situated under the paraglossæ which it bears, is an elongated, unpaired, chitinous organ, the median furrows of which however probably indicate its derivation from a paired condition. Three regions may be distinguished: a terminal, free portion (Plate **1**, Fig. 3, *gls.*), an intermediate region with which the paraglossæ are fused, and a basal part, consisting of a pair of supporting stalks (*pd.*, Plate **2**, Fig. 10, Plate **3**, Figs. 22, 23). The free portion is oval in cross section (Plate **4**, Fig. 28, *gls.*); viewed from above (Plate **3**, Fig. 23) it terminates in front in an oval transparent lobe, across the end of which is a subterminal dorsal fold or ridge (Fig. 23, *pli.*), which interlocks with the labrum (Plate **1**, Fig. 3). The upper surface of the terminal lobe is provided on either side with a curving row of minute teeth (Fig. 23, *de.*) borne upon a thickened chitinous ridge. A median dorsal groove is present, in the course of which occurs what appears to be an opening (Fig. 23, *of.*) into the interior of the glossa. The intermediate region bears the paraglossæ, the basal halves of which merge with the glossa to form a single body; the cavity of either paraglossa also becomes confluent with that of the glossa (Plate **4**, Fig. 29). The lateral surfaces of the glossa are strongly concave (Plate **4**, Fig. 29), and receive the maxillæ, which lie adjacent to it. The maxillæ normally approach each other in the space left free between the upper surface of the end of the glossa and the under surfaces of the paraglossæ (Plate **1**, Fig. 3). The glossa is prolonged behind into a pair of slender, diverging, chitinous stalks or legs, by von Stummer-Traunfels termed the "Stützgerüst" (Figs. 10, 22, 23, *pd.*$'$). The enlarged base of each bears some resemblance to a human foot (*pd.*). The toe of the foot, which underlies the cardo of the maxilla, is attenuated into a long ligament which bends around the base of the cardo and attaches itself upon the outside of the base of the stipes (Fig. 10, *lig.*). The dorsal edge of the stalk is extended and modified to form a second ligament (*lig.*$'$), which, as previously stated, unites with a ligament from the toe of the cardo, a suture remaining to indicate where the two ligaments united.

The glossa is lined with a layer of well developed pigmented epithelium, containing large oval nuclei (Plate **1**, Fig. 3). A central tubular cavity is left, however, which is a branch of the general body cavity. The possible glandular nature of the tongue will be discussed later.

LABIUM.

The labium, or lower lip (Plate **3**, Fig. 24), is a single plate, formed by the union of two lateral plates, as indicated by a conspicuous median suture. Either half of the labium is divided by sutures into three distinct regions. The anterior region (*plp.*) bears five prominent tubercles, from the apex and sides of which project several subulate bristles. The intermediate region (*men.*) is of lunate form, thickly chitinized along the mesal margin, hinged along the posterior curving suture, and bears a few setæ. The posterior and most extensive region (*sb'men.*) is almost divided into two sclerites by an oblique suture, which however becomes obsolete at its posterior end. This third region is laterally fixed to the clypeus, is posteriorly distinguished from the gula by a deep oblique suture, and bears a number of setæ, many of which are barbellate. The halves of the labium are firmly fused together, except anteriorly, and are not easily separable; but the fusion involves only the ventral margins of the mesal faces of both plates, in such a way that a trough or gutter is left within the buccal cavity (Fig. 25, and Plate **4**, Figs. 28, 29, *sul.*). At the posterior end of the median longitudinal suture begins the *linea ventralis* of Tullberg (Fig. 24, *ln. v.*), an external median ventral gutter formed by two thin longitudinal ridges of chitinous cuticula, the margins of which approach each other without uniting, as is shown by transverse sections (Figs. 26 and 27). This linea ventralis may be traced back along the median ventral line of the body as far as the lobes of the ventral tube, which is a median appendage of the first abdominal segment; between the body segments, however, the linea ventralis suffers considerable interruption. I shall return to this peculiar structure when considering the glands of the head.

The morphology of the labium of Collembola has never been elucidated, and is difficult to understand, even after careful comparison with other orders of insects. I am at present able to offer only a few suggestions upon the subject. The glossa and paraglossæ have no connection with the labium, although fused with each other. Labial palpi have been regarded as absent by other authors, yet the anterior regions of the labium, which are doubtless tactile in function, may perhaps be palpi in a morphological sense also. If a maxillary palpus of this same insect with its setigerous tubercles be imagined as having become sessile, through a shortening of the stalk, we have a counterpart of the terminal lobe of the labium. I see no serious objection to considering the two remaining sclerites of either side as mentum and submentum, although the presence of a nearly obsolete suture, tending to divide each submentum into two sclerites, certainly complicates the matter.

The movements of the labium are effected by five pairs of muscles, of which three are elevators and two depressors. I shall describe these muscles as they appear in successive sagittal sections, beginning at the median plane.

1. *Posterior depressor.* This is the shortest of the labial muscles, and is inserted on the ventral wall close to the median plane (Plate **1**, Fig. 3, and Plate **3**, Fig. 25, *1. dep. p.*). This muscle arises from the dorsal surface of the thick chitinous wall of the salivary duct and runs forward, downward, and inward to its insertion. It opens the mouth by pulling upon the under surface of the lower lip. All the lateral muscles are seen tranversely sectioned in Plate **4**, Figures 28–31.

2. *Mesal elevator.* This muscle runs along the upper and inner margin of each half of the labium (Figs. 3 and 25, *2. lvt. ms.*). The insertion is at the anterior extremity, and the origin close beside that of the preceding muscle, on the same chitinous duct. The function is to close the mouth by diminishing the extent of the inner surface of the labium.

3. *Anterior depressor* (Fig. 3, *3. dep. a.*). In origin, course, and function this muscle is similar to the posterior depressor; it is more lateral, however, and is inserted somewhat in advance of its companion.

4. *Middle elevator.* This muscle (Figs. 3 and 25, *4. lvt. m.*), which is longer than any of the preceding, arises from the posterior arm of the tentorium, bends downward, follows the inner wall of the labium directly forward, and terminates at the distal extremity of the labium. The function of the muscle is like that of the mesal elevator.

5. *Lateral elevator.* This is the longest and most lateral of the labial muscles (Fig. 25, *5. lvt. l.*). As to insertion and course it is similar to the middle elevator, but its origin is more posterior and dorsal, being upon the dorsal chitinous surface of the salivary duct. The principal difference between the three elevators described is that, by reason of their different insertions, they may raise different portions of each terminal movable lobe of the labium.

The labium is supplied by the third pair of nerves from the infra-œsophageal ganglion; the nerves originate a little to one side of the median plane from the ventral part of the ganglion, and pass forward, downward, and outward into the dorsal portion of either half of the lower lip. The labium is lined with a single layer of confluent, pigmented, hypodermal cells, with moderately large, round nuclei. Beneath the bristles of either half of the labium is a cluster of large oval nuclei, which belong to filiform cells exactly like those of the labrum; ganglionic cells may also be distinguished, which bear the same relations as those described for the upper lip.

THE CEPHALIC GLANDS.

The glands in the head of Orchesella comprise two pairs, the principal pair lying in the base of the head and occupying most of the region behind the maxillæ (Plate **1**, Fig. 2, *gl.*). Each of the larger glands consists of a single tube, which is thrown into several longitudinal convolutions. The deeper half of the tube is of larger caliber than the remainder, and constitutes the secretory part (Plate **4**, Fig. 32, *gl.*), while the more superficial half is distinctly smaller in caliber and simply conductive in function (Fig. 32, *dt.*). The chitinous evacuating duct of either side finally runs forward and downward on the mesal side of the gland, passing just beneath the maxillar evagination and trending toward the median plane. The ducts open separately on either side of the extreme proximal portion of the labial cleft (Plate **3**, Fig. 25, *dt.*). As the mesal surfaces of the two halves of the labium are fused together along their ventral edges only, a trough or gutter (*sul.*) is left above the line of fusion, through which the secretion may run forward to the mouth opening.

The epithelium of the glandular portion consists of large polygonal cells (Plate 4, Fig. 33), containing large oval nuclei. The granular cytoplasm is confined to the base of each cell, where it forms a dense, deeply staining mass; the portion of the cell adjacent to the lumen of the gland contains a clear non-staining substance, which sometimes appears to occupy large vacuoles and is probably secreted fluid. A delicate chitinous intima may be distinguished as well as a thin basement membrane. The dorsal wall of the gland proper is connected to the ventral wall of the maxillary pocket by columnar cells (Fig. 33) with small oval nuclei and fibrous cell body. These are probably modified hypodermis cells; between them may be seen unmodified cells, which are flattened against the cuticula.

Transverse sections show the evacuating duct to be chitinous throughout its whole length (Fig. 34), the component cells being indicated by small, round nuclei only. The basement membrane is thin, but the chitinous intima is thick.

In my account of the anatomy and function of the principal cephalic glands, I differ widely from Fernald ('90) and also from Willem et Sabbe ('97). According to Fernald ('90, p. 63), a curious anatomical relation exists between the "salivary glands" and the ventral tube or "vesicle" of Anurida maritima. I give the author's own words: "Passing forward [from the cleft of the abdominal vesicle] on the ventral median line of the body to a median cleft in the lower lip is a small tube, in the formation of which both hypodermis and cuticula take part. In the posterior portion of the head are a pair of glands which resemble salivary glands and which I regard as their homologues here. From these glands a duct leads forward and soon fuses with its fellow, and the median duct thus formed passes along the under surface of the buccal cavity to a median cleft of the lower lip, where, instead of emptying into the mouth, it turns downward and joins the ventral tube just described. This remarkable relation of the parts concerned I am unable to explain, although sure that no error of observation was made."

Willem et Sabbe ('97, pp. 131, 132) have recently offered an explanation of the peculiar relation which Fernald described but left without an interpretation; they claim that the ventral tube of Smynthurus is an adhesive organ, covered with a glutinous substance and add: "Ce liquide est sécrété, comme l'a annoncé Fernald pour Anurida maritima, par deux glandes situées dans la tête, chez Sminthurus fuscus, elles sont logées dans la région postérieure de la cavité céphalique et occupent les protubérances verticales postérieures de la tête. Chacune d'elles est constituée par un tube contourné qui, dans sa région glandulaire, se composé de cellules plates à gros noyaux et à bordure striée; le conduit excréteur, plus étroit, débouche à l'extrémité postérieure de la fente médiane de la lèvre inférieure. Ces glandés, découvertes chez Macrotoma flavescens par Tullberg, qui les considérait comme glandes salivaires, ont été figurées ensuite chez *Lipura* [Aphorura] ambulans par Nassonow qui les fait se déverser dans la cavité buccale; elles ont été signalées chez Anurida maritima par Fernald, qui a découvert leur véritable rôle. De l'orifice de la glande jusqu'au tube ventral, la sécrétion suit une gouttière chitineuse incomplète, qui court sur la ligne médiane de la face inférieure de la tête et du thorax, en passant entre les pattes; elle descend le long du tube ventral pour aboutir au sillon qui sépare les deux lobes de cet organe."

I do not deny these observations upon Anurida and Smynthurus, especially in the face of Fernald's positive assertion, — I have not examined those genera with reference to this question, as to do so would take me beyond the scope of this paper, — but I have been unable to confirm the observations in the case of Orchesella. In this species there is no common median duct, although the approximating sides of the labial cleft might possibly be mistaken for such. I find no distinct opening through the labium into the *linea ventralis;* this structure is, as I have described, and as Willem et Sabbe admit, "une gouttière chitineuse incomplète," being always more or less open (Plate **3**, Figs. 26, 27) throughout its length, and moreover becoming more or less interrupted between the body segments. In short, it is doubtful if it can have the function of conveying even a viscid fluid. Furthermore, the exsertile processes of the ventral tube are themselves well provided with unicellular glands already described by Sommer ('85), but disregarded by Willem et Sabbe ('97), sufficient to furnish the viscid secretions. It is my opinion, then, that the larger cephalic glands of Orchesella are truly salivary glands, as are those of Macrotoma [Tomocerus] and Lipura [Aphorura] in the opinion of Tullberg and Nassonow.

The second pair of glands lie close to the skull on either side of the head, between the bases of the mandible and maxilla. Each gland consists of a somewhat conical mass of secreting cells converging downward to a chitinous duct which follows the skull down, between the mandible and maxilla, becoming triangular in cross section, and opens through the lateral wall of the mandibular pocket, about half way down the mandible.

The glandular cells (Plate 4, Fig. 35, *gl.*) are polygonal, with large oval nuclei; the cytoplasm forms a close network, the interspaces of which contain a clear substance.

The transition is abrupt between the gland and the duct, which ends blindly (Fig. 35, *dt.*). The end of the duct, however, is provided with many pores, which facilitate the passage of secreted fluid through the thick, chitinous wall of the duct. The mouth of the duct is distinctly marked by ectodermal pigment, which is reflected from the wall of the buccal cavity and lines the lumen of the duct for a considerable distance (Fig. 31, *lu.*).

The pivot of the mandible (*cdx.*), resting in its stirrup, abuts against the gland, as shown in Figure 35. This leads me to think that the lubrication of the pivot may possibly be an incidental function of the gland.

This pair of glands evidently corresponds to a pair described for Smynthurus by Willem et Sabbe ('97, p. 132), who state, however, that "Les conduits excréteurs des différentes cellules d'un même côté se réunissent en un canal collecteur qui, de la base de la mandibule, descend obliquement pour se terminer dans la partie supérieure de la cavité buccale, dans l'angle formé par la mandibule et l'hypopharynx." In Orchesella, the gland cannot be said to open in the same place.

Regarding the possibility of the existence of a lingual gland, I may say that the base of the glossa is lined with epithelial cells which are unusually large and contain large oval nuclei (Plate **1**, Fig. 3). There is apparently a median opening, or at least a very thin place on the upper wall of the glossa (Plate **3**, Fig. 23, and Plate **4**, Fig. 28, *of.*), but I have not been able to trace its relation to underlying tissues on account of the extreme delicacy and brittleness of the glossa, resulting in unavoidable distortions in the process of sectioning. On the other hand, the central cavity of the glossa is undoubtedly a part of the general body cavity, so that the evidence in favor of the tongue being glandular is at most very slight.

The Physiology of the Mouth-Parts.

Almost complete ignorance of the physiology of the mouth-parts has been but the natural consequence of an incomplete knowledge of their anatomy. Obviously, very little can be learned by direct observation or experiment; much may be inferred, however, from the structure and relations of the organs. I have already described the action of the muscles which are concerned, and may now briefly trace the history of the food until the stomach is reached.

Orchesella cincta is a common species among decomposing leaves and in moss; it is most abundant among decaying pine needles and twigs, upon which it feeds. The stomach usually contains minute irregular fragments of wood, and the insect thrives when confined in a glass tube with a moistened piece of decaying pine wood.

The observing Dr. Fitch ('63) is the only naturalist who has given any account of the feeding habits of Collembola. I quote his observations ('63, p. 672) upon Smynthurus hortensis: "These Garden Fleas are so minute that the human eye without the aid of glasses is wholly unable to inspect their movements. The following observations will therefore be the more interesting to the reader. It is some years since that I noticed several of these insects on a piece of new pine board lying in the garden. Wondering what they could find to attract them to that situation, where I thought the odor of any turpentine in the wood would rather make it repulsive to them, I was able to observe their operations by approaching a magnifying glass to them gently, so as not to alarm them and cause them to skip away, — the light colored surface of the new wood enabling me to inspect their movements much more accurately than could be done were they standing upon a darker colored ground. Several of them were noticed, here and there, to have grasped in their mouths what appeared to be an exceedingly minute flexible fibre of the wood, fine as a fragment of a spider's web; and they were pulling backward, at the same time shaking their heads slightly, evidently to tear off these fibres. One of the fore legs was frequently used to crowd this fibre more and more into the mouth, whenever it became peeled up and too long to pull upon to advantage. Everything indicated that it was for the purpose of food that they were thus tearing off this fine fuzz from the surface of the new board. At one place was a small black spot in the board, caused apparently by some old disease in the wood at this point, which rendered it more soft and palatable to the insects, for two of them were here busily occupied in gnawing the particles of matter from the surface, as it seemed."

The stout setæ which project from the labrum, palpi, and labium, and surround the mouth, are probably tactile in nature. It is possible that the food is moistened with saliva before being taken into the mouth, as the median trough of the labium is well adapted to convey saliva to the border of the mouth.

In order to seize food, the mandibles leave their sockets and are protruded a little from the mouth. The tips of the mandibles, by lateral movements, grasp fibres of decaying wood, which are held between the terminal incisive teeth, the four teeth of the left mandible interlocking with the five of the right one. The food is pulled into the mouth by the retraction of the mandibles, assisted by the upper and lower lips, then meets the secretions poured into the buccal cavity by the two pairs of glands, and is grasped by the claws of the terminal maxillary lobes, which move laterally; the entire maxilla may also perform lateral movements. The maxillæ are situated on either side of the tongue, and their tips interlock in the space left between the glossa and paraglossæ, so that the retraction of the maxillæ — which is slight, however, as contrasted with that of the mandibles — must pull the food along the dorsal surface of the glossa, and through the space which intervenes between the paraglossæ. In this operation, the laciniæ brush along the surface of the glossa, which is curved so as to conduct the food between the paraglossæ. On the concave dorsal surfaces of the paraglossæ the food meets the grinding faces of the mandibles, the upward rotary movement of which may carry it to the projecting teeth of the paraglossæ. I have sometimes found particles of wood held between the teeth of the paraglossæ and those of the epipharynx, which is opposite. The coarse ventral teeth of the mandibles crush the woody fibres preparatory to a finer comminution by the denticulated molar surfaces. In the grinding process, the powerful adductors play the principal part, supplemented by rotary movements and possibly also by forward and backward rubbings. The downward rotary movement is much stronger than the reverse, judging from the size and number of the muscles concerned in the two acts. During mastication the mandibles are probably withdrawn into their chitinous sockets, where the pivots encounter firm resistance. The pivots are perhaps lubricated by glands already described.

The comminuted food of the pharynx is sucked into the œsophagus. This occurs by the constriction and subsequent dilatation of the fore gut. Once within the œsophagus, the food may be forced back by peristaltic action, resulting from the successive contraction of constricting muscles, until the stomach is reached, where a valve prevents the return of the food into the gullet.

Although Collembola are classed as mandibulate insects, it is evident that they are also suctorial. The Collembola are closely related to Campodea, a generalized type which is regarded as the representative of a primitive form from which more specialized insects have been derived. As already suggested by Lubbock, we may imagine the primitive insect to have possessed mouth-parts resembling those I have described, capable of further modification in either the mandibulate or suctorial direction. Indeed, the latter modification has already occurred in the Collembolan genus Neanura.

In conclusion, I desire to thank Mr. Samuel Henshaw, whose knowledge of entomological literature has been of great service to me. I wish to acknowledge my special indebtedness to Professor Mark; for his careful and kind supervision have been my greatest aid and encouragement.

BIBLIOGRAPHY OF THYSANURAN MOUTH-PARTS.[1]

Bourlet.

'39. Mémoire sur les Podures. Mém. Soc. Sci. Agric. Arts, Lille. Pt. 1, pp. 347–417. 1 Pl.

Bourlet.

'41–'42. Mémoire sur les Podurelles. Mém. Soc. Sci. Agric., etc. Nord. Douai. Also separate, Douai, 1843, 78 pp, Pl. 1.

Fabricius, J. C.

1777. Genera Insectorum. [pp. 101–102.]

Fernald, H. T.

'90. Studies on Thysanuran Anatomy. (Prelim. comm.) Johns Hopk. Univ. Circ. Vol. 9, pp. 62–63.

Fernald, H. T.

'90^a^. The Relationships of Arthropods. Studies Biol. Lab. Johns Hopk. Univ. Vol. 4, pp. 431–513. Pls. XLVIII.–L.

Fitch, A.

'63. Eighth Report on the Noxious and other Insects of the State of New York. Albany, N. Y.

Grassi, B.

'86. I progenitori degli Insetti e dei Miriapodi. L' Japyx e la Campodea. Memoria II. Atti Accad. Gioen. Sci. Nat. Catania. Ser. 3, Tom. 19, pp. 1–67. Tav. I.–V.

Grassi, B.

'86[a]. I progenitori dei Miriapodi e degli Insetti. Memoria III. Contribuzione allo studio dell' Anatomia del genere Machilis. Atti Accad. Gioen. Sci. Nat. Catania. Ser. 3, T. 19, pp. 101–124. 1 Tav.

Grassi, B.

'86[b]. I progenitori dei Miriapodi e degli Insetti. Memoria IV. Cenni Anatomici sul Genere Nicolatia. Bull. Soc. Entom. Ital. An. 18, pp. 173–182. Tav. VII., VIII.

---

[1] This Bibliography includes the works on Thysanura as well as Collembola, and also the titles of articles relating to the cephalic glands of Collembola.

Grassi, B.

'87. Anatomia comparata dei Tisanuri e considerazioni general sull' organizzazione degli Insetti. Atti Accad. Lincei, Roma. Ser. 4. Mem. Vol. 4, pp. 543-606. Tav. I.-V.

Grassi, B., e Rovelli, G.

'89-'90. I progenitori dei Miriapodi e degli Insetti. Memoria VI. Il sistema dei Tisanuri fondato soprattutto sullo studio dei Tisanuri italiani. Nat. Sicil. An. 9, pp. 25-41, 53-68, 77-87, 105-124. Tav. 1, 2.

Haliday, A. H.

'64. Japyx, a new Genus of Insects belonging to the Stirps Thysanura, in the Order Neuroptera. Trans. Linn. Soc. Vol. 24, Pt. 3, pp. 441-447. Pl. 44.

Laboulbène, A.

'65. Recherches sur l'Anurida maritima, insecte Thysanoure de la famille des Podurides. Ann. Soc. Entom. France, Sér. 4, T. 4 (1864), pp. 705-720. Pl. 11.

Laboulbène, A.

'65. Description et anatomie d'un insecte maritime (Anurida maritima) qui forme un genre nouveau dans l'ordre des Thysanoures et la famille des Podurides. Compt. Rend. Seanc. Mém. Soc. Biol. Paris. Sér. 4, T. 1 (1864), Mém. pp. 189-206. Pl. 1.

Latreille, P. A.

'32. De l'organisation extérieure et comparée des insectes de l'ordre des Thysanoures. Nouv. ann. mus. hist. nat. Paris. Sér. 3, T. 1, pp. 161-187.

Lubbock, J.

'62. Notes on the Thysanura. Pt. I. Smynthuridæ. Trans. Linn. Soc., Vol. 23, Pt. 3, pp. 429-448. Pls. 45, 46.

Lubbock, J.

'73. Monograph of the Collembola and Thysanura. Ray Soc. 255 pp. 78 Pls.

Meinert, F.

'65. Campodeæ: en familie af Thysanurernes orden. Naturh. tidsskr. Ræk. 3, Bd. 3, pp. 400-440. Tab. XIX.

Translation. On the Campodeæ, a Family of Thysanura. Ann. Mag. Nat. Hist., Lond. Ser. 3, Vol. 20, pp. 361-378. Figs. 1867.

Nassonow, N.

'87. The Morphology of Insects of Primitive Organization. Studies Lab. Zool. Mus. Moscow, pp. 15-86. 2 Pls. 68 text figs. (In Russian.)

Nicolet, H.

'41. Recherches pour servir à l'histoire des Podurelles. Extr. Nouv. Mém. Soc. Helv. Sci. Nat. Neûchatel. Vol. 6, 84 pp. 9 Pls. Also separate, '43. Ibid. T. 4. 88 pp. 9 Pls.

Olfers, E. de.
'62. Annotationes ad Anatomiam Podurarum. Diss. inaug. Berolini. 34 pp. 4 Lith. Pls.

Oudemans, J. T.
'87. Bijdrage tot de Kennis der Thysanura und Collembola. Amsterdam. 104 pp. 3 Pls.

Translation. Beiträge zur Kenntniss der Thysanura und Collembola. pp. 147–226. Taf. I.–III. Amsterdam, 1888.

Packard, A. S.
'71. Bristle-tails and Spring-tails. Amer. Nat. Vol. 5. pp. 91–107. Figs. 23–40. Pl. 1.

Rovelli, G. [See **Grassi, B., e Rovelli, G.**]

Sabbe, H. [See **Willem, V., et Sabbe, H.**]

Sommer, A.
'84. Ueber Macrotoma plumbea. Beiträge zur Anatomie der Poduriden. Inaug. Diss. Göttingen. Also Zeitschr. wiss. Zool., Bd. 41, pp. 683–718, Taf. XXXIV., XXXV. 1888.

Stummer-Traunfels, R. R. von.
'91. Vergleichende Untersuchungen über die Mundwerkzeuge der Thysanuren und Collembolen. Sitzungsb. Akad. Wissensch. Wien, Bd. 100, Abth. 1, Heft 4, pp. 216–235. 2 Taf.

Tullberg, T.
'72. Sveriges Podurider. Kongl. Svensk. Akad. Handlingar, Stockholm. Ny Följd. Bd. 10, No. 10. 70 pp. 12 Pls.

Willem, V., et Sabbe, H.
'97. Le tube ventral et les glandes céphaliques des Sminthures. Ann. Soc. Ent. Belgique. T. 41. pp. 130–132.

EXPLANATION OF PLATES.

[All figures are of Orchesella cincta L.]

ABBREVIATIONS.

Note. — Each muscle is numbered in agreement with the text.

a.	Anterior.
abd.	Abductor.
add.	Adductor.
at.	Antenna.
atc.	Articulation.
bac.	Rod.
br.	Arm.
br. a.	Anterior arm.
calc.	Shoe.
car.	Cardo.
cav. buc.	Buccal cavity.
cdx.	Pivot.
cht.	Chitinous.
cl. gn.	Ganglion cell.
clyp.	Clypeus.
cpt.	Head.
cra.	Cranium.
crs. ba.	Basal ridge.
c'stt.	Constrictor.
cta.	Cuticula.
cx.	Heel.
d.	Dorsal.
de.	Teeth.
dep.	Depressor.
dil.	Dilator.
dt.	Duct.
e'phy.	Epipharynx.
e'th.	Epithelium.
exp.	Expansion.
f.	Frontal.
fac.	Surface.
ga.	Galea?
gl.	Gland.
gls.	Glossa.
gn. inf'œ.	Infra-œsophageal ganglion.
gn. su'œ.	Supra-œsophageal ganglion.
gu.	Gula.
h'drm.	Hypodermis.
i.	Intima.
i'cis.	Incisive.
l.	Lateral.
la.	Plate.
lab.	Labium.
lbr.	Labrum.
lcn.	Lacinia.
lig.	Ligament.
ln. v.	Linea ventralis.
lu.	Lumen.
lvt.	Elevator.
m.	Middle, median.
m....m.	Median line.
mb. ba.	Basement membrane.
md.	Mandible.
men.	Mentum?
mol.	Molar.
ms.	Mesal.
mu.	Muscle.
mx.	Maxilla.
n.	Nerve.
nat.	Natural size.
nl.	Nucleus.
ocl.	Ocellus.
œ.	Œsophagus.
of.	Orifice.
or.	Mouth.
p.	Posterior.
pa'gls.	Paraglossa.
pd.	Foot.
pd'.	Footstalk.
phy.	Pharynx.
pig.	Pigment.
pi'my.	Perimysium.
pli.	Fold.
plp.	Palpus.
pr'j.	Projection.
pr'j. con.	Conical projection.
pr't.	Protrusor.
ret.	Retractor.
rot.	Rotator.
sb'men.	Submentum?
set. sns.	Sensory bristle.
sta.	Stirrup.
stp.	Stipes.
sul.	Trough.
sut.	Suture.
tnd.	Tendon.
tnt.	Tentorium.
v.	Ventral.

PLATE 1.

Fig. 1. External aspect of the mouth. × 116.

Fig. 2. Diagram of the head, seen from the right side, to show the relations between certain organs. × 55. The small figure in a circle represents the natural size of the head.

Fig. 3. Reconstruction from sagittal and parasagittal sections of the left half of the head, imagined as seen from the right side. The numbers 28, 29, 30, and 31 refer to figures of Plate **4**, bearing corresponding numbers, which represent transverse sections made in the positions of the numbered lines of this figure. × 220.

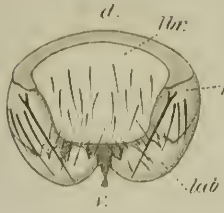
Fig. 4. Transverse section of the œsophagus. × 530.

Fig. 5. The tentorium, viewed from the right side; reconstructed from serial sagittal sections. × 220.

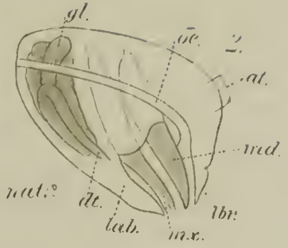
Fig. 6. Dorsal aspect of the tentorium; reconstructed from frontal sections. × 220.

Fig. 7. Sagittal section passing through the tentorium and adjacent structures. × 440.

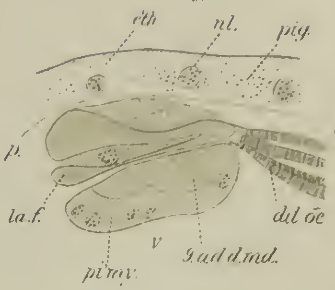
Fig. 8. Parasagittal section of the labrum. × 220.



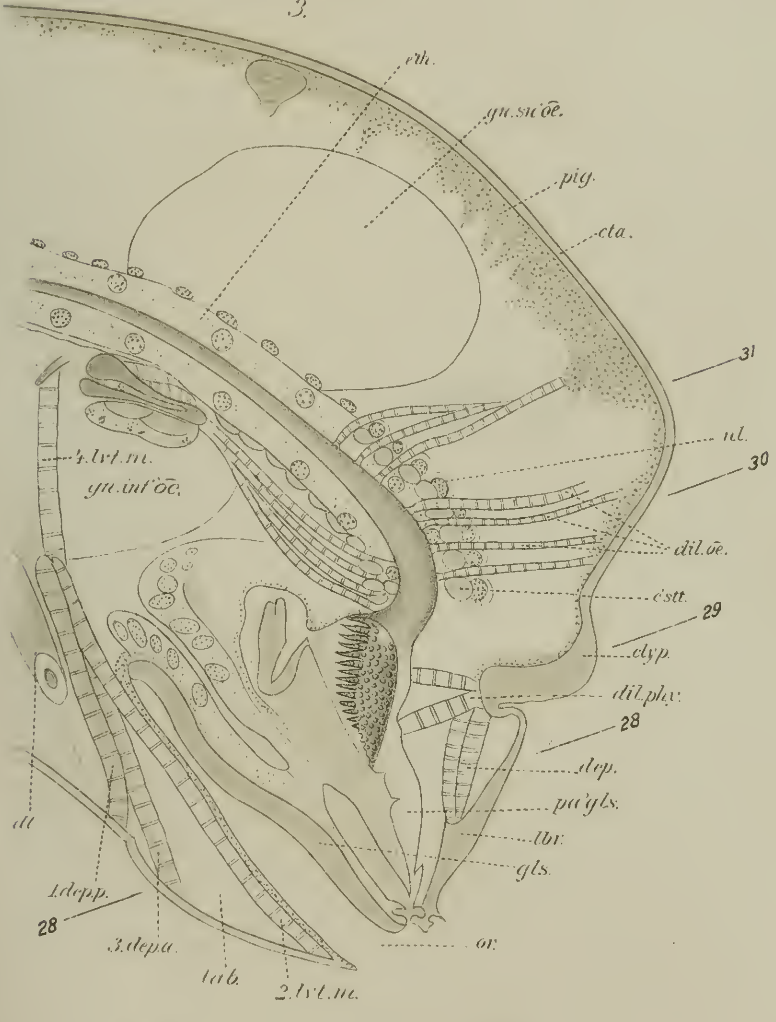
1.



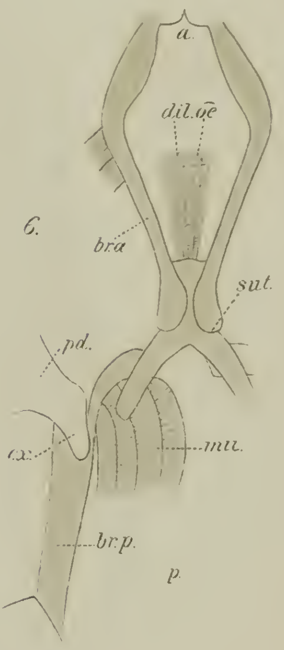
2.



7.

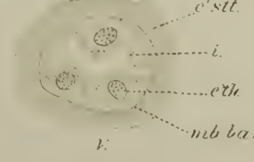


3.

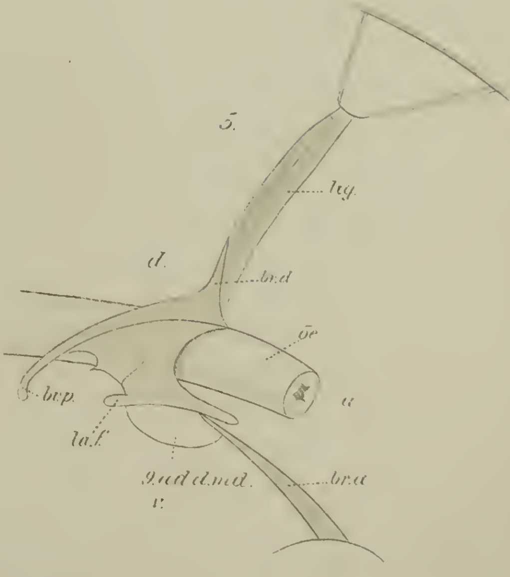


6.

8.



4.



5.

J.W.F. del. [illegible]

PLATE 2.

Fig. 9. Internal aspect of the labrum and clypeus, to show the epipharynx. × 220.

Fig. 10. Dorsal aspect of the internal mouth-parts, *in situ;* the paraglossæ are omitted. From dissections and potash preparations. × 116.

Fig. 11. Ventral aspect of the apex of the right mandible. × 440.

Fig. 12. Ventral aspect of the molar region of the right mandible. × 440.

Fig. 13. Dorsal aspect of the base of the left mandible, *in situ;* from a dissection. × 440.

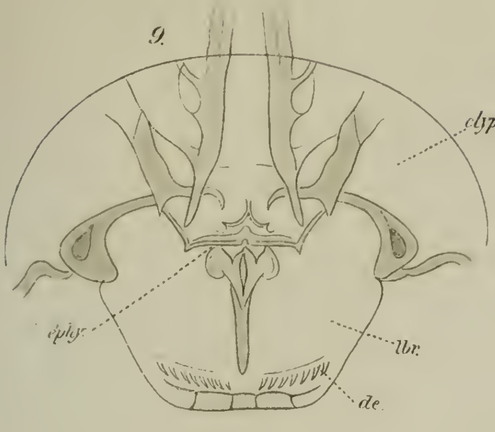
Fig. 14. Dorsal aspect of the left mandible with its muscles. Reconstructed from serial sections, aided by dissections. × 116.

Fig. 15. Ventral aspect of the right mandible, to show certain muscles, and to supplement Fig. 14. From a dissection. × 116.

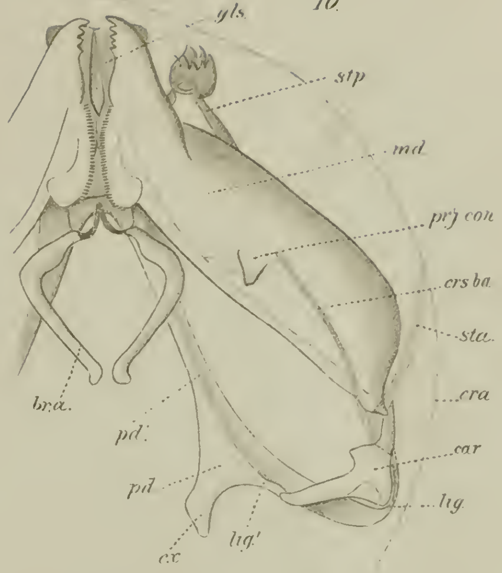
Fig. 16. Posterior aspect of a transverse section of the right mandible, cut near the anterior angle of the triangular orifice. × 220.

Fig. 17. Three ganglion cells from within a mandible. × 530.

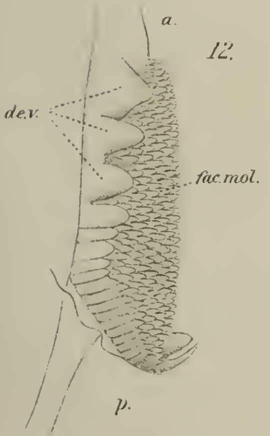
9.



10.

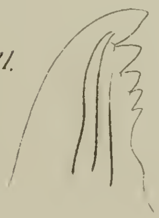


12.

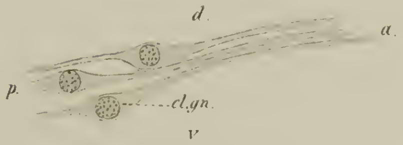


13.

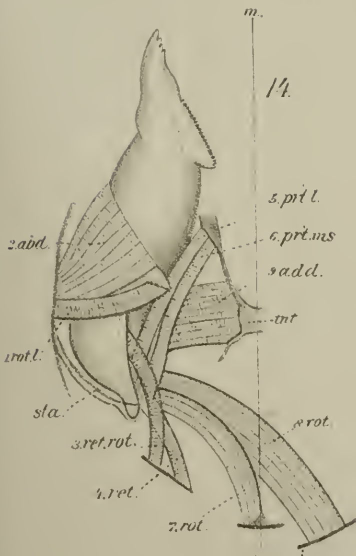
11.



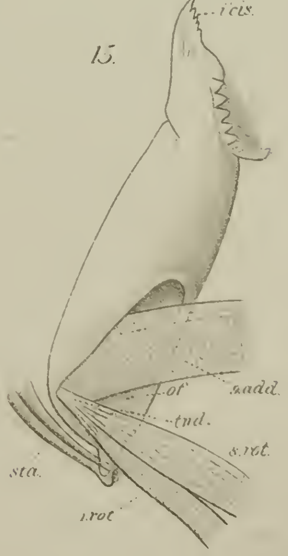
17.



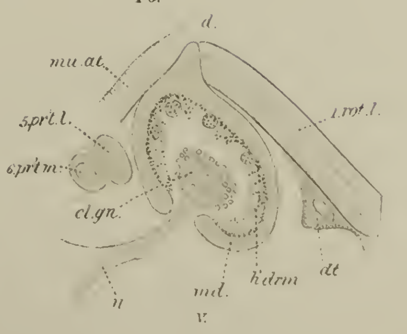
14.



15.



16.



J.W.F. del.

PLATE 3.

Fig. 18. Dorsal aspect of the framework of the left maxilla; from a dissection. × 116.

Fig. 19. Dorsal aspect of the head of the right maxilla; from a dissection. × 530.

Fig. 20. Dorsal aspect of the left maxilla, with most of its muscles. Reconstructed from serial sections, aided by dissections. × 116.

Fig. 21. Dorsal aspect of the more ventral portion of the left maxilla; supplementary to Fig. 20. From serial sections and from dissections. × 116.

Fig. 22. Dorsal aspect of the right paraglossa, with underlying glossa; from dissections. × 440.

Fig. 23. Dorsal aspect of the glossa; from dissections. × 440.

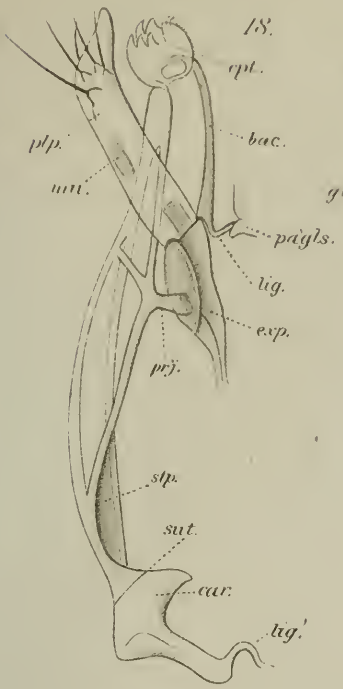
Fig. 24. Ventral aspect of the right half of the labium; from a dissection. × 220.

Fig. 25. Dorsal view of the left half of the labium; reconstructed. × 220.

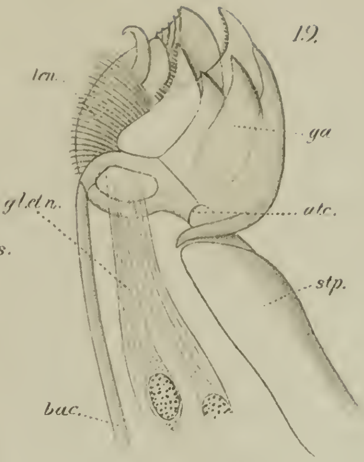
Figs. 26 and 27. Transverse sections of the *linea ventralis*. × 530.

FOLSOM-MOUTH PARTS ORCHESELLA PLATE 3.

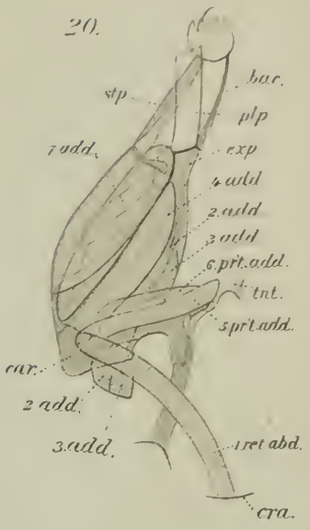
18.



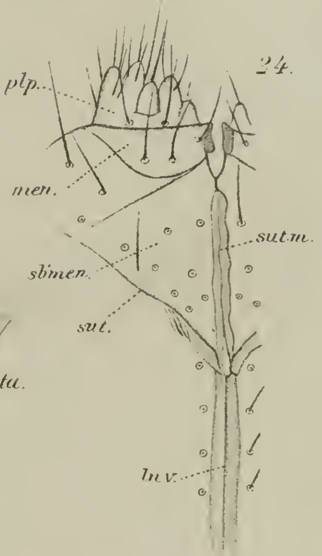
19.



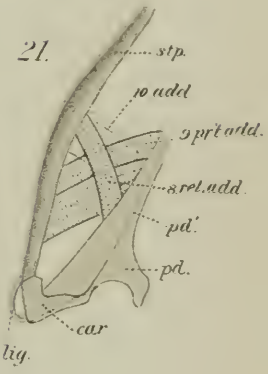
20.



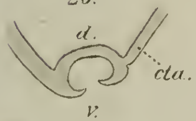
24.



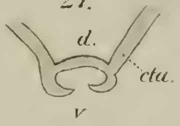
21.



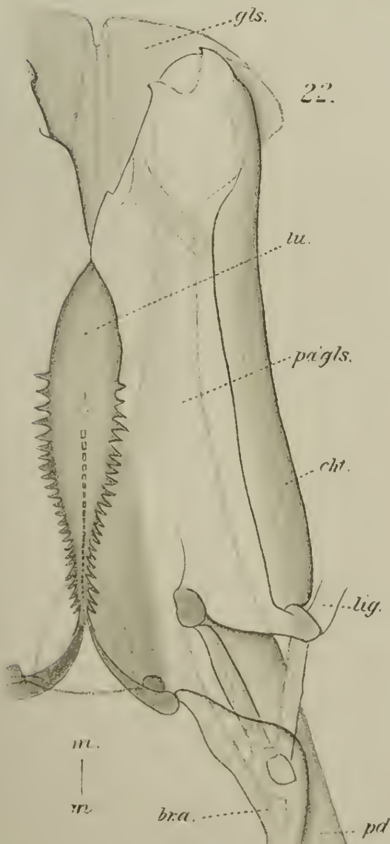
26.



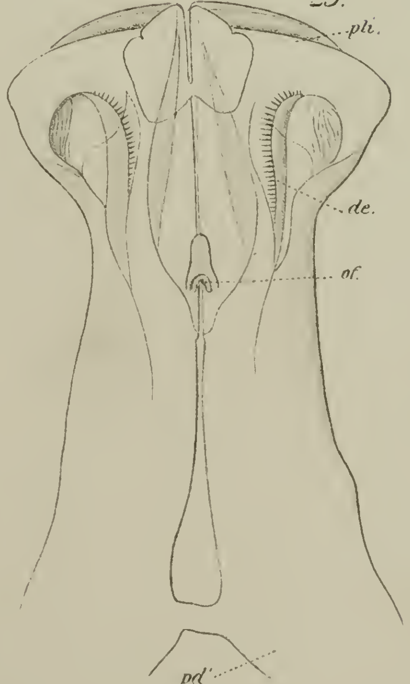
27.



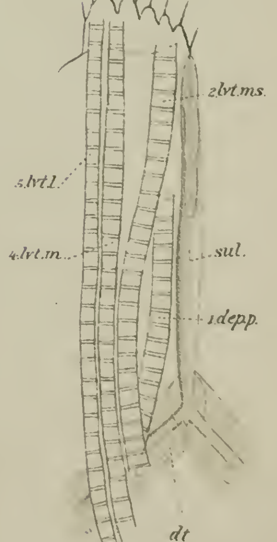
22.



23.



25.



J.W.F. del.

B. Meisel, lith Boston.

PLATE 4.

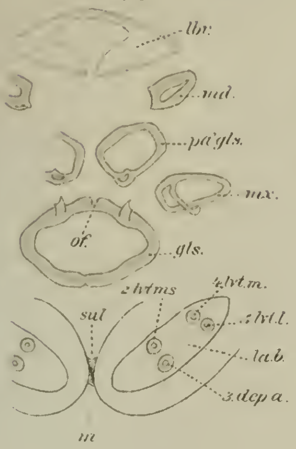
Figs. 28–32. Sections nearly transverse to the mouth-parts, numbered in sequence, beginning near the mouth, and cut approximately in directions indicated by the numbered lines of Plate **1**, Fig 3. Figs. 28–31, × 220; Fig. 32, × 116.

Fig. 33. Transverse section through a secretory region of one of the larger cephalic glands. × 440.

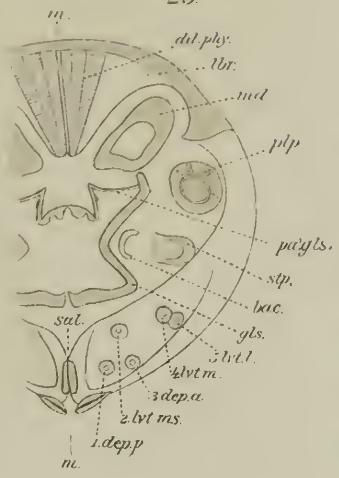
Fig. 34. Transverse section of an evacuating duct of the same gland. × 440.

Fig. 35. Sagittal section of one of the pair of smaller cephalic glands. × 220.

28.

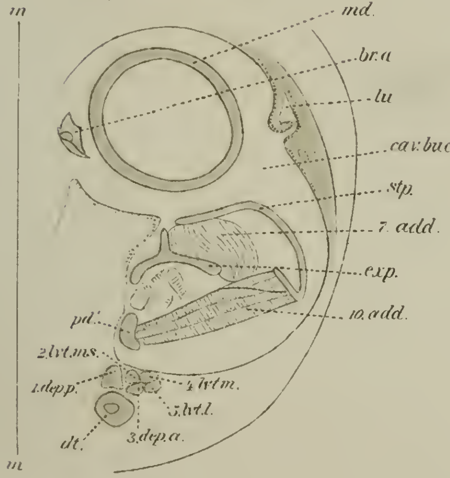


29.

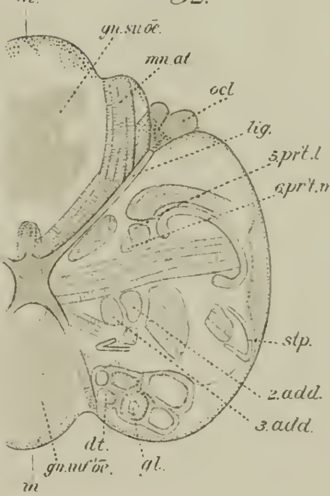


30.

31.

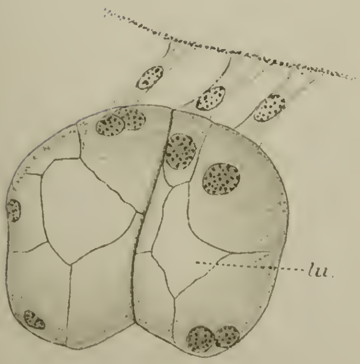


32.



34.

33.



35.

J.W.F. del.

A. Meisel, lith. Boston.

No. 3. — *Studies from the Newport Marine Laboratory. Communicated by* Alexander Agassiz.

XLII.

Longitudinal Fission in Metridium marginatum Milne-Edwards.

By G. H. Parker.

From early times double specimens of different species of Metridium have been observed and recorded. Thus in the last century Dicquemare ('75, p. 229, Tab. VI. Fig. 2) described and figured a specimen of M. dianthus with two complete oral disks. Similar specimens were observed by Johnston ('47, p. 233), who called them monstrosities, and interpreted them as cases of coalescence brought about by the gregarious habit of the species. Thorell ('59, p. 10) and Gosse ('60, p. 20) likewise mentioned specimens with two disks as monstrosities, though Gosse also expressed the opinion that they were due to a tendency to spontaneous division. Foot ('63, p. 64), who confirmed the observations of his predecessors on the occurrence of animals with two oral disks, also recorded the discovery of a specimen with two mouths on one disk and further stated that these aberrations from the normal form are merely to be considered as monstrosities. G. Y. and A. F. Dixon ('91, p. 20), in reporting the occurrence of specimens with two disks as well as those with two mouths on one disk, mention them likewise as monstrosities. Carlgren ('93, p. 109), after stating his belief that longitudinal division is not uncommon in M. dianthus, adds : "Mehrere Forscher scheinen Formen mit zwei Mundscheiben als monströse ansehen zu wollen. Es kann doch wohl als eine begonnene Längsteilung, die nicht zu Ende geführt ist, betrachtet werden."

Double specimens of M. marginatum were observed as early as 1847 by Professor Louis Agassiz, among whose unpublished drawings are three figures, two of which (Plate I. Figs. 2, 3) bear this date and probably represent two views of the same animal ; the third figure (Fig. 1) bears the date of 1860. These figures were unaccompanied by any notes bearing on the question of fission, but in the "Seaside Studies," published in 1865 by Elizabeth C. Agassiz and Alexander Agassiz ('65, p. 11), longitudinal fission is stated to occur in this species.

Finally, Torrey ('98, p. 347), who studied the Californian species M. fimbriatum, described double specimens which he believed to be in process of fission.

The material upon which the present paper is based consisted of ten specimens of Metridium marginatum, collected in part by myself and in part by others. The sources of this material are acknowledged in the account of the specimens given with the description of the figures. Here each specimen has received a distinguishing letter. To the gentlemen whose names are mentioned as having obtained certain specimens for me, I wish to express my indebtedness. I am also indebted to Dr. H. C. Bumpus, Director of the Laboratory at the United States Fish Commission Station at Wood's Hole for many courtesies shown me while working at the station, and I am under special obligations to Mr. Alexander Agassiz for the privilege of working at the Newport Laboratory, and for the use of unpublished drawings made for Professor Louis Agassiz.

The animals collected were for the most part stupefied by means of magnesium sulphate in sea water, Tullberg's well known method, and subsequently hardened in chromic acid and dissected by hand.

The specimens naturally fall into two groups: first, those with two mouths on one disk, of which there were two examples, specimens A and B (Plate II. Figs. 6 and 7); and secondly, those with two complete oral disks, of which there were eight, C to J (Plate II. Figs. 4 and 5, Plate III. Figs. 8–14).[1] The two specimens (Plate I. Figs. 1–3) figured by Professor Agassiz belong also to this group. These two groups were not only distinguished by external anatomical differences, but also by certain internal characteristics. In both representatives of the first group the œsophageal tubes were Y-shaped, the single inner end opening into the gastrovascular cavity and the two outer ends opening each through a mouth. In specimen A (Plate II. Fig. 6) the bifurcation was close to the oral disk and the œsophagus was for the greater part of its extent a single flattened tube. In specimen B (Fig. 7) the œsophagus was double excepting at its extreme inner end, so that its form is perhaps more correctly described as V-shaped. In all the specimens in the second group the œsophageal tubes were entirely distinct from their super-

---

[1] One of these eight, specimen J, was sacrificed in an attempt to rear it; hence I have been able to study the internal anatomy of only seven such specimens.

ficial to their deep ends (Plate III. Figs. 8–14). In the material at hand, then, completely distinct disks were always associated with completely separate œsophageal tubes and single disks bearing two mouths with only partially separate tubes.

Although the œsophageal tubes have been described as though they were either entirely distinct or united only through their own substance, in two of the nine animals studied there were special membranes attaching one tube to the other. In specimen C (Plate III. Fig. 8) the two tubes were held together by a single membrane which extended from their oral to their pedal ends, but which failed of connection with the inner surfaces of both oral and pedal disks. In specimen B (Plate II. Fig. 7) two such membranes were present and extended from the region where the œsophageal tubes united almost to the oral disk. Both membranes were closely attached to the tubes, and were deficient only next the oral disk; consequently the cavity which they enclosed was entirely cut off from the gastrovascular cavity except near the oral disk, where it opened freely over both membranes. Although the membranes in these two specimens had the general appearance of mesenteries, they lacked the characteristic muscle bands and mesenteric filaments. Membranes much like these, but in one case bearing mesenteric filaments, have been observed in M. fimbriatum by Torrey ('98, p. 347).

In all specimens excepting B, F, and H, each mouth was monoglyphic; in B (Plate II. Fig. 7) and F (Plate III. Fig. 11), each animal had a monoglyphic and a diglyphic mouth; in H (Plate III. Fig. 13) one mouth was monoglyphic and the other aglyphic. In those cases where the œsophageal tubes were united, A and B, the siphonoglyphs were, notwithstanding this union, distinct throughout their whole lengths. The siphonoglyphs of any double animal apparently do not occupy random places, but are usually arranged symmetrically with reference to the assumed plane of division. This is easily seen in Figures 8, 10, 12, and 14 (Plate III.). Its significance in connection with fission has been pointed out by Torrey ('98).

Of the complete mesenteries the directives were always in pairs, and always attached to the siphonoglyphs. Their arrangement consequently corresponded to that of the siphonoglyphs, and hence need not be described. The non-directives were also always in pairs, though not infrequently one member of such a pair was incomplete. This occurred in eleven cases in a total of 107, or in about 10% of the mesenteries in the specimens examined. Including under the head of pairs of complete mesenteries those cases in which only one member of a pair is complete, the number and general distribution of the non-directives is indicated in the following tabulation.[1]

Specimen	A	B	C	D	E	F	G	H	I	
Left Directive Pair	1	1	1	1	1	1	1	1	1	
Intervening Non-directive Pairs	1	2	3	2	1	2	3	16	3	= 33
Right Directive Pair	1	1	1	1	1	1	1	0	1	
Non-directive Pairs	8	2	16	7	8	3	13	0	5	= 62
Additional Directive Pair . .		1				1				
Non-directive Pairs		6				6				= 12
Total Non-directive Pairs										107

The numbers of non-directives in the animals with two mouths bear an important relation to those of animals with single mouths. In an enumeration of the mesenteries in the latter, made some time ago (Parker, '97), I found that in 131 specimens the pairs of non-directives were never fewer than three and never more than fourteen, and that the average was about five and a half pairs (5.6+) for each individual. In the nine double-mouthed specimens the non-directives were never fewer than eight pairs, nor more than nineteen, and the average was a little less than twelve (11.9—) for each individual. It thus appears that the double-mouthed specimens have almost exactly twice as many non-directive mesenteries as the single-mouthed ones.

As can be seen from the tabulation already given, as well as from the figures, the non-directives are unevenly but characteristically distributed, there being usually a large group on one side and a small group on the other side of the pairs of directives, called rights and lefts. Even in specimens B, F, and H (Figs. 7, 11, and 13), where the directives are more or fewer than two pairs, this same peculiarity in distribution may be said to exist. In another respect the distribution of the non-directives is remarkably regular. In specimen I (Plate III. Fig. 14) a pair of non-direc-

---

[1] In this table the term left directive pair is applied to the pairs of directives toward the left in the figures on Plate III., and to those toward the bottom in the figures on Plate II. The corresponding pairs on the other œsophageal tubes are called right directive pairs. Right and left have in this connection only this simple descriptive significance.

tives is so placed that, while they start from nearly the same place on the outer wall, they pass to different œsophageal tubes. The pair opposite these has similar connections, so that at this stage the assumed plane of division may be said to pass through primary entocœls on both sides. The same is true of G (Fig. 12), and Torrey ('98, Plate XXI. Fig. 1) figures what seems to be a similar case, though in his description (p. 347) he mentions only *one* pair of mesenteries as divided between the œsophageal tubes. Apparently there is some discrepancy here, but whether it is the description or the figure which is faulty, it is impossible to say. In the remaining specimens examined by me, the division plane always lay in primary ectocœls. It is noteworthy that in the nine cases studied none showed the plane of division passing through a primary ectocœl on one side and a primary entocœl on the other. In this respect the specimens were always perfectly symmetrical, a condition which may hold for other Actinians, as suggested by the symmetrical division of Zoanthus thomensis as described by Koch ('86, p. 33).

The incomplete mesenteries formed what were usually irregular groups in the primary ectocœls. Their arrangement seemed to bear so little on the question of division that I have not attempted a description of them. In the figures of transverse sections the incomplete mesenteries are either represented in full in a given primary ectocœl or their presence is indicated by x. Primary ectocœls not marked in one or other of these ways contained no incomplete mesenteries.

Of the double-mouthed specimens whose sexes could be determined, four were females and three were males. No evidence of hermaphroditism was observed, though the specimens were carefully scrutinized in this respect. Obviously the double-mouthed condition is not peculiar to either sex.

The interpretations that have been placed upon these double-mouthed specimens have already been stated. Johnston's idea that they have arisen by the fusion of two originally independent individuals seems to me entirely unwarranted. M. marginatum is represented by individuals showing extreme variations in color and markings, and yet the two members of all double specimens seen by me have been strikingly similar. If fusion were the means of forming double animals, particolored combinations ought occasionally to occur, but such I have never seen.

There remain then the two suggestions of monstrosities and of stages of fission. To test which of these was the correct interpretation, I attempted to watch the process in what might be assumed to be a dividing individual. This animal was found at Wood's Hole, August 6th, 1898, and was kept under observation there during August and later at Beverly Bridge till October 3d of the same year, a period of some eight weeks. During this time the animal was kept in open sea water in a marked locality, not in a laboratory aquarium, which my former experience had taught me might be unfavorable. When first seen its pedal disk measured about three centimeters in diameter. It had two complete oral disks, one of which had a monoglyphic and the other a diglyphic mouth. The cleft between the two oral disks was a deep one, and I hoped soon to witness the separation of the two individuals. When about eight weeks after capture it was last seen, it had increased in size so that its pedal disk was nearly seven centimeters in diameter, but the cleft between the two parts had in no wise increased. The specimen then unfortunately disappeared from its locality. The fact that it grew considerably shows that it was under approximately normal conditions, and yet so far as fission was concerned the animal was essentially at the same stage at the end of the eight weeks as at the beginning. This coincides with the experience of Torrey ('98, p. 351), who in describing longitudinal fission in M. fimbriatum states that he has "not observed a single instance of full severance of individuals, though a number of dividing polyps have been kept in the laboratory for nine months." Thus direct evidence of actual fission is wanting.

If now we turn to the specimens which have thus far been described, it must be admitted that they can be arranged in a series passing from less to more completely divided individuals. This in itself, however, affords no more grounds for concluding that M. marginatum reproduces by longitudinal fission than a similar series of partially double mammals would establish longitudinal fission for these animals. To make the proof conclusive the final products of the process must be found.

As a rule, the larger specimens of M. marginatum are sessile animals.[1] In large specimens that had undergone division the offspring ought therefore to be found together. M. marginatum further shows great variability in its colors and markings; hence such natural pairs might thus be distinguished from their neighbors, for the two descendants would of course inherit directly the surface markings of their progenitor.

A search was made for natural pairs at Beverly Bridge, a locality

---

[1] According to my own observation the locomotor activity of this species becomes rapidly less as the size increases. A specimen whose diameter was about 5 mm. moved as much as 9 cm. in twenty-four hours. A second one whose average diameter was about 2 cm. never moved more than 1 cm. in a day, and a large one whose diameter was about 8 cm. showed no perceptible movement in fifteen days.

where the species was represented by thousands of individuals in easily accessible positions. The search was facilitated by the fact that often a given pile or plank was covered with individuals of almost exclusively one type of coloration; almost all in one restricted location were orange-colored, or brown, or whitish, etc. This is doubtless due chiefly to reproduction by fragmentation from the edge of the pedal disk, a non-sexual process which insures to the offspring the minute characteristics of the parent. My object was to find pairs of animals individually separate, but situated next each other and strikingly similar in color and markings, though entirely unlike those surrounding them. Such instances, if found, would afford strong evidence in favor of the actual occurrence of longitudinal fission. A search of some three hours' duration, in which between two and three thousand specimens were inspected in their attached positions, resulted in the discovery of six such natural pairs. These were pairs which fulfilled the requirements of the case in every respect, in that they were composed each of two animals strikingly similar in size and coloration, and entirely isolated from others of a like kind by a surrounding group of individuals unlike them. What seemed to be natural pairs of this kind were often met with in other places, but as it was important to accept only pairs that were well isolated, and as these would naturally not occur frequently, it is not surprising that only six such pairs were found.

The six pairs were placed each in a separate bottle and transferred to the laboratory for further study. On examination all proved to be monoglyphic except one individual, which was diglyphic. The arrangement of the complete mesenteries is indicated as follows: —

$$\text{First Pair}\quad \begin{cases} \mathrm{D}-2-3-4-5-6-7. \\ \mathrm{D}-2-3-4-5-\frac{6}{2}-7-8. \end{cases}$$

$$\text{Second Pair}\quad \begin{cases} \mathrm{D}-2-\mathrm{D}-4-5-\frac{6}{2}-7. \\ \mathrm{D}-2-3-4-5-6-7. \end{cases}$$

$$\text{Third Pair}\quad \begin{cases} \mathrm{D}-2-3-4-5-6-7. \\ \mathrm{D}-2-3-4-5-6-7. \end{cases}$$

$$\text{Fourth Pair}\quad \begin{cases} \mathrm{D}-2-3-4-5-6-7-8-9. \\ \mathrm{D}-2-3-4-5-6. \end{cases}$$

$$\text{Fifth Pair}\quad \begin{cases} \mathrm{D}-2-3-4-5-6. \\ \mathrm{D}-2-3-\frac{4}{2}-5-6. \end{cases}$$

$$\text{Sixth Pair}\quad \begin{cases} \mathrm{D}-2-3-4-5. \\ \mathrm{D}-2-3-4-5-6. \end{cases}$$

The first pair were found attached to a large mussel shell, and were killed and hardened without being disturbed from their natural positions. The arrangement of their siphonoglyphs and mesenteries is shown in Figure 15 (Plate III.). So far as the anatomical peculiarities of this and the five other pairs are concerned, they might well be considered as animals that had undergone division.

A further important feature of the six pairs was that in all cases members of the same pair were of the same sex. Of the six pairs, three were female and three male. This uniformity is precisely what would be expected, if these pairs arose by longitudinal fission, but quite the reverse of what we should anticipate had they been the result of accidental juxtaposition. This evidence seems to me to favor strongly the view that longitudinal fission is a regular method of increase in M. marginatum, though it does not exclude the possibility of some of the double-mouthed forms being true monstrosities. It is, however, not my belief that the specimen which was watched by me some two months and which did not progress in division was a monstrosity. I am rather inclined to Torrey's opinion, that the process of longitudinal fission is an extremely slow one. This accords with what we know of the length of life of Actinians, some having outlived human beings.

In all the double-mouthed specimens which I have examined the two partial individuals were of about equal size, so that longitudinal fission in M. marginatum may be justly described as equal. In no case have I ever observed any evidence of distinctly unequal longitudinal fission, though one of the specimens figured by Agassiz (Plate I. Figs. 2 and 3) shows some considerable inequality. In this respect M. marginatum seems to be strikingly different from M. fimbriatum, which according to Torrey ('98) divides more usually by unequal than by equal longitudinal fission.

In longitudinal fission, obviously, certain fundamental changes must occur: new siphonoglyphs and new complete mesenteries, both directive and non-directive, must be developed. In the material which I have studied I have been able to discover no trace of the formation of new siphonoglyphs. The usual symmetrical arrangement of two of the siphonoglyphs in each double animal suggests a process of division by which one original siphonoglyph gives rise to two by longitudinal splitting, as described by Torrey ('98). This is very likely one of the initial steps in longitudinal fission, though it is not necessarily essential, as the condition of specimen H (Plate III. Fig. 13) shows where the original siphonoglyph obviously did not divide.

Of the formation of new directives I have seen absolutely nothing. The production of new complete non-directives is possibly indicated in several cases. In specimen C a curious condition was observed, which is shown in the diagram (Plate III. Fig. 8). Two complete mesenteries start from the column wall, but unite before they reach the œsophageal wall. The cavity which they enclose may be called a primary entocœl so far as their longitudinal muscles indicate, but it contains two incomplete mesenteries which pair off with the united complete ones. The condition might be interpreted as due to the splitting of a complete mesentery and the supplementary development of incomplete ones, though this interpretation is not without objections. I am more inclined to look on the condition as purely abnormal. In another case, the mesentery marked 1 in Figure 7 (Plate II.), whose mate is incomplete, is itself complete only through a small portion of its oral length. This might be a mesentery originally incomplete, which by active growth had completed itself in the oral region. A second similar case was observed among the six natural pairs already mentioned. Beyond these meagre facts, I observed nothing suggestive of the methods by which new complete mesenteries may be formed.

In all the specimens examined by me the fission was progressing from the oral toward the pedal pole of the animal, never in the reverse direction, as described by McCrady ('59, p. 275) for Actinia cavernosa, by Carlgren ('93, p. 31) for Protanthea simplex, and as may also occur in Cereactis as described by Wilson ('89, p. 38), who however did not place this interpretation on what he saw. The direction of fission in M. marginatum corresponds to that generally found in M. fimbriatum as described by Torrey ('98).

The kind of individuals produced by equal longitudinal fission in M. marginatum can be easily inferred from the foregoing account. They are usually monoglyphic, though occasionally diglyphic, possibly on rare occasions aglyphic. A pair of directive mesenteries is regularly attached to each siphonoglyph. The animals possess the usual number of complete non-directive mesenteries. These, however, do not show the regular hexamerous arrangement often met with in this species, but are as a rule very irregularly disposed. As I have elsewhere indicated (compare Parker, '97, pp. 263, 264), M. marginatum is represented by two chief types: a diglyphic one often characterized by a strictly hexamerous arrangement of its mesenteries and a monoglyphic one in which amongst other forms three sub-types, distinguished respectively by having five, six, and seven pairs of non-directives, may be recognized. The animals produced by longitudinal fission may come under any of these heads except the regularly hexamerous diglyphic form, to which about one fifth of the numbers of specimens ordinarily collected belong. While I can confirm Torrey's ('98, p. 357) statement that diglyphic and monoglyphic individuals may arise by the same mode of non-sexual reproduction, I believe he has gone too far when he denies any possible correlation between these structural types and the methods of reproduction. Since no mode of non-sexual reproduction has been shown to give rise to a hexamerous diglyphic specimen, and since this type is represented by about one fifth of the number of individuals in the species, it seems to me still possible that this may be the result of sexual reproduction.[1] The value of this suggestion must, however, await further investigation. Should it prove true, much of the irregularity in the arrangement of the mesenteries in Metridium would be associated with non-sexual reproduction.

SUMMARY.

The double specimens of Metridium examined had either two mouths on one oral disk or two complete oral disks. In the former cases the œsophageal tubes were incompletely divided (Y- or V-shaped); in the latter, there were two completely distinct tubes.

The mouths of the double specimens were usually monoglyphic, sometimes diglyphic, and in one instance aglyphic. Two siphonoglyphs were usually placed symmetrically to the supposed plane of division.

A pair of directive mesenteries was always attached to each siphonoglyph. There were about twice as many non-directive mesenteries in double specimens as in single ones.

In any given case the assumed plane of division passed through either two primary ectocœls or two primary entocœls, never through a primary entocœl on one side and a primary ectocœl on the other.

The double specimens were either male or female, and showed no evidence of hermaphroditism.

They are not due to fusion.

---

[1] In briefly discussing this question, Torrey ('98, p. 357) has quoted me in a somewhat misleading way. It is true that I suggested that the monoglyphic and diglyphic types might have the value of varieties, and also that they might be correlated with the methods of reproduction, but this was not done in one breath, as might be inferred from Torrey's statement. I mentioned the possible interpretation as varieties on page 269 of my former paper (Parker, '97), and, after stating my disinclination to accept this interpretation, I suggested on page 270 the possibility of correlation with the methods of reproduction. Why Torrey should have combined these two suggestions as one, and why he should have used quotation marks for a piece of composition which is not mine, remain to be explained.

While some may be monstrosities, the occurrence of natural pairs shows that longitudinal fission takes place.

This process is probably extremely slow.

While monoglyphic and irregular diglyphic specimens may be produced by this and other non-sexual processes, the production of regular hexamerous diglyphic specimens by non-sexual methods has not been observed. Such specimens number about one fifth of all collected, and may be the products of sexual reproduction.

Cambridge, January 13, 1899.

PAPERS CITED.

Agassiz, E. C., and Agassiz, A.

'65. Seaside Studies in Natural History. Boston. Ticknor and Fields. viii + 155 pp.

Carlgren, O.

'93. Studien über nordische Actinien. Kongl. svenska Vet-Akad. Hdlgr. N. F., Bd. XXV. No. 10, pp. 1–148, Taf. I.–X.

Dicquemare, J. F.

'75. A Second Essay on the Natural History of the Sea Anemonies. Phil. Trans. Roy. Soc., London, Vol. LXV., 1775, pp. 207–248, Tab. VI.

Dixon, G. Y., and Dixon, A. F.

'91. Report on the Marine Invertebrate Fauna near Dublin. Proc. Roy. Irish Acad., 3d Ser., Vol. II. pp. 19–33.

Foot, F. J.

'63. Notes on the Astræacea of the Coast of Clare. Proceedings of the Natural History Society of Dublin, for the Sessions 1859–1862 (inclusive). Vol. III. pp. 63–69.

Gosse, P. H.

'60. Actinologia Britannica. A History of the British Sea Anemones and Corals. London. Van Voorst. xl + 362 pp., 12 Pls.

Johnston, G.

'47. A History of the British Zoophytes. Second Edition. London. Van Voorst. xvi + 488 pp., 74 Pls.

Koch, W.

'86. Ueber die von Herrn Prof. Dr. Greeff im Golf von Guinea gesammelten Anthozoen. Inaugural-Dissertation. Bonn, Carl Georgi. Pp. 36, 5 Taf.

McCrady, J.

'59. Instance of incomplete longitudinal Fission in Actinia cavernosa Bosc. Proceed. Elliott Soc. Nat. Hist. Charleston, S. C. Vol. I. pp. 275–278.

Parker, G. H.

'97. The Mesenteries and Syphonoglyphs in Metridium marginatum Milne-Edwards. Bull. Mus. Comp. Zoöl., Vol. XXX. pp. 259–273, 1 Pl.

Thorell, T.

'59. Om den inre byggnaden af Actinia plumosa Müll. Öfversigt af Kongl. Vetenskaps-Akademiens Förhandlingar. Vol. XV. 1858, pp. 7–25, Tab. I.

Torrey, H. B.

'98. Observations on Monogenesis in Metridium. Proceed. California Acad. Sc., 3d Ser., Zoölogy, Vol. I. pp. 345–360, Pl. XXI.

Wilson, H. V.

'89. On the Occasional Presence of a Mouth and Anus in the Actinozoa. Johns Hopkins University Circulars. Vol. VIII. pp. 37, 38.

EXPLANATION OF FIGURES.

All figures were taken from specimens of Metridium marginatum Milne-Edwards. In the figures of transverse sections the dotted lines represent the axes of the mouths projected upon the plane of section. All complete mesenteries are drawn. The incomplete mesenteries usually form more or less irregular groups in the primary ectocœls. Each primary ectocœl containing incomplete mesenteries either has these mesenteries represented in it or is marked with x; any primary ectocœl not designated in one or other of these ways contained no incomplete mesenteries.

PLATE I.

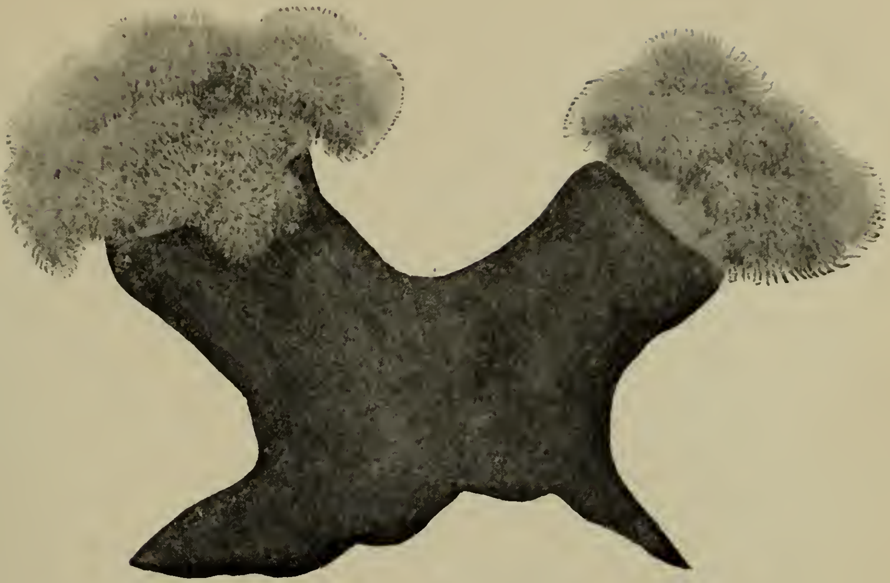
Reproductions of figures of double specimens from the unpublished drawings of Professor Louis Agassiz.

Fig. 1. Side view of a specimen with two oral disks. The original drawing is marked, "Alive in Aquarial Gardens, May, 1860." Drawn by J. Burkhardt.

Fig. 2. Oral view of a partly contracted specimen with two oral disks. The two disks show a greater difference in size than is usual with this species.

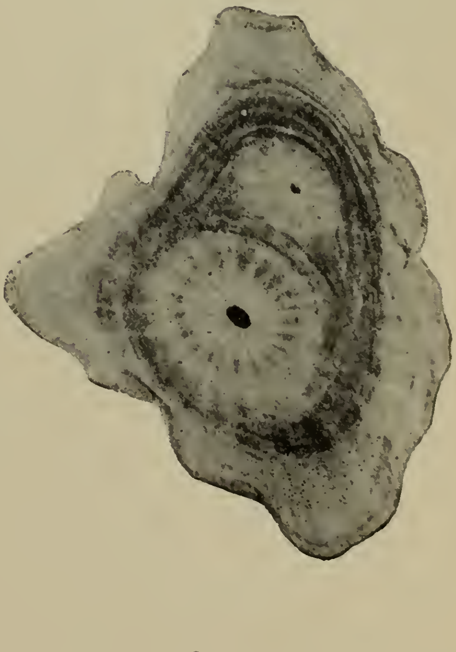
Fig. 3. Oral view of what is probably the same animal as that shown in Figure 2, but in a more contracted state.

The original drawings from which Figures 2 and 3 were taken were on the same sheet of paper, which was marked, "Boston, Sept. 28, '47." Drawn by W. H. Tappan.



1

2



3

Boston Eng. Co.

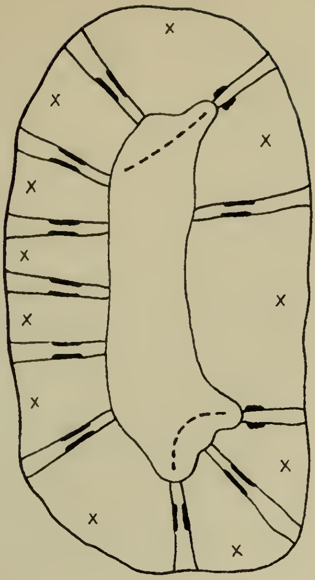
PLATE II.

Fig. 4. Lateral view of specimen D, with two complete oral disks, collected by the writer and S. F. Williams at Beverly Bridge, Mass. The arrangement of the internal parts of this specimen as seen in transverse section is shown in Figure 9 (Plate III.). Female. Natural size.

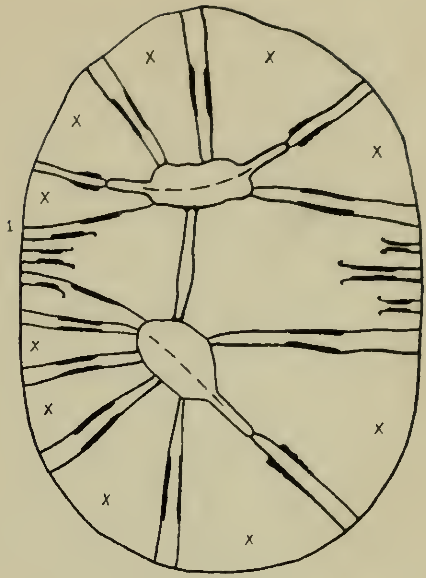
Fig. 5. Oral view of the same specimen as that shown in Figure 4. Slightly enlarged.

Fig. 6. Transverse section of specimen A, with one oral disk and two mouths. The section is taken at a level at which the œsophagus is single. Orally from this the œsophagus becomes double, each tube leading to a mouth opening. Sex not determined. Collected by B. H. Van Vleck at Cape Ann, Mass. × 2.

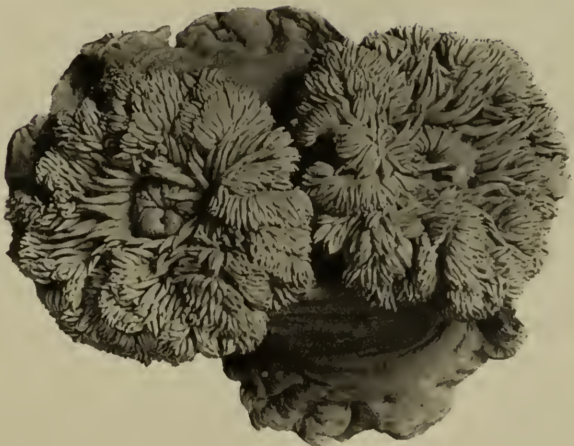
Fig. 7. Transverse section of specimen B, with one oral disk and two mouths. The cavities of the two œsophageal tubes were entirely distinct except near the extreme aboral end, where the two tubes united to form a single œsophagus. The œsophageal tubes are connected with each other by a pair of membranes which resemble mesenteries without differentiated muscle bands. These membranes extend from the region in which the two œsophageal tubes separate almost to the oral disk. The cavity between them opens into the gastrovascular cavity orally, since both membranes are deficient in that region. Mesentery 1, though complete orally, is incomplete through more than half of its pedal length. Collected by the writer at Wood's Hole, Mass. Female. × 3.



6



7



5

4

C. Bullard, photo.

Heliotype Co. Boston

PLATE III.

All the specimens shown on this plate, except those represented in Figure 15, had each two complete oral disks and two distinct œsophageal tubes.

Fig. 8. Transverse section of specimen C, in which the two œsophageal tubes are connected by a single membrane which reached neither the oral nor the pedal disks. Collected by the writer at Wood's Hole, Mass. Male. × 1.5.

Fig. 9. Transverse section of specimen D, also shown in Fig. 4 (Plate II.). Female. × 2.

Fig. 10. Transverse section of specimen E, collected by B. H. Van Vleck at Cape Ann, Mass. Sex not determined. × 2.

Fig. 11. Transverse section of specimen F, collected by C. W. Prentiss at Wood's Hole, Mass. Male. × 3.

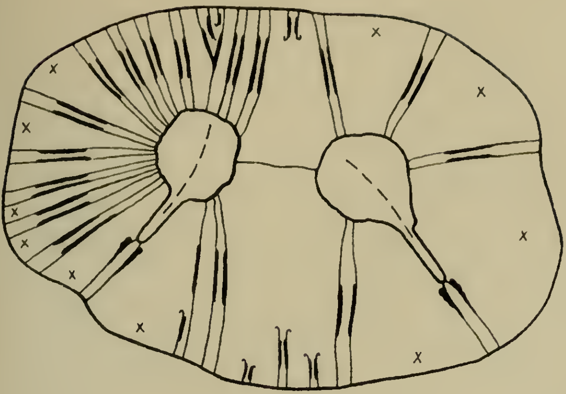
Fig. 12. Transverse section of specimen G, collected by J. I. Hamaker at Newport, R. I. Female. × 2.

Fig. 13. Transverse section of specimen H, collected by R. H. Johnson at Wood's Hole, Mass. Female. × 2.

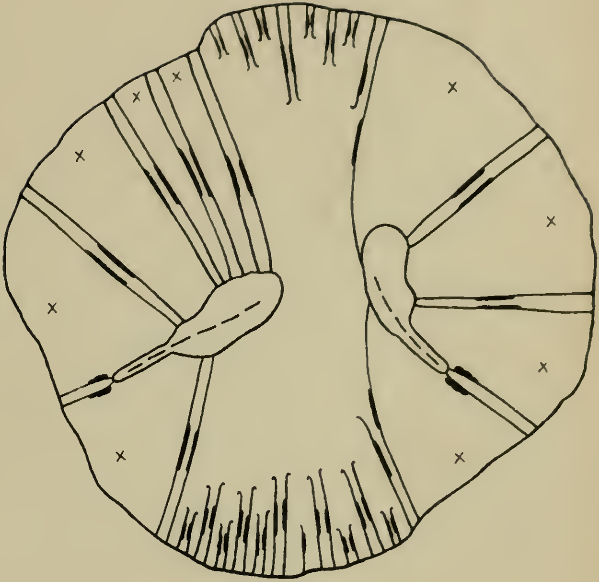
Fig. 14. Transverse section of specimen I, collected by the writer at Wood's Hole, Mass. Male. × 2.

[Specimen J, collected by the writer at Wood's Hole, Mass., was lost in an attempt to rear it.]

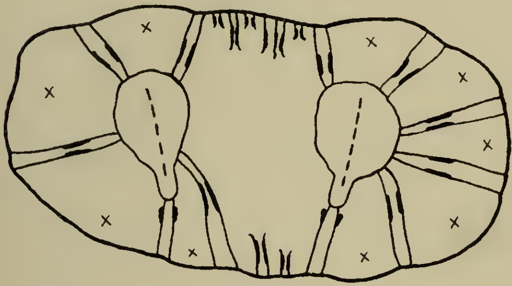
Fig. 15. Transverse section of a natural pair of individuals, showing their mutual relations so far as positions of siphonoglyphs, etc. are concerned. The two specimens, which were entirely separate. were killed and preserved without being removed from the shell on which they were found.



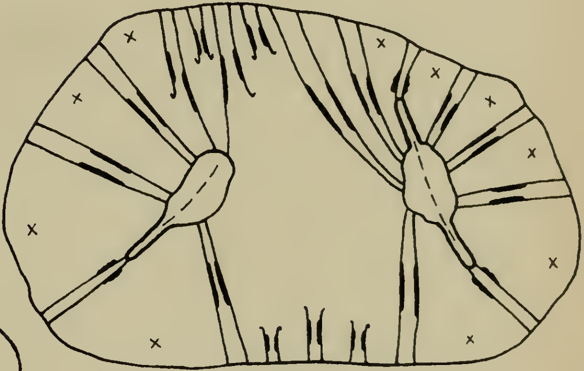
8



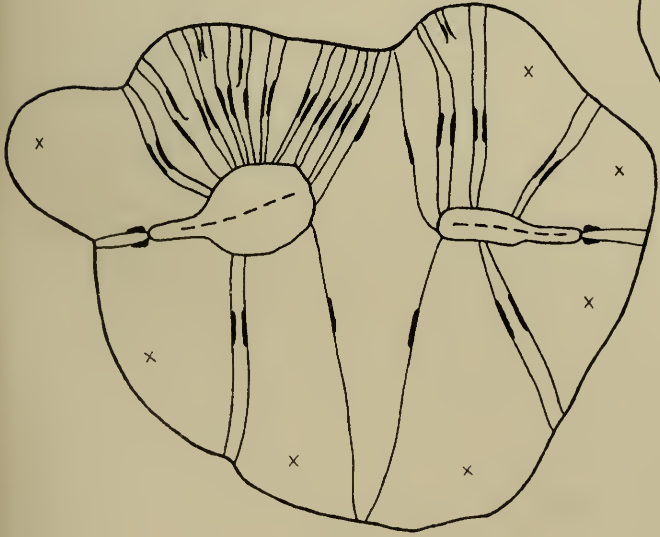
9



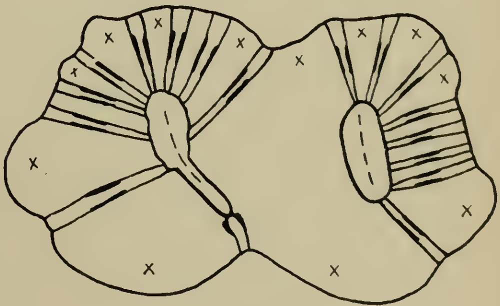
10



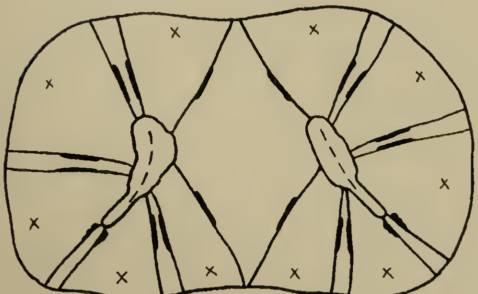
11



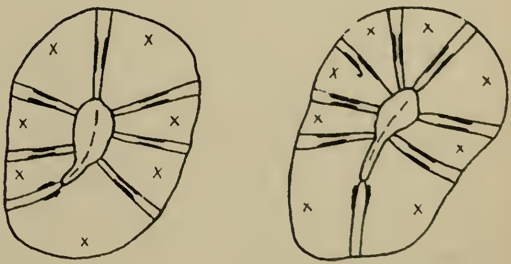
12



13



14



15

G.H.P., del.

Heliotype Co., Boston.

No. 4. — *Ovogenesis in Distaplia occidentalis* Ritter (*MS.*), *with Remarks on Other Species.*[1] By Frank W. Bancroft.

CONTENTS.

I. Introduction.

The Distaplia material here described was collected by Professor William E. Ritter at Pacific Grove, California, during the summer of 1896, and is much of it in an excellent state of preservation. Davidoff's ('89, p. 118) corrosive-acetic mixture, picro-acetic acid, picro-sulphuric acid, and Perenyi's fluid were used for fixing, and of these the first was by far the best, and yielded excellent results.

---

[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College, under the direction of E. L. Mark, No. XCVIII.

For the name of the species I am also indebted to Dr. Ritter, who has kindly allowed me to quote his manuscript name, *Distaplia occidentalis.* With the material at my disposal, which, for the most part, consists of only pieces of colonies, and these from but one of the many localities where the species has been encountered, it would be unwise to attempt a complete diagnosis. I will, therefore, endeavor to give only a few of what seem to be the distinctive features.

The colonies vary in shape, being both incrusting and pedunculate; in the latter case they are often mushroom-shaped. The color also varies; in preserved specimens it may be whitish, salmon-yellow, brownish, or purple. The zoöids are small, adult ones exceeding 3 mm. by a few micra only, and they are always hermaphrodite, ovary and testis being well developed at the same time. The ramifications of the pyloric gland do not end in swollen ampullæ. The stomach, though nearly smooth on the outside, is thrown into irregular folds within, so that in whole preparations it has a reticulated appearance. The test is composed of the thin walls of numerous lacunæ. It contains many ectodermic vessels, and these do not anastomose. These characters easily separate *D. occidentalis* from *D. magnilarva* (Delle Valle, '82, p. 200; Lahille, '90, p. 157), *D. lubrica* (Drasche, '83, pp. 22–23), *D. vallii*[1] (Herdman, '86, pp. 128–132), and *D. livida* (Sars, '50, p. 154; Huitfeld-Kaas, '96, p. 11). It appears to be distinguished from *D. clavata* (Sars, '50, p. 154; Huitfeld-Kaas, '96, p. 11) by the great length, 6 cm. of the narrowly clavate colony. This leaves *D. rosea* (Delle Valle, '82, p. 202; Lahille, '90, pp. 174–175; Caullery, '95, p. 8) and *D. intermedia* (Heiden, '93, pp. 348–349), with which our species seems to be closely related. If *D. intermedia* is found to have unisexual zoöids, then this character will separate it from *D. occidentalis.* If, on the other hand, the colonies examined by Heiden were not fully mature, and the zoöids become hermaphroditic later, then his species and *D. rosea* must be united. Thus we get *D. rosea* as the closest, and a very close, relative of *D. occidentalis.* In fact, the only differences seem to refer to characters of minor importance, such as the range in shape and color of the colonies, and the inequalities on the inner surface of the stomach.

---

[1] If, as Herdman says (pp. 128, 130), *D. vallii* contains no bladder cells in the test which "consists of a homogeneous matrix in which are scattered numerous small test cells and larger pigment cells (Plate XVIII. Fig. 4)," then this species must be considered rather distantly related to the other members of the genus, for in all of these in which the structure of the test has been examined, it has been found to be lacunar.

But, as has already been said, I have not made the extended observations necessary to place beyond doubt the position of *D. occidentalis.*

The Styela and Chelyosoma material was mostly collected by myself, at various places along the California coast, during the summers of 1894 and 1895, and studied about a year later. Four fixing media were used, — Flemming's fluid, picro-sulphuric acid, glacial acetic acid, and Perenyi's fluid, and of these the last gave the best results.

The investigation of the Styela and Chelyosoma material was done for the most part at the University of California, and that of Distaplia entirely at Harvard University during the college years of 1896–97 and 1897–98.

The stains used for the last species were mostly iron hæmatoxylin and a combination of methyl green and acid fuchsin, adapted from Auerbach's ('96, p. 414) method B a. These two methods supplement each other very nicely, and render the use of others almost superfluous; the hæmatoxylin demonstrating most morphological features splendidly, while the chemical constitution is brought out well by the methyl green and fuchsin. The iron hæmatoxylin was employed in the usual way; fresh solutions of the stain were found to give decidedly the best results, but for some things, such as nucleoli, which take a fresh solution too strongly, older ones are often to be preferred. In using the double stain, sections were first treated in a mixture containing two parts of a 0.1% aqueous acid fuchsin solution, to which a little acetic acid had been added, and three parts of a 0.1% solution of methyl green. They were left in this mixture for about fifteen minutes, and then immersed in a 0.1% solution of methyl green for a few minutes longer. From the stain the sections were transferred directly to 90%, and then to absolute alcohol, xylol, and balsam. No especial care is necessary in order to get a satisfactory differentiation. In addition to the two stains mentioned, List's ('96, pp. 480–487) potassium ferro-cyanide methods were also employed, but yielded no very satisfactory results. They will be discussed later.

The sectioning of the younger ova presents no difficulties, but the older ones, which, with the exception of the germinative vesicle, are pure yolk, are exceedingly difficult to deal with, on account of the crumbling of the yolk, and for them no satisfactory method was found. However, all of the material that I had access to had been preserved in 80% or 90% alcohol for some time, so that I did not have an opportunity of testing the effect of preservation in weaker grades of alcohol, formalin or paraffine. As a rule, the whole colony was sectioned, but when dealing with the maturation stages, the best results were obtained by dissecting out the ova, and then leaving them for a very short time in the higher grades of alcohol, xylol, and paraffine. Four minutes in each of the former, and three in the paraffine, melting at 50° Centigrade, secured a good penetration, but did not entirely prevent crumbling. Painting the sections with flexible collodion was resorted to, but while this held together the section that was being cut, it also pulled part of the yolk out of the next section, and imperfect series resulted. Double imbedding with celloidin and paraffine was also tried, but this made the yolk too brittle, so that I am still in quest of a satisfactory method for this material.

The sections were cut 6 μ thick, and fastened to the slide with tap water, which was evaporated at about 36° after the sections had been stretched by subjection to a slightly higher temperature. This method gave perfectly satisfactory results, and possesses the immense advantage of leaving no foreign substance on the slide.

I wish to express here my thanks to Dr. E. L. Mark, under whose direction this research has been carried on, and to whose constant kindness the credit of much that may be of value therein is due.

II. Sexual Organs.

1. Development in Distaplia occidentalis.

Old colonies which had already reached sexual maturity are the only ones in which I have studied the development of the sexual organs. In such colonies, all of the buds, even the smallest and least differentiated, possess the fundament of the ovotestis. Figure 1 (Plate 1) represents a section through such a bud. The large germ-cells, which indicate the presence of the ovotestis, are situated entirely on one side of the flattened inner vesicle, and all of the evidence indicates that this side is dorsal; for, as soon as the axes of the bud are established by the development of the other organs, the ovotestis is found to lie in the mid-dorsal line. The rather indiscriminate mingling of the young oögonia and primordial follicle cells, and the superficial[1] position of the oögonia as contrasted with the deeper position of the less differ-

---

[1] Following Julin ('93, p. 95), I use the terms *superficial* and *deep* as relating to the position of the structure in question with reference to the whole individual. *Peripheral* and *central* are used only to describe position with reference to the organ itself.

entiated cells, which will go to make up the testis, are characteristic of all the younger buds. On the other hand, the amount of separation of the ovotestis from the inner vesicle is subject to considerable variation. In the bud figured, the two apparently are fused in places, but in other buds, which are entirely similar in all other respects, the line of demarcation of the ovotestis from the inner vesicle is most distinct. In these cases it is seen that all the mesodermic elements on the dorsal side of the inner vesicle, with the exception of a few scattered cells, are contained in the fundament of the ovotestis. The conclusion, then, to be drawn from the examination of the undifferentiated bud is that the possibility of an endodermic origin for some of the unspecialized cells of the ovotesticular fundament must be conceded; but certainly the greater part, and perhaps the whole of it, is derived from the mesoderm.

So far as the spaces between the cells of the ovotestis are concerned, the figure represents a rather unusual condition, since in most cases the fundament forms a compact mass. But on account of the unusual separation, this bud demonstrates very clearly that in this stage Distaplia has no "assise périphérique" such as Julin ('93, p. 97) and Floderus ('96, p. 175) found in the youngest stages examined.

In slightly older buds, where the fundaments of the intestine and epicardium are present, the only change in the ovotestis is due to a few of the ova having increased in size and assumed more distinctly the characters of the oögonium. Its position is still dorsal, but it occupies only the posterior end of the dorsal side of the bud. At still later stages, even after the peribranchial sacs are quite large, the ovotestis is apparently fused with the posterior end of the dorsal tube. This connection is often very puzzling; in one series, for instance, the lumen of the dorsal tube extends quite to the ovotestis, the latter appearing as a thickening of the dorsal tube. In buds of these stages there is considerable variation in the disposition of the organs, the ovotestis being placed slightly to one side of the dorsal tube or directly behind it, or even dorsal to its posterior end. Accordingly, I am inclined to believe that the apparent union between these two organs is not significant, but due rather to their close approximation and to oblique sectioning. This position is further strengthened by the fact that both before, immediately after, and even occasionally during, this stage, the ovotestis is completely isolated from all other organs. Whenever the ovotestis is thus isolated, it is produced anteriorly into a genital strand, which occupies very nearly the mid-dorsal line. It seems likely, then, in view of the very general isolation of the sexual organs observed in the early stages, that the whole of these organs is produced by the growth of the ovotesticular fundament of the undifferentiated bud.

In older buds the genital organs are always distinctly separated from the other organs, and the differentiation of ovary from testis is speedily accomplished. Figures 2 and 3 (Plate 1) represent two consecutive cross-sections through a stage in which this separation is going on. In Figure 2, the posterior section, there are two well-defined masses of cells which in Figure 3 are united, the only indication of the future separation being a slight notch on one side of the fundament. The splitting takes place from behind forwards, and appears to be accomplished by a rearrangement of the cells in situ, and the secretion of a structureless membrana propria between the two masses. Preceding the actual separation, however, there is a differentiation consisting in the fact that the smaller cells, which will produce the testis, are always situated deeper than the others, and this, as Figure 1 shows, is characteristic even of the earliest stages. Both ovary and testis are usually solid masses of cells at this stage, and for some time later, but occasionally one or both of them may develop a lumen (Plate 1, Fig. 3), though in the case of the testis it is never well defined.

Figure 4 (Plate 1) gives a longitudinal section of a somewhat later stage, the ovary and testis being completely separated from each other, but both still attached to a common genital strand (*fun. gen.*). The latter extends from the anterior ends of the genital organs to the left peribranchial sac, with the walls of which it fuses. It is much thicker and shorter in the earlier than in the later stages, when the distance that it has to traverse becomes greater.

An examination of Figures 2, 3, and 4 shows that at this stage there is a well-defined tendency for the long axis of the peripheral nuclei of the testis or testicular part of the ovotestis to occupy a tangential position. This marks the beginning of the peripheral epithelium that bounds the testis at all later stages. In the ovary, however, such a peripheral layer is absent in this stage, as in the earlier ones, so that the young oögonia or their follicles extend to the surface of the organ. This is exactly the condition found by van Beneden et Julin ('85, p. 334) for the same stage of these organs in Perophora. Their figures (6 *a* and 6 *b*, Planche XVI.) show the peripheral layer well differentiated in the testis, but not in the ovary, though the two organs are still connected.

The fundaments of the oviduct and vas deferens are at first formed by the splitting of the genital strand, which is progressively converted from behind forward into vas deferens and oviduct. But with the growth of the bud, the undifferentiated portion of the strand is stretched more and more, until it becomes a single row of cells attached end to end, which connects the last differentiated portions of the two ducts with the peribranchial epithelium.

From this time on cell-multiplication must take place pari passu with the separation of the ducts. But as no mitoses were encountered, it is useless to speculate as to whether this multiplication is accomplished in the region of the genital strand, the differentiated ducts, or the mass of cells where the three join. Even before the ducts are separated throughout their whole length a histological difference is apparent, the nuclei of the oviduct cells being more flattened and taking a fainter stain than those of the vas deferens. Another point of interest is that, contrary to what obtains in other species, both ducts are solid strands, which do not acquire a lumen until much later.

While the ducts are being separated, the testis increases in size and entirely covers the deep side of the ovary, so that in cross-section it appears as a crescent, the tips of which abut against the ectoderm on either side of the ovary. Later it becomes divided up into the eight or more testicular pouches which are characteristic for the species. Meantime the ovary increases in size and acquires a lumen, on the deep side of which most of the ova are situated. With these last changes all the essentials of the adult structure are reached, but the position of the sexual organs with respect to the axes of the animal, and the point of union of the genital strand with the peribranchial sacs, still undergo some change.

In young buds with small peribranchial sacs, which have not yet united to form the median cloaca, and without a trace of stigmata, the sexual organs are situated in the mid-dorsal line, and also in the intestinal loop which has developed around them. At this stage the œsophagus opens into the right posterior corner of the branchial sac and the anus is near the left posterior corner, so that the whole of the post-pharyngeal digestive tract is in a frontal plane. The genital strand extends forward in the median line and joins the tip of the left peribranchial sac, where this comes nearest to the sagittal plane. Later the point of union of the genital strand with the peribranchial sac migrates still farther to the left, so that it comes to lie much nearer to the anus. Now, as the bud grows and assumes the adult shape, the whole abdomen is so twisted that right becomes ventral, left dorsal, and the loop of the digestive tract occupies the sagittal plane. By means of this twisting, the anus becomes dorsal and the point of union of the genital strand with the peribranchial sacs migrates from the left through the cloaca to the right peribranchial sac; and thus the adult relations of the organs are acquired.

Conclusions.

From this account it follows that the development of the sexual organs in Distaplia occidentalis agrees with that of the three species described by van Beneden et Julin ('85, pp. 328–349) and of Ciona intestinalis described by Floderus ('96, pp. 173–181) in the following important respects: —

1. The whole of the sexual organs of the adult is developed from a single solid mass of cells of mesodermic origin, which during the later period of its existence is connected with the cloaca by a genital strand.
2. The ovary is separated from the testis by a splitting of the primitively single fundament which proceeds from behind forward. The separation of the two ducts takes place in the same manner, though here growth must intervene. The ovary and oviduct always lie on the superficial side of the testis and vas deferens.
3. The cavity of the ovarial fundament is formed in such a way that the germinative epithelium lies in its deeper wall.

Distaplia occidentalis differs from the species mentioned in that: —

1. The ovary and testis are usually solid, and the ducts always so, at the time when they are separated from each other.
2. The genital strand is at first quite thick, and decreases in diameter as the bud grows.
3. The fundament of the ovotestis is present in the youngest stages, whereas in the other species it appears quite late in ontogeny.

With the development of these organs in Styelopsis grossularia studied by Julin ('93), that of our species has less in common, because in the two the ovaries and testes are of a different type. In Distaplia, and the four species with which it has been compared, the ovary is distinctly separated from the oviduct proper, in the walls of which no ova arise, while in Styelopsis the deep wall is given over to the production of ova throughout the whole extent of the oviduct. Furthermore, in Styelopsis the testis is divided into a number of lobes, each one opening separately into the peribranchial cavity, whereas in the other species it is a single organ with a single long duct. Accordingly, there is no genital strand at all in Styelopsis, and the separation of ovary from testis takes place from the middle towards both ends; in the other respects mentioned, however, this genus agrees with Perophora, Phallusia, Clavelina, and Ciona.

With respect to the presence of a peripheral epithelium surrounding the developing ovotestis, there is more variation. In Perophora and Distaplia this is present in the testis but not in the ovary, while in Clavelina, according to the figures of van Beneden et Julin ('85, Planche XV., Figs. 9, 10, and 13), in Styelopsis and in Ciona it is encountered in both. This distribution is very suggestive, for the first two genera have rather small zoöids, and a simple structure, while the last three are much larger, produce many more sex cells, and are more highly specialized. It seems, then, that it is only in the larger and more complex ascidians that this peripheral epithelium is formed around the developing ovary.

For the explanation of the fact that the oögonia are present in the undifferentiated Distaplia bud, we must undoubtedly look to the fact that in this genus, as in Botryllus, the life of the individual zoöid is very short, so that apparently it would not have time to mature an ovum if the latter were to start from a wholly undifferentiated cell, and consequently it receives the ovum in a slightly elaborated form. In these two genera, however, the structure and development of the sexual organs seem to be entirely different, as according to Pizon ('92–'93, pp. 257–271), the ovary and testis of Botryllus arise from separate fundaments, and no real ovary is formed at all, but merely a few follicles attached by separate stalks to the peribranchial sacs.

Distaplia also agrees with Botryllus and disagrees with all other species in which the matter has been studied in that the fundaments of the sexual organs and their ducts are usually solid. This condition is probably the direct result of the early development of these organs necessitating their being blocked out in solid masses before enough cells to form vesicles were available.

On the whole, however, it is evident that the development of the sexual organs in our genus conforms to the type first described by van Beneden et Julin for Perophora, Clavelina, and Phallusia, and deviates rom it only in minor respects due to the simpler structure and short flife of the zoöids in Distaplia.

2. Structure in the Adult.

a. *In Distaplia occidentalis.*

This species of Distaplia is always hermaphroditic, no unisexual zoöids such as have been described for D. magnilarva having been encountered. Nor is there any provision for the prevention of self-fertilization by means of protandry or protogyny. The testis is found to be functionally active for a much longer period than the ovary, for spermatozoa are always found in the vas deferens from the time the oldest ova are about half grown until after the usual number of eggs, two, has been laid.

The development of the genital organs in zoöids of the same size varies considerably according to the condition of the colony. If the oldest zoöids of a colony are laying eggs or have recently done so, then all the younger ones and the older buds have their sexual organs more fully developed than in individuals of the same size in colonies which possess no mature sexual products. In the undifferentiated buds, however, the same conditions obtained in all the colonies.

The position of these organs is on the right side of the intestinal loop. When partially developed, they do not extend beyond the intestine, either anteriorly or posteriorly, but when maturity is reached, they project beyond it in both directions. In this condition the ovary occupies the extreme hind end of the zoöid and is entirely posterior to the loop. The testis, which is much more voluminous, is also mainly posterior to the loop, but its extreme anterior end is usually within it.

Concerning the finer structure of the ovary, recent investigators are not entirely in accord. Corresponding to the fact that in the development of this organ a peripheral epithelium is described by Julin and Floderus, which the earlier investigators had not mentioned, there is a similar disagreement about the adult structure. But here the difference is of much more importance, for Julin, in tracing the peripheral membrane into the adult ovary, arrives at an idea of the relation of the germinative epithelium to the peripheral wall essentially different from that of his predecessors. Van Beneden et Julin ('85, pp. 350, 358) and Maurice ('88, p. 456, 464) had found that the superficial wall of the ovary passed insensibly into the germinative epithelium occupying the lateral edges of the organ. The deeper[1] wall, which is

---

[1] There can be no doubt that in van Beneden et Julin's Figure 14 (Planche XV.) the wall of the ovary of Clavelina rissoana that is placed uppermost and described

formed by a cylindrical epithelium in both Clavelina rissoana and Fragaroides, and to which the stalks of the older follicles are attached, is considered as having developed from the germinative epithelium. According to this view, then, both the germinative epithelium and the cylindrical epithelium connecting with and forming the stalks of the follicles[1] are merely differentiations from the wall of the ovary and not additional structures. In other words, the ovary is but a specialized part of the oviduct.

On the other hand, Julin (p. 95) finds that in Styelopsis the superficial wall of the ovary connects with a thin limiting epithelium and not with the germinative epithelium. The latter represents an additional element lying within the cavity formed by the two peripheral epithelia and not represented at all in the *oviduct* of such forms as Clavelina and Fragaroides. As the ova increase in size, they push the limiting epithelium before them, and retain their connection with the rest of the ovary by means of it. Thus, according to this author, the outermost layer of cells surrounding the ovum and continuous with the stalk is not, as has been formerly supposed, derived from the germinative epithelium, and is not part of the true follicular covering of the egg.

Floderus, though he finds a limiting epithelium in the young ascidian, does not agree with Julin concerning the structure of the adult. He finds that the germinative epithelium continues into the epithelium of the superficial wall (p. 187), that the epithelium which he thinks corresponds to Julin's limiting epithelium does not connect with the superficial wall (p. 185), and that the stalks of the ova connect with their follicles (p. 190).

But little evidence in favor of Julin's contention has been found in the ovary of Distaplia occidentalis, which has essentially the structure

(p. 351) as "la voûte de cette même cavité" is the deep or ventral wall. Maurice (p. 459) takes it for granted that this wall is dorsal, and points out the difference that would exist between Clavelina and Fragaroides on this point. Floderus (p. 183–184) discusses the question fully and concludes that although van Beneden et Julin do not state explicitly which side is dorsal, the description and the position of the figure when compared with the other figures on the plate compel us to believe that the authors consider the "voûte" dorsal. However, leaving the question of the intention of the authors aside, the ventral position of the germinative epithelium in the *fundament* of the ovary in C. rissoana and of the ovarian follicles in the adult ovary of C. lepadiformis, described by Floderus, point conclusively to the fact that the same condition must obtain in the adult C. rissoana.

[1] I propose in future to call the characteristic tissue constituting this epithelium stalk tissue.

described for the same organ in Fragaroides. It consists of two sacs, the first of which is an enlargement of the posterior end of the oviduct, and whose cavity may be designated as the lumen of the ovary proper (Plate 1 Fig. 5, *lu. ov.*). On the deeper wall of this sac is situated the germinative epithelium, which occupies the greater part of its extent. When viewed from within the animal, this epithelium presents an oval outline with its long axis running in an antero-posterior direction. The second sac, whose cavity is spoken of as the lumen of the stalk tissue, is situated on the deep side of the first one, and its lumen connects with that of the ovary proper by a narrow passage in the stalk, which is inserted in the deep wall of the ovary proper at about the centre of the oval patch of germinative epithelium. Figure 5 represents a cross-section through both these cavities and the stalk connecting them.

In our species the adult ovary is composed of three tissues (Plate 1, Figs. 5, 6). First the thin pavement epithelium comprising the superficial[1] wall of the organ (*par.′*). Usually it forms also the lateral edges and is often continued so as to constitute part of the deep[1] wall (Plate 1, Figs. 5, 6, 7, *par.″*). It is directly continuous with, and of the same histological structure as the wall of the oviduct, both being very thin and devoid of cilia.

Secondly, the germinative epithelium and the older ovarian follicles developed from it. The former sometimes appears as directly continuous with the superficial wall, but more often, especially when the ova are a little larger (Figs. 5, 6, 7), they seem to lie enclosed within a peripheral epithelium which is itself continuous with the superficial wall. The ova, which are the only indication of the germinative epithelium, are very few, the total number in an adult zoöid being usually under twenty. Occasionally a very small oögonium, or an ovum that may perhaps be considered undifferentiated (Fig. 5, *ov'go.*), is found within the superficial wall, but in the great majority of cases they are confined to the deeper wall. Here they are usually so arranged that the older the oögonium the nearer it is to the middle of the wall to which the stalk tissue is attached (Fig. 5). There are very few or no primordial ova in the epithelium, so that physiologically it is really no germinative epithelium at all, but merely a repository for the youngest oögonia. It is very interesting to note, however, that this repository of oögonia takes on the same relations to the rest of the ovary that the functional germinative epithelia of the more specialized

---

[1] Used in the technical sense defined on page 62.

genera assume. In Distaplia occidentalis this arrangement of the oögonia, and even their existence there, has reference to the phylogeny of the genus rather than to present usefulness, for the usual number of eggs laid by a zoöid is two, or at most three, and since in the adult there is no provision for budding, all the younger oögonia must degenerate with the zoöid and go to waste.

Thirdly, there is the stalk tissue (Figs. 5, 6, *tis. pd.*), which is directly continuous with the germinative epithelium or its peripheral membrane, and also by means of the follicular stalks with the follicles of all the older ova (Plate **3**, Figs. 14, 15, *tis. pd.*). This, in its typical condition (Figs. 5, 15), is a cylindrical epithelium with rather irregular oval nuclei and a thick, structureless basement membrane on its peripheral surface. The stalk tissue surrounds a cavity (Fig. 5, *lu. pd.*) that is usually somewhat larger than the true cavity of the ovary, with which it connects by a narrow stalk. This stalk joins the rest of the ovary in the region of the germinative epithelium, so that a series of cross-sections presents exactly the same appearance as in Fragaroides. Posteriorly the deep wall is composed of a continuous germinative epithelium; about the middle of the epithelium the cavity of the stalk tissue connects with the cavity of the ovary proper and divides the germinative epithelium so that in a cross-section of this region it looks like a paired structure (Plate **1**, Fig. 5). Anteriorly the entire centre of the deep wall is made up of germinative epithelium as it is posteriorly. As a result of this structure, it is seen that the stalk tissue does not connect with the flat pavement epithelium comprising the wall of the oviduct. The cavity of the stalk tissue extends posteriorly behind that of the ovary proper, and has the follicles attached to it in such a way that the oldest ovum is usually the most posterior one. From this account it follows that the ovary, though not a paired organ, is a symmetrical one; but even this is not always the case. Occasionally the stalk tissue, instead of being inserted near the centre of the deep wall, joins the latter near one side, so that it connects with the superficial wall on one side and the germinative epithelium on the other.

The question as to whether in Distaplia occidentalis there is a limiting membrane which is distinct from the germinative epithelium, seems to be answered negatively. The condition mentioned above, and represented in Figures 5, 6, and 7, where the ova project strongly into the cavity of the ovary, seems to indicate that the germinative epithelium is bounded peripherally by a limiting membrane.

But it is impossible at this stage to tell whether the side of the ovum next to the periphery of ovary is covered by but one cell layer, the follicle, or by a limiting epithelium in addition to this. I have never been able to differentiate a limiting epithelium in this position, but the failure could not justify one in denying its existence. When it comes to the formation of the follicular stalk, however, evidence is obtained that is conclusive, for we get the external epithelium of the ovary, which should extend around the ovum independently of the follicle, connecting with it in the clearest possible manner (Plate **3**, Figs. 14, 15). Figure 14 shows part of a young ovum that is entirely outside of the ovarian wall, but which is not yet attached to it by a stalk. On the left the ovum is attached to the germinative epithelium, as the tangential section of a much younger egg (*ov'go.*) shows. On the right it joins stalk tissue which has not yet assumed its typical appearance. Between the two are cells which make up both the follicle and the wall of the ovary, and will probably differentiate into follicle and stalk tissue. Figure 15 represents the same region in an older ovum, where the stalk tissue presents its characteristic structure and is seen to be directly continuous with the follicular epithelium. From these facts the conclusion seems justified that in the adult Distaplia ovary, just as in the developing one, we have no peripheral limiting epithelium.

One feature that is not usually encountered in other species, but is quite conspicuous in the ovary of this one, is the corpus luteum (Fig. 5, *cp. lut.*). This structure is merely the part of the follicular covering of the egg which remains behind when the latter is extruded from the ovary. It will be described in detail after the origin of its constituent elements has been considered.

The oviduct (Plate **2**, Fig. 9, *ov'dt.*) is a narrow, thin-walled tube extending up the right side of the abdomen and in immediate contact with the ectoderm. Throughout its extent the vas deferens (*va. df.*) is closely appressed to its deep wall. The most striking peculiarity of the oviduct is that its diameter, even when distended by the passage of an ovum, is very much less than the normal diameter of the ripe egg. Accordingly, when the egg is passing through the duct, it is greatly distorted, assuming the shape of a sausage (Plate **3**, Fig. 17). In this figure the ovum occupies a part of the oviduct, all of the cavity proper of the ovary, and also the entire cavity enclosed by the stalk tissue and its own follicle. The point where the stalk tissue joins the germinative epithelium lining the deep wall of the ovary proper is well indicated by the constriction at *pd.* Figure 16 shows the normal size of the ovum before laying.

b. Observations on Other Species.

I have examined sections of the adult ovary in several other species, and describe the condition in two of these, on account of the light it throws on our conception of the fundamental structure of the ascidian ovary.

The first of these species is Styela montereyensis,[1] whose ovary presents a structure similar to, but not identical with, that described for Styela rustica by Floderus (p. 185–186). The ovaries are four elongated tubes, two on each side, which open at their anterior ends into the atrial cavity. The superficial wall is composed of a ciliated epithelium, which connects with a germinative epithelium at the lateral edges. The deep wall is much folded in an irregular manner, and is composed of a thin pavement epithelium with occasional small oögonia contained in its thickness. At times portions of the deep wall, where these oögonia are crowded together, look a good deal like germinative epithelium. I am convinced, however, that this is not the case, for nowhere in the deep wall are oögonia of the smallest size and undifferentiated ova, such as exist in the two lateral germinative epithelia, encountered. The presence of these small oögonia outside the germinative epithelium is due to the fact that the latter sometimes gives off its oldest oögonia after the younger ones, which are thus carried out into the deeper wall before they are really ready, and remain in it for a considerable period, while they are reaching the size at which they project beyond the pavement epithelium. All the older oögonia are situated on the deep side of this epithelium, presumably attached to it by their follicular stalks, though these are but seldom seen. In each of these four ovaries, then, we have essentially the same structure that exists in Clavelina and Styelopsis, where the ovary is single and situated in or near the sagittal plane. Furthermore, it is likely, though not proven, that these four ovaries are developed from separate fundaments, for in a very much younger stage (Plate 2, Fig. 12), when the whole of the deep wall is made up of the germinative epithelium, and the primordial ova are still dividing,

---

[1] This is one of the commonest of our California ascidians. It was first described by Dall ('71, pp. 157, 158) as *Cynthia montereyensis*, and subsequently by Fewkes ('89, pp. 134, 135) as *Clavelinopsis rubra*. Ritter ('93, p. 39) placed it in its proper genus, *Styela*.

and the vas deferens opens into the oviduct instead of the atrium, these organs occupy the same relative position as in the adult.

The second species is Chelyosoma productum, Stimpson ('64, p. 161). Here the structure is similar, but not identical, to that described by Floderus (p. 187) for the genera Ascidia, Ascidiella, and Corella. The ovary is much branched, occupying the superficies of the viscera, and also extending in between the stomach and intestine and covering their deeper surface. In each lobe, however, the conditions are different from those in the genera mentioned, in that the germinative epithelia are in two strands, which are usually entirely separated from each other except at the ends of the lobes, where they fuse. In the great majority of cases, especially where the lobes are superficial, they are so flattened that they are parallel to the surface. One of the walls thus formed, which is usually the superficial one, has its median part formed of a cubical epithelium with long cilia, and on both sides of this are situated the germinative epithelia with the largest ova away from the median line. Occasionally the germinative epithelia are broad enough to reach the lateral edges, but these are usually formed by the ova that are just large enough to extend beyond the wall of the ovary. The other wall is made up of the same kind of ciliated epithelium, and to it all the follicles of the older ova are attached. Here again, then, we have the essential structure of Clavelina and Styelopsis, but developed in each of the lobes of an irregularly branching ovary. It must be said, however, that although the structure of the two walls is quite constant, their position with respect to the surface of the animal is somewhat irregular. The position is most constant in the superficial lobes, but even here only about 76% have the wall containing the germinative epithelia superficial, while in about 14% it occupies the deeper position; and in the other 10% the plane of the lobe is approximately at right angles to the surface. In the lobes that extend between the stomach and intestine, and over their deeper side, the variation in orientation is still greater, depending more upon the adjacent organs than upon the surface of the animal.

c. *General Considerations.*

Floderus (p. 250) established the law that in forms with bilateral arrangement of the germinative epithelia the development within the same takes place from without inward. In general this holds good for the three species studied, though some exceptions are encountered. It would be equally true to extend the law from the germinative epithelia to the whole ovary, but the case of the deeper lobes of the Chelyosoma ovary shows that its applicability is limited to ovaries, or their parts, that have a superficial position. Stated in its most general form, then, the law of growth within the ascidian ovary of the regular type seems to be that:

In general, in ovaries or parts of ovaries having a superficial position and bilateral symmetry, whether the germinative epithelium is double or not, development takes place from the median line of the superficial wall towards the deeper parts of the animal.

Another general question is whether the Clavelina type of ovary, with two separate germinative epithelia, should be considered more primitive than that of Distaplia and Fragaroides, where a single germinative epithelium occupies the greater part of the deep wall. It seems to me that the condition in Distaplia is more primitive, for it occurs in smaller and simpler species, and is in itself a simpler condition. Furthermore, this contention is borne out by the young Styela ovary (Plate **2**, Fig. 12), where the germinative epithelium occupies the whole deeper wall of the ovary, though it is double in the adult. It is, however, possible that both the condition in Fragaroides and Styela may be the result of a secondary fusion; and Julin's work on Styelopsis, where the germinative epithelium is formed from two single rows of cells extending along the lateral edges of the ovarian fundament, and proliferating primordial ova and oögonia towards the middle line, favor this view. In Styelopsis the two epithelia thus formed do not come near enough to fuse, but it may be that they do in other species. In Distaplia, however, there is certainly no fusion, for the germinative epithelium is single from the first. There is about the same number of oögonia in the undifferentiated bud that there is in the adult, so that the whole ontogeny of these cells consists in rearrangement and growth. A few of these oögonia commence to increase in size at a very early period, and, as these are usually near the middle of the deeper wall, it is here that the first follicle and consequently the stalk tissue is formed. But we should expect that occasionally an ovum near the edge would commence to grow first, and accordingly we actually do find that in a few cases the stalk tissue is attached near the lateral edge of the ovary. In fact, from the study of the development in Distaplia, one gets the impression that the bilateral symmetry is accidental, depending upon the fact that usually the first ovum to grow will be somewhere near the centre of the deep wall. But that this cannot be true for other species, and may not be true in this one, is shown by the fact that in Clavelina, Ciona, and Styelopsis the doubling of the germinative epithelium occurs before the oögonia are formed.

III. Incubatory Pouch.

1. Historical Summary.

Almost all compound and social Ascidians have some provision for retaining their eggs within the colony until the larvæ developed from them are ready to enter upon their free swimming existence. The organ where this is accomplished is usually called an incubatory pouch, but its structure varies much in different groups. Usually the pouch is merely a slight enlargement of one peribranchial sac, into the bottom of which the eggs are laid, and from whose top the fully formed larvæ escape. Occasionally, however, as in Glossophorum sabulosum described by Lahille ('90, p. 203), the pouch consists in the terminal enlargement of the oviduct. Distaplia and Colella, and probably also the allied genus Julinia, Calman ('94), present an extreme development of incubatory pouch, which consists of a large diverticulum connecting with the dorsal edge of the zoöid by a narrow stalk. Within the enlarged terminal part of the pouch the eggs and embryos are always arranged so that the youngest are at the bottom; but how they got there has been somewhat of a puzzle to ascidiologists. Delle Valle ('81) published the first account of this structure; he supposed that the ripe ova reached the peribranchial sac and were put into the pouch together, and then fertilized. The retardation that the spermatozoa would experience in travelling down the pouch and getting past the first ova he thought accounted for the greater development of the embryos near the mouth of the pouch. The next investigator of the subject was Herdman ('86), who studied this organ in Colella pedunculata and allied species. He describes the pouch (p. 89) as "merely an enormous diverticulum of the peribranchial or atrial cavity" and remarks that the neck is so narrow that ova can pass in but that the larvæ cannot escape. He explains the arrangement of the embryos within the pouch by supposing that the ripe eggs all reach the peribranchial sac, are there fertilized and subsequently put into the pouch in order, the one last fertilized going first. But he says that he has no evidence for this, as eggs have never been found in the peribranchial sac. Since then no investigator, so far as I know, has attempted to account for the arrangement of embryos in incubatory pouches of the

Distaplia type. Calman ('94, p. 10), however, in describing the genus Julinia, which is closely related to Distaplia, gives a description of a spherical vesicle attached to the dorsal side of the thorax which he believes to be an incubatory pouch, though no eggs or embryos were found in it. The most significant thing about his account is that the lumen of the oviduct seems to be continuous with that of the pouch.

2. Observations.

The incubatory pouch in Distaplia occidentalis is not so large as in some other members of the genus. It usually contains two embryos, and never more than three, according to my experience, while in D. magnilarva, according to Delle Valle's figure ('82, Fig. 5), the pouch may contain as many as eight. The conditions vary in different colonies; in some the pouches contain but one or two embryos, while in others three is the predominating number. The pouch is attached to the posterior dorsal region of the thorax, a little to the right of the median line, and when fully formed, though still attached to the zoöid, it extends posteriorly about as far into the colony as the zoöid itself.

A careful examination of the structure of the pouch shows that it is not merely a diverticulum from the peribranchial sac, but consists of two parts which, for descriptive purposes, may be called the oviducal and the peribranchial portions, though I do not know that they have been developed from the oviduct and peribranchial sac respectively. The oviducal part is a narrow tube, the anterior end of which connects with the oviduct, and the posterior end with the bottom of the pouch. Anteriorly the peribranchial portion is a narrow tube opening into the posterior dorsal corner of the right peribranchial sac. Posteriorly, however, it is enlarged to form the pouch proper, in which the developing embryos are lodged. Figure 8 (Plate **2**) represents a young pouch in which the relation of the oviducal (*brs. ov'dt.*) to the peribranchial portion (*brs. pi'brn.*) is shown. Both portions are of course covered by the evaginated ectoderm (*ec'drm.*). The relations of the stalk of the pouch to the zoöid are best shown by means of cross-sections (Plate **2**, Figs. 9, 10, 11). The most posterior section (Fig. 9) shows the stalk entirely separated from the zoöid and imbedded in the common test. Its oviducal portion (*brs. ov'dt.*) is seen to be nearest to the part of the zoöid containing the oviduct (*ov'dt.*). As the series is followed anteriorly, the ectoderm of the stalk first joins that of the zoöid and then the wall of the oviducal portion becomes continuous with that of the oviduct (Fig. 10, *ov'dt.*). Figure 11 is taken from another zoöid and shows the opening of the peribranchial portion of the stalk into the right peribranchial sac. As the pouch is completely separated from its zoöid long before the larvæ are mature, the only function of this peribranchial orifice is to serve as a passage for the spermatozoa. The vas deferens (*va.df.*), which is closely applied to the deep wall of the oviduct until the latter joins the oviducal part of the pouch, extends much farther forward and opens into the cloaca near the anus. It is thus seen that the oviducal portion of the pouch is a continuation of the oviduct into the pouch, and that the egg never reaches the peribranchial sac at all, but is conveyed directly to the bottom of the pouch.

The lumen of the oviducal part of the pouch is even narrower than that of the oviduct, so that here too the egg is greatly elongated in its passage. Figure 18 (Plate 3) shows an egg the greater part of which has just entered the pouch; but a small portion of it has not quite emerged from the oviducal tube, and can be seen as a small projection from the rest of the ovum. From the fact that there are no muscles present in the pouch, and none but the heart muscles in the abdomen, and because the ovum has shrunken away from the walls of its conducting tube in preserved specimens, I believe that this compression is not due to the killing reagent, but represents a normal condition.

I have not been able to discover the pouch at the very beginning of its development, and so cannot say whether it is formed as an evagination from the peribranchial sac, from the oviduct, or from both. It is probable, however, that even if the first stages were found it would be difficult to settle this matter, so that a comparative anatomical investigation of the subject in Colella, for instance, where all grades of pouch formation obtain, would be more profitable. I have, however, found the fundament when it was only a short cylindrical outgrowth about 150 μ long. At this stage it presents all the essential features of the adult except that the pouch proper is very little enlarged. In fact Figures 9 to 11 (Plate 2) were taken from a stage but little older than this. Zoöids with pouches in this condition are about 2 mm. long, that is about two-thirds grown. The vas deferens, however, is filled with spermatozoa apparently ready to be discharged. Subsequent development consists in a swelling of the pouch, and an elongation of its stalk, so that the whole structure moves posteriorly into the colony at some little distance from the zoöid producing it. When the bottom of the pouch is at about the level of the stomach, the first ovum enters it; when the last ovum has entered, its end is about at the level of the posterior extremity of the zoöid.

None of the pouches containing the older embryos are ever found connected to zoöids, and as no adult zoöids are ever encountered without pouches, it is evident that the zoöids from which the older pouches arose have degenerated, and that those found in the colony along with these older pouches belong to a subsequent generation. As a matter of fact, degenerating zoöids are not infrequently encountered, and in close proximity to them are seen the pouches with which they were probably connected. Most of the growth of the embryos takes place after the degeneration of their mother; accordingly the pouch is much enlarged, becoming even longer than the adult zoöid was, and the narrow anterior stalk apparently swells up to the size of the pouch proper. The whole structure migrates through the test until its anterior end finally comes into close connection with one of the common cloacal cavities, through which the fully developed larvæ reach the exterior.

IV. Envelopes of the Ovum.

So many summaries of this subject have been published, and such a good one by its most recent investigator, Floderus, that a detailed discussion of the literature would be superfluous. In fact the whole subject has been left in a very satisfactory condition by this author, who was the first to discuss the evidence for the formation of the follicle cells and test cells, both from within the ovum and from sources which are external to it. Accordingly, much that I have determined is confirmatory of his results, and of those of earlier investigators. However, as it was from the genus Distaplia that Davidoff ('89) drew what is probably the strongest evidence for the intraovular origin of the test cells, it seems worth while to discuss the conditions in this genus.

1. Primitive Follicular Epithelium.

Concerning the development of the primitive follicular epithelium (van Beneden et Julin, '85, p. 357), I can confirm the account of Floderus and all the other investigators of the subject since van Beneden et Julin's time. The epithelium is formed from the primordial follicle cells found in close proximity to the oögonia in the earliest stages

(Plate **1**, Figs. 3, 4; Plate **2**, Fig. 12, *cl. fol. pr.*). Even in the undifferentiated bud (Fig. 1), there are found among the oögonia smaller nuclei that will probably give rise to nuclei of follicle cells. As the oögonium increases in size, these cells multiply and form a continuous epithelium around it (Plate **1**, Fig. 7; Plate **3**, Figs. 21, 23, 13). Julin ('93, pp. 106–109) states that the first follicle is composed of three cells, one of which is the sister, and the others the products of division of the cousin of the ovum; and also (p. 123) that the entire follicle of later stages is derived from these three cells. In our species, where the ovogenesis is not so rapid, and there is plenty of time for a rearrangement of the cells, there is no evidence showing that the formation of the follicle is so precise; and the fact that in one instance a small ovum has been found in the follicle of an older one (Plate **3**, Fig. 26) seems to show that the follicle is made up from any cells that happen to be in the vicinity of the growing oögonium.

The stalks connecting the younger follicles to the germinative epithelium and the older ones to the stalk tissue are, as has already been shown, differentiations from the germinative epithelium which connect with the follicle, and are not derived from a limiting epithelium of the ovary. However, even before the stalk of the follicle is completely established the differentiation of the primitive follicle into secondary follicle cells and test cells has begun.

2. Test Cells.

Davidoff, in studying the origin of the test cells in D. magnilarva, found evaginations of the wall of the germinative vesicle, and concluded that these are constricted off to form the vesicular structures present in the cytoplasm of the ovum. These vesicles, he says, sometimes appear empty and sometimes have a chromatic spot within them. Their peripheral membrane stains very lightly, but as they move towards the periphery of the ovum, they progressively take a deeper stain and develop chromatic granules until they become the fully developed nuclei of the test cells. Later their cytoplasm is formed from portions of the cytoplasm of the ovum. Caullery ('94, p. 600), who worked on the ovogenesis of D. rosea, does not confirm Davidoff's results, but says that the test cells arise from the follicular cells by mitosis. He does not, however, give the evidence upon which this statement is based.

a. Evidence for the Intraovular Origin of the Test Cells.

I have observed much of the evidence upon which Davidoff bases his account, but do not consider it strong enough to establish his contention. As a rule the wall of the young germinative vesicle is perfectly smooth (Plate **3**, Figs. 20–23, 13), but in quite a number of cases it is thrown into folds. A rather extreme instance of this folding is shown in Figure 19 (Plate **3**), which, however, represents well the most characteristic feature, which is that the folds usually occur at the ends of an oval germinative vesicle. The long axis of the germinative vesicle is often parallel to the edge of the knife used in sectioning, so that in these cases the folding may be due to the shoving of the section in cutting, but in other cases this cause cannot be invoked. Davidoff's figures represent the folding as being most pronounced at the ends of the germinative vesicle, but not limited to that region. In D. occidentalis, however, I found no cases of such extensive folding as he has shown.

Other structures that probably influenced Davidoff's conclusions, and are sometimes associated with the folding, are the cytoplasmic vacuoles near the germinative vesicle (Plate **3**, Fig. 19). Oblique sectioning and a faint stain, such as the borax carmine used by Davidoff is liable to give, might combine to obscure the conditions so that the vacuole would appear to be part of the germinative vesicle. It may be that some of the nuclear evaginations seen by Davidoff were formed in this way; but, even if what he figures are actually evaginations from the germinative vesicle, it would not follow that they represented a normal condition. Thus the presence of the vacuoles (Fig. 19) just opposite to the *in*foldings of the membrane seem to show that both are artifacts due to some shrinking process.

These vacuoles, however, are certainly some of the structures which Davidoff has considered nuclear buds *separated* from the germinative vesicle. In younger ova, where all of the cytoplasm takes a much deeper stain, these vacuoles may have a stained periphery and thus resemble a nucleus very closely (Plate **3**, Fig. 22, *vac.*).

The intravitelline bodies, from which Fol ('83), Sabatier ('84), and Roule ('85) have derived both follicle and test cells, and Pizon ('93, pp. 284–290) the test cells only, and the true nature of which Floderus first elucidated, are also present in Distaplia (Plate **1**, Fig. 7; Plate **3**, Figs. 22, 23; Plate **4**, Fig. 28, *cp. ia'vt.*), though they are much smaller and occur less frequently than in Ciona. These bodies are often, though not always, surrounded by a clear area, probably due to shrinkage, and especially when they are small, the combination looks very much like the nuclei with pale membranes and central chromatic spots figured by Davidoff ('89, Taf. 5, Figs. 6, 7). But the irregular occurrence of the clear area, the lack of a chromatic membrane in the later stages, and the absence of transitions between them and the test cell nuclei, show that they cannot be nuclei, and have nothing to do with the formation of the test cells.

b. Evidence for the Follicular Origin of the Test Cells.

The first indication of the formation of the test cells is found in the form and position of certain nuclei in the primitive follicle. Whereas at first all the nuclei of the primitive follicle are oval, when viewed in section, later one is occasionally encountered which is nearly spherical and projects some distance into the cytoplasm of the ovum (Plate **3**, Fig. 13, *cl. fol.*). The space between the nucleus and the egg cytoplasm I do not suppose to be occupied by the hyaline cytoplasm of the forming test cell, as Floderus does in similar instances (p. 234), but consider it as due primarily to shrinkage. In some instances I believe that clear spaces thus formed were *partially* occupied by cytoplasm during life; but in these cases I think that there was nothing but the thinnest possible layer of cytoplasm between the follicle nucleus and the egg, for in my most satisfactory preparations of this stage, where the follicular cytoplasm is stained, none is usually encountered in this place (Plate III., Figs. 24, 25). Here it is seen that the stained cytoplasm of the follicle is not quite half as thick as the clear spaces in Figure 13, and that even here shrinkage vacuoles are occasionally present. They also show that in Distaplia no structureless membrane, or chorion, has as yet been secreted on the inner surface of the follicle, the line of demarcation between this surface and the ovum being merely the cell membrane of the follicle cells.

Figures 24 and 25 are from an ovum that is slightly older than that shown in Figure 13, and in the height of test-cell production. About half the follicle cells have rounded up, and either are on their way to become test cells, or have actually become such. A majority of these can be seen to be in cytoplasmic connection with the follicle. A perfect series of the stages in the process can easily be made out, from the enlarged follicle nucleus that is still in contact with the outer membrane of that layer, through cases of progressive migration of the nucleus and its accompanying cytoplasm into the ovum (Plate **3**, Fig 24, *cl. tst.*) to the condition where the test cell is entirely within the latter, but still connected by a narrow strand with the follicle (Plate **3**, Fig. 24; Plate **4**, Fig. 27, *cl. tst.′*), and finally to that where it is entirely disconnected from the follicle, and the chorion passes between the two (Fig. 27).

The way in which the test cells develop here is essentially that given by Morgan ('90) and Floderus (pp. 234, 235), but the evidence in the three cases differs slightly. Morgan has differentiated the boundaries between the adjacent follicle cells, which neither Floderus nor I have found, and has seen the cytoplasm of the forming test cell extending between the follicle cells quite to the peripheral membrane of the latter. Floderus finds both the follicle cell and the developing test cell within a clear space, which he considers hyaline cytoplasm. I find that in favorable instances the cytoplasm of the follicle and test cells stains, and the two are seen to be in connection. When, however, the cell boundary between them can be detected (Fig. 25), the test cell cannot be seen to extend quite to the periphery of the follicle, but lies on its central surface. In this respect Distaplia differs from the forms studied by Morgan, for the first step in the formation of the test cell in Distaplia seems to be a displacement of the whole follicle cell towards the inner surface, and only subsequently does its separation take place.

Julin (p. 123), in describing the ovogenesis of Styelopsis, says that there is an almost simultaneous mitotic division of all the follicle cells, and when the products of this division come to rest, they are arranged in two layers, the inner of which consists of test cells. Caullery ('94, p. 600) agrees with Julin in deriving the test cells from the follicle by mitosis. I have never seen any mitotic figures in the follicle or test cells of Distaplia occidentalis, but do not doubt that they occur. It is likely, however, that in this species the process is not accomplished as Julin describes it, for after the mitosis there must be a differentiation taking place, by means of which the nuclei of the prospective test cells become larger and more spherical than the remaining follicle nuclei.

Shortly after the origin of most of the test cells, the chorion is secreted between these cells and the follicle (Plate **4**, Fig. 27); even this, however, does not destroy the cytoplasmic connections of all the test cells, and occasionally the union can be seen at much later stages. With the formation of the chorion, the differentiation of the primitive follicle into secondary follicle and test cells appears to be complete, and the large subsequent increase in the numbers of the latter must be due to their division. There is no reason to doubt that they divide by mitosis, for at this stage they have a perfectly healthly appearance, and in fact Davidoff (pp. 131–132) has described and figured mitoses of both test and follicle cells in D. magnilarva.

c. Degeneration of the Test Cells.

The degeneration of the test cells in Distaplia is a much simpler process than that occurring in some ascidians, consisting, as Davidoff has shown, in the vacuolation of the cytoplasm. The cellular nature of the product is always evident, as the distinctive character of the nucleus is never lost, though this organ is forced into a peripheral position and changes its appearance slightly. This degenerative vacuolation begins in our species at about the same time as the yolk formation (Plate **4**, Fig. 28) and is completed (Plate **5**, Fig. 30) before the last changes in the yolk occur. Figure 29 (Plate **4**) shows a few test cells in which the process is just beginning. At this stage the test cells are often numerous enough to form a double row about the periphery of the ovum (Fig. 28), but sometimes they form only a single row. As the ovum passes through the oviduct into the pouch, it seems to contract somewhat, forcing the test cells out, and the yolk bodies between which they were formerly situated become arranged so as to form a smooth surface at the periphery of the ovum (Plate **5**, Fig. 31). However, in spite of this tendency, there is occasionally enough pressure exerted upon the test cells to force them partly into the yolk again.

Up to this time the nucleus has changed little if any, but from now on further changes in the test cells are almost entirely confined to this organ. During the growth of the embryo, the nucleus loses most of its chromatin, its membrane only staining, and becomes compressed between the cell membrane and adjacent vacuoles (Plate **5**, Figs. 32, 34).

d. Fate and Function of the Test Cells.

Among the early investigators the belief that the test of the larval ascidian was formed by the test cells was universal, and it was on this account that Kupffer ('70, p. 122) applied this name to them. In 1872, however, Herting ('72) showed that the test first appeared as a thin layer next to the ectoderm of the larva and entirely within the so-called test cells, which took no part in the process. This view has been generally accepted from that time; but quite recently a vigorous supporter of the older theory has been found in Salensky ('92, '94, pp. 441–449, '95, pp. 618–621).

This author, finding that in Salpa and Pyrosoma cells which are derivative of the follicle take a large part in the formation of the embryo, turns to the compound ascidians expecting to find there the beginnings of the same process. Accordingly, he makes out that in the compound ascidians the test cells, or kalymmocytes, as he calls them, have a function to perform during the life of the embryo, though this differs in different cases. In representative species of the genera Fragarium, Amarœcium, and Circinalium he found a placenta attaching the embryo to the wall of the cloaca, and the fœtal part of this structure was derived from transformed test cells. In Distaplia magnilarva, Diplosoma, and Didemnum these cells have the function of forming the test of the larva, the whole of it being derived from the test cells in Diplosoma, but only a part of it in the other two genera.

In Distaplia, which is the only genus in which this process need concern us, Salensky finds that at the time when the test is forming, the test cells flatten out against the ectoderm of the larva so that in places they form continuous layers. These he thinks secrete the cellulose matrix ('92, pp. 113–114) and then metamorphose into the cells lining the lacunar spaces with which the test is honey-combed. The test, he thinks, continues to grow in the same way, having layer after layer of test cells added to its outer surface. Caullery ('94, p. 600), the only other author who has studied this subject since the publication of Salenky's first article ('92), comes to the conclusion that the test cells take no part in the formation of the test, but does not give any evidence.

In examining Distaplia occidentalis, an appearance was quite frequently noted that looked very much as if there were unmodified test cells within the test itself. But when examined more carefully, the substance within which the test cells were contained was found at stages before there was any test being formed, and even before the egg had segmented. It was also found within the cavities of some of the older embryos, and was then concentrated on the same side of all the cavities. If in these cases the substance was situated on the left side of the cavities, then that on the outside of the embryo was always on the left side and vice versa. Thus there was every reason to believe that the substance surrounding the test cells was a coagulum that had been thrown down by the fixing reagents, and had reached its characteristic arrangement by means of gravity. From Salensky's ('92, p. 113) statement that in an early stage the changing test cells are separated from one another by a homogeneous substance that looks very much like test matrix, I have thought that he might possibly have had some more refined form of a similar coagulum before him; but I cannot for a moment suppose that the true nature of a state of affairs such as exists in my preparations would have escaped him.

The flattening out of the test cells against the ectoderm and test mentioned by Salensky, I find to be due to pressure from without. Wherever the inner follicular epithelium is close to the embryo, as on its sides, for instance, there the test cells are much flattened against the surface (Plate 5, Figs. 32, 34, *cl. tst.*); but where the epithelium is lifted from the surface, as in the triangular space it leaves when passing over the tail, the great majority of the test cells are spherical. Occasionally, however, oval ones are found here with their sides next to the ectoderm or test, but in such cases the extreme flattening that occurs on the sides has never been seen. Moreover, in reviewing quite a number of series I have been unable to discover any transitions between the test cells and cells within the test, or any cases in which the peripheral layer of the test matrix was not perfectly distinct from the superimposed test cells. Thus no evidence at all has been found that is favorable to Salensky's view of the test formation.

So much for the interpretation of Salensky's results. Concerning the actual method of test development I must say that I think it can be shown that the test in Distaplia is formed in such a way that the test cells cannot be instrumental in producing it.

The first tunicin, or animal cellulose, that is laid down is that forming the tail fin, which is quite well developed at a time when no other tunicin can be detected either on the tail or the body of the embryo. Now the test matrix of the fin has no cells within its substance, and so must have been formed by the activity of cells that are outside of it. As it is attached to the ectoderm on one of its three sides, and as the test cells are in contact with only about half of the surface of the other two, and are usually not pressed against it, and as these cells are in no way different from any of the other test cells, there is very little ground for believing the test matrix of the tail to have been secreted by the test cells.

On the body of the embryo an examination of the early stages shows that here the whole thickness of the test is quite small, much less than the thickness of a test cell, even though the latter is pressed against the test by the follicular epithelium (Plate **5**, Fig. 32, *tst.*). In spite of this fact, however, the outer layer of the test matrix is quite thin, and under it the beginnings of the first lacunæ (*lac.*) are seen. Occasionally we see cells (Fig. 32, *cl. ms'drm.*) within the lacunæ, but these have none of the characters of the test cell, whereas they do resemble some of the mesenchyme elements very closely. It seems hardly possible, then, that the test cells can have had anything to do with forming this structure. Moreover, in following the series through ten sections, 6 μ thick, not another cell is found within the test of this region. It is seen therefore that the first tunicin and some of the first lacunæ are formed from the ectoderm, not only without the intervention of the test cells, but also without the aid of *any* cells lying within the test substance.

With further increase in the thickness of the test the lacunæ increase in size, and many mesoderm cells wander into them, and into the matrix between them (Plate **5**, Figs. 33, 34, *cl. ms'drm.*). These cells often flatten out against the lacunar wall, and line it for a variable distance, but in the test that is about as thick as the test cells; this condition is rarer than at a later period, when there are several layers of lacunæ.

During the whole of the development, up to the time when the larva is extruded, the test cells are often closely pressed against the test; but there appears to be no marked decrease in the number of these elements, though, of course, on account of the greater size of the embryo, in the later stages they become more widely separated. In this species, then, the evidence points strongly to the conclusion that the test cells have nothing whatever to do with the formation of the test, but that the matrix of the latter, together with its lacunæ, is formed from the ectoderm, and that its cells are mesodermic elements that have subsequently wandered in.

What, then, is the function of the test cells in Distaplia, if they have nothing to do with the formation of the test, and what is the function of these cells in general? Many authors are not satisfied with their rôle in nourishing the ovum, but think that they must be functionally active as long as they remain near the growing embryo. Thus, Salensky ('92, pp. 109–110) says: "Es wurde vielmehr still schweigend angenommen, die Testazellen hätten keine Bedeutung bei der Bildung des Embryos der Ascidien. Ein solcher Schluss war für mich von Anfang an nicht ganz befriedigend." Floderus, after a careful discussion of the literature, so far fails to realize the true nature of these cells that he says (p. 244): "Ich halte es für wahrscheinlich, dass die Testazellen eine Art von rudimentären Bildungen sind, welche nunmehr eine unbedeutende Rolle spielen, allein einstweilen dürfte man die Frage nach ihrer eigentlichen Function und ihrer richtigen Deutung gewissermassen als eine offene bezeichnen können."

In considering the function of the test cells, it should always be borne in mind that they are *follicle cells* derived from other follicle cells, and as such their mission is to convey nourishment to the ovum. The fact that they lie under the chorion, and imbedded in the cytoplasm of the ovum, does not remove them from this category, but merely puts them in a more favorable position for conveying food to the egg cell. Starting as normal and vigorous cells in the follicular epithelium, their activity is so great that degenerative changes in the shape of vacuolation appear in them, while the follicle cells proper still retain their normal appearance. The early occurrence and complexity of these processes offer the best possible evidence for the intensity of the activity. It is not surprising, therefore, and I think we have no right, *a priori*, to expect that cells which have worked so hard that they have lost their vitality — cells in which degenerative changes have set in — should become further involved in the developmental processes of the embryo.

3. Secondary Follicular Epithelium.

For some time after its complete differentiation this epithelium is comparatively thin with flattened nuclei (Plate **4**, Fig. 27). Soon, however, as the cells multiply, the epithelium thickens, and the nuclei assume a spherical shape (Plate **3**, Figs. 26, 15, *e'th. fol.*). The increase in cells continues, so that soon they must arrange themselves in two layers (Plate **4**, Fig. 28). At about this stage morphological differentiation sets in, and the inner nuclei fail to take the stain strongly, thus becoming somewhat paler than before (Fig. 28, *nl. e'th. fol. i.*). All cell multiplication now seems to cease, for with the subsequent growth of the ovum the thickness of the follicle decreases, probably on account of stretching (Plate **5**, Fig. 30). But in spite of this thinning out the follicle does not become one cell thick, as Davidoff maintains (p. 136). On the contrary, there are two quite distinct kinds of nuclei (Fig. 30), and it is probable that at this stage the inner and outer follicular epithelia are differentiated, but so closely pressed together that the only indication of the differentiation consists in the nuclei.

4. Inner Follicular Epithelium.

It must be confessed that while the egg is still in the ovary the nuclei of this layer are hard to find, and do not appear to be numerous. Moreover, in the latest ovarian stages, where the follicle is even thinner than in Figure 30, they are still less apparent. But later developments show conclusively that we here have to do with the nuclei of the inner follicular layer; for when the egg has left the ovary it is covered by only a thin pavement epithelium with pale nuclei at rather distant intervals (Plate **5**, Fig. 31, *e'th. fol. i.*), while all the darker nuclei of the outer follicle remain behind in the corpus luteum (Plate **1**, Fig. 5; Plate **6**, Fig. 47). This inner epithelium persists, and covers the embryo during the whole of its life within the colony, and becomes so stretched in the later stages that even the nuclei are obliterated. It is thus seen that, contrary to what Davidoff believed (p. 138), there is in Distaplia a splitting of the secondary follicle into an outer and an inner epithelium, which is actually accomplished only when the egg leaves the ovary, though the two layers are probably, and their nuclei certainly, differentiated some time before. Thus, in Distaplia, the results of van Beneden et Julin on the origin and fate of these two epithelia are completely confirmed.

5. Outer Follicular Epithelium and Corpus Luteum.

As has already been said, one of the distinguishing features of this layer is the comparatively deep stain that its nuclei take. Another characteristic, which is just beginning to appear in Figure 30 (Plate **5**), but is much more distinct later, is that part of the cytoplasm also takes a very deep stain. Tangential sections through the follicle of ova that have reached the maximum size, about 300 μ, show this stained cytoplasm situated in irregular patches around a central nucleus. In sections of the newly formed corpus luteum (Plate **6**, Fig. 47) this cytoplasm comes out very distinctly.

The corpora lutea (Fig. 5) are often conspicuous features of the Distaplia ovary, as they are at first about 80 μ in diameter, and remnants of them persist until an embryo of forty or fifty cells is developed from the ovum formerly contained within them. When first formed, this structure is a thick walled vesicle with a rather small cavity opening into the lumen of the ovary. Almost the whole thickness of the wall is composed of the cells of the outer follicle, which are pressed together and elongated radially. Figure 47, which represents part of the wall of a corpus luteum which the hind end of the ovum has just left, shows most of the deeply stained cytoplasm of each cell located between its nucleus and the periphery of the organ. Peripherally, this cytoplasm seems to be attached to the hyaline membrane (*mb. prp.*) surrounding the whole structure. This membrane is nothing but a local differentiation of a similar covering of the ovary and all its products, the consideration of which has been postponed until now.

Distaplia seems to have a special aptitude for the secretion of structureless membranes, for they cover the surfaces of nearly all the visceral organs. In the case of the ovary and its products, the membrane can usually be demonstrated with ease. Both the connective-tissue cells and the epithelium of the ovary itself seem to participate in the secretion. Origin from the first source is to be inferred both from the frequency with which strands of connective tissue are seen to join and extend along the wall of the ovary (Plate **1**, Fig. 6, *fun. con't. tis.*); and also from the fact that often the connective tissue cells themselves are found on the wall of the ovary. That the membrane is also in part secreted by the cells of the ovary is proved by its general occurrence, but principally by the fact that on the periphery of the stalk tissue, where we have the greatest number of cells per unit of area, it is exceptionally developed, being much thicker than at other places (Fig. 5, *mb. prp.*). It occurs also on the surface of the follicles, varying much in thickness, but being in general best developed on those that are about half grown. On the surface of the oldest follicles are found here and there very flat nuclei that are probably derived from wandering cells almost imbedded in this membrane. It is probably nuclei of this kind, and the structureless membrane containing them, that Julin considers to be the remnant of the limiting epithelium of the ovary surrounding the follicle; for he says that this limiting epithelium has gradually become hyaline.

On the newly formed corpus luteum this basement membrane (Plate **6**, Fig. 47, *mb. prp.*) is thicker and more conspicuous than on any other part of the ovary, except some of the stalk tissue, and it is of special importance in attempting to explain how the ovum is pressed through the ovary into the oviduct. This pressure cannot be due to muscles, as there are none in the abdomen except those of the heart. Nor can an increase of blood pressure in the whole abdomen, due either to long-continued beating of the heart in one direction, or to the contraction of thoracic muscles, be invoked in explanation. For while this might burst the follicle by pressing it against the ectoderm and modifying its spherical shape, it would also tend to press the oviduct out flat against the ectoderm, and so could hardly be effective in moving the ovum into the oviduct. The only other available force is one resident within the follicle of the ovum, and this might lie either in the outer follicular epithelium or the membrana propria. I think that at first both of these structures are the active agents; but the irregular crowding together of the follicle cells in the corpus luteum seems to show that, during the later stages of the process, at any rate, the cells have no active function. Finally, then, by this method of exclusion, we come to the membrana propria as par excellence the active agent in forcing the ovum into the oviduct, and find that there is considerable direct evidence for this view. In the first place, both follicular epithelium and membrana propria are presumably under tension in the largest eggs, being formed by the stretching of structures that were formerly thicker and of less area. Secondly, the membrana propria of the corpus luteum is perfectly homogeneous and quite thick; and it is very improbable that a membrane which was formerly very much thinner, and covered an area about fourteen times its present extent could assume this condition unless it had been under tension, upon the removal of which it could contract into its present shape. Thirdly, it has the appearance of elastic substance, being thrown into the folds characteristic of such material. These folds, however, may in part be due to the irregular pull exerted on the membrane by some of the follicle cells attached to it. When once the ovum is started on its course up the oviduct, the continuation of its progress seems to be effected by the contractions of the oviducal epithelium, but the main force in the initiation of the process seems to be the elastic tension of the membrana propria of the follicle.

As soon as the ovum has entirely passed out of the ovary, the corpus luteum begins to degenerate. The first change consists in the dissociation of the deeply stained cytoplasm formerly associated with the nuclei (Fig. 5). Strands of this material are still encountered, but the characteristic arrangement is lost. At about the same time the nuclei themselves appear paler, and the wandering mesoderm cells on the surface of the structure are flattened against it, and together with the membrana propria form an investing capsule (Fig. 5). Next comes the constriction of the stalk of the corpus luteum, by means of which it is separated from the stalk tissue. During this process the lumen may or may not disappear, but after the distinct epithelial connection with the stalk tissue is lost, the corpus luteum remains connected therewith for some time by irregular strands of cytoplasm or connective tissue.

Within the isolated corpus luteum many vesicles are formed containing nuclei in various stages of chromatolytic degeneration, while outside the vesicles are other nuclei, which, though staining faintly, appear to be in a healthy condition. It seems, then, that some of the cells of the corpus luteum retain their vitality and digest their neighbors, for the functional nuclei are so numerous as to make it improbable that they have all penetrated the thick membrana propria from without.

Cases have been encountered where this cutting off from the ovary has already taken place when the ovum that left the corpus luteum is in the two or four cell stage. On the other hand, the same condition has been found when the youngest embryo in the incubatory pouch contained about sixteen cells. From this time on, the remnant of the corpus luteum becomes smaller and smaller, still remaining a compact mass; but finally, when the ovum has divided into about sixty cells, it disintegrates and disappears.

6. Observations on Styela montereyensis.

In this species the development of the follicular membranes progresses in much the same way as in Distaplia, but it is more difficult to follow. The presence of a separate outer follicular epithelium, however, is easily seen at a comparatively early stage; but, as is usual with the simple ascidians, this epithelium is much thinner than the inner follicle.

The most interesting events in the life of the follicle of this species are the degenerative changes which take place in the test cells, and those of the inner follicular epithelium. In the latter the process is comparatively simple, and consists only in the development of a large refractive body in the cytoplasm of the cell. It is first seen at a stage when the yolk is fully formed, and the maximum size of the ovum is nearly reached, and appears as a small speck in the cytoplasm, so close to the nucleus that it may have been extruded from the latter. It rapidly increases in size, until, just before the egg leaves the ovary, it is nearly as large as the nucleus of the cell and is surrounded by a lighter area, which may, however, be due to shrinkage. Together with this area it is about the size of the nucleus, which now occupies an excentric position. It does not take nuclear stains well, but when a safranin, gentian violet, and orange triple stain is used, it is colored an opaque brown, that makes it the most conspicuous object in the ovary. This body can have no reference to any future function of the cell, for, very shortly after the egg enters the water, into which it is extruded, all of the follicle cells are lost, and the egg is covered only by the chorion, with a few cellular fragments adhering to its outer surface. It seems rather to be some product of the intense metabolism of the cell, which the latter is attempting to get rid of, or to deposit in some innocuous form.

The degenerative changes in the test cells are much more complex, ending in a product that looks like Figure 46 (Plate 5) when stained with a nuclear stain, and like Figures 42 and 43 (Plate 5) when overstained in safranin. The latter stain brings out the essential structure more clearly, and by means of it we see that the test cell has resolved itself into a number of vesicles (*vs.*), each one of which contains a central refractive, faintly staining corpuscle (*cp. c.*). The number of vesicles varies from seven or eight to twice that number. They are remarkably uniform in size, and when well stained it is only very rarely that one is encountered which lacks the corpuscle, though it often happens that nuclear stains do not bring out the corpuscles at all satisfactorily. At the centre of the cell there is accumulated another substance, which sends out thin lamellæ between the vesicles. In hæmatoxylin preparations (Plate 5, Figs. 44–46), the central substance appears homogeneous or finely granular, but safranin demonstrates within it quite a number of very deeply staining bodies that sometimes occupy almost the whole central space (Fig. 43). Of the nucleus, not a trace can be seen, for, as will be shown presently, the central bodies just mentioned are not composed of nuclear material.

The first step in the formation of these complex test cells begins early, not very long after the formation of the test cells themselves, and before the yolk granules appear. The first change noticed is an irregular vacuolation of the cytoplasm (Plate 5, Figs. 35, 36). Within many of these vacuoles are seen bodies (*cp. ia'vac.*) which look much like the central corpuscles of the vesicles of the final product, so that it is most natural to suppose that the vesicles are developed from the vacuoles of the earlier stage. But the conditions subsequently encountered do not bear out this supposition.

The next step consists in further vacuolation, which is still more irregular. Some of these vacuoles are much larger than any of the vesicles of the final stage (Plate 5, Fig. 37), and occasionally three-quarters of the cell will be taken up by an immense vacuole crowding the smaller ones and their central bodies to one end. Furthermore, nearly half of the vacuoles have no stained bodies within them, and these bodies themselves have increased in size, so that instead of being comparable to the central corpuscle, they are nearer the size of the entire vesicle of the final stage (Plate 5, Figs. 37, 41). At this stage there are two kinds of stained bodies, — those within the vacuoles (*cp. ia'vac.*) and those included in the lamellæ between the vacuoles (*cp. ia'll.*). Safranin (Fig. 37) does not allow one to distinguish between these, but the triple stain of safranin, gentian violet, and orange does, giving the intravacuolar bodies a light yellow, and the intralamellar ones a deep purple color. At a slightly earlier stage the intravacuolar bodies also take the purple stain, so that it may be that these two structures have a common origin. The nucleus takes part in none of these changes. It is occasionally seen in safranin preparations (Fig. 38, *nl.*), and hæmatoxylin shows it to be practically unchanged, and universally present at considerably later periods (Plate 5, Fig. 44).

The next and most important stage is that in which some of the intravacuolar bodies have acquired a central more deeply stained corpuscle. Their size is about the same as before, but they stain more faintly (Fig. 38). In the next stage (Plate 5, Figs. 39, 40) all of these bodies have developed a central corpuscle; they now take a still fainter stain, and have approximated still more closely in size to the vesicles of the final stage. In fact they resemble the latter so closely that most of the transitional stages from one to the other are found among the test cells of a single ovum. As these bodies acquire their final dimensions, they assume a peripheral position, crowding the remains of the intravacuolar cytoplasm towards the centre, in which are contained the deeply stained intralamellar bodies that treatment with safranin makes so prominent (Plate 5, Figs. 42, 43).

The nucleus, which from the start of the process has a peripheral position, persists almost unchanged until the vesicles have become thoroughly established (Fig. 44). It is still oval, but stains more faintly than before. Later still, while the vesicles remain entirely unchanged, the nucleus slowly degenerates, becoming at first paler, and distorted by the pressure of the vesicles (Fig. 45), and then refusing to take the stain altogether, but persisting as an irregular peripheral refractive patch (Fig. 42, *nl.*), which finally seems to vanish entirely (Fig. 46).

This process, like that in the follicle cells, has no prospective meaning, for the test cells take no part in the development of the embryo. In life they have a decided yellow color in this species, while the yolk is green, so that, in the living embryo, they can be detected easily, floating in the space between the embryo and the chorion, and are seen to be left behind at the time of hatching. The process must rather be considered as entirely degenerative, perhaps a futile attempt to conform to the changed conditions and protect the cell from the disastrous results of its active metabolism, by means of which the ovum is nourished. It seems well to emphasize the intensity of this metabolism.

V. Ovum.

1. Cytoplasm.

As is usual in ascidians, the cytoplasm of the young Distaplia ova is filled with rather large granules that take a nuclear stain with avidity (Plate 1, Fig. 4; Plate 3, Figs. 21, 22), but while the test cells are being formed the stain becomes fainter and fainter, until it almost vanishes. Together with the decrease in stainability, there is a decrease in the size of the granules (Plate 3, Figs. 23, 13), until at last they become so inconspicuous as to be negligible quantities (Plate 4, Fig. 27). In later stages again they appear to become more marked, but it is difficult to correlate the changes with the size of the ova, for there is so much individual variation. It is clear, however, that after the cytoplasm has ceased to stain deeply, good preservation will often enable one to detect a cytoplasmic network, the nodal points of which give the appearance of granules (Plate 3, Fig. 26; Plate 4, Fig. 28). This condition comes out more distinctly in the later stages figured, but indications of the same thing are seen earlier, and the reticulum probably exists even where it is obscured by the deep stain. The network persists up to the time of the formation of the yolk bodies, and is present in the central part of the ovum when the periphery already contains much yolk (Fig. 28).

In Distaplia magnilarva Davidoff ('89, p. 155) did not find any stages in the process of yolk formation, and hence concludes that the yolk bodies are formed simultaneously throughout the whole extent of the ovum. In our species, however, stages are often encountered in which the yolk bodies are present at the periphery only (Fig. 28). Here the largest yolk bodies are scattered amongst the test cells, and as the germinative vesicle is approached they become progressively smaller, until near the centre there is a gradual transition into the cytoplasmic reticulum. However, where the yolk is forming the whole of the cytoplasm seems to be converted into that substance, for the intervals between the yolk bodies are not occupied by the cytoplasmic reticulum, — which at this stage takes a distinct though faint stain, — but by a confused mass of substance, all of which has the characteristic hyaline appearance of the yolk bodies, in which, however, no structures of definite shape have been formed. After the yolk bodies are fully established, the absence of undifferentiated cytoplasm between them is still more marked, for, like Davidoff, I have been unable to discover trace of any other substance between them (Plate 5, Figs. 30, 31; Plate 6, Fig. 50). When fully formed, the yolk bodies are of very large size for ascidian material, and of various shapes. Those apparently first formed are oval or spherical, while those of later development are angular and occupy the spaces left by the first ones.

Yolk formation begins when the ovum is about half grown (150 μ in diameter), and all of the cytoplasm is transformed into yolk some time before the maximum size (about 300 μ) is reached. During the growing period that follows the earliest stage at which all the cytoplasm is converted into yolk, there is a little clump of yolk around the germinative vesicle which has but indistinctly broken up into yolk bodies (Plate 6, Fig. 49), and it may be from the periphery of this clump that the new yolk bodies producing the increase in size are formed. Ova possessing this clump of undivided yolk average about 200 μ in diameter.

Later this clump becomes completely broken up into yolk bodies (Fig. 50). But none of these are spherical, as is usually the case in other regions, all being more or less elongated in a radial direction. It is probable that growth continues even after this central yolk has broken up, for the range in size of ova in this condition is from 230 μ to 326 μ. It is impossible to determine the diameter of the mature ovum, because, as soon as it begins to leave the ovary, it is immediately deformed, and even in the pouch it is oval instead of spherical. But it is not probable that the mature ovum would exhibit so much variability.

2. Germinative Vesicle.

The chromatin in the young germinative vesicle is usually situated next to the membrane, while in the centre no structural elements of any kind can be detected (Plate 1, Fig. 4, *ov'go.*). The chromatic granules are sometimes of uniform size (Fig. 4, *ov'go.*), but usually there is one which is much larger than the rest, and destined to become the nucleolus (Fig. 1, *ov'go.*). At this period all of the granules, including the prospective nucleolus, are differentiated similarly — taking a bluish tint — with the methyl green and acid fuchsin double stain. Soon achromatic fibres make their appearance. At first mainly peripheral, and inserted on the chromatic granules and the membrane, they soon come to traverse the centre of the vesicle. It is rarely, however, that chromatin is found upon them (Plate **1**, Fig. 3, *ov'go.*). At the same time that the achromatic network becomes differentiated, the largest chromatin granule increases in size, and becomes more nearly spherical and not so closely approximated to the membrane. Although it still takes the same stain as the other granules, the disparity in size and its regular shape justify us in calling it the nucleolus. Its later development will be discussed in a separate section.

The further changes that occur in the growth of the rest of the germinative vesicle consist entirely in the elaboration of the achromatic network and the chromatin granules upon it. The achromatic fibres are not always seen, especially in the later stages, but staining in iron hæmatoxylin brings out the chromatic elements very distinctly (Plate **3**, Fig. 13; Plate **4**, Fig. 27; Plate **6**, Fig. 48). The latter form a reticulum extending through all parts of the germinative vesicle, the complexity of the structure increasing with the size of the vesicle, and culminating in the condition shown in Figure 48 (Plate **6**).

In addition to the reticulum, many isolated granules are found throughout the vesicle and especially on its membrane. While all these granules when stained with iron hæmatoxylin are very deeply colored, and resemble closely the chromatic structures described for other eggs, still, strictly speaking, we are not justified in calling them chromatin; for chromatin is that substance which takes the chromatic or basic aniline stain when treated with a combination such as methyl green and acid fuchsin. Malfatti ('91), in testing the electivity of this stain for known chemical substances, found that free nucleic acid was stained pure green; nucleins, which contain less phosphorus, were colored blue, while substances with still less phosphorus took the red stain. Thus, as nucleic acid and the nucleins are derived from the nucleus, it becomes highly probable that chromatin is made up of these substances.

Now, when the germinative vesicle of this stage is treated with the stain mentioned, the network that is so distinct in hæmatoxylin preparations is colored red, and the only substance staining green is contained within the nucleolus, which will be considered later. During the growth of the nuclear reticulum, then, there appears to be a concentration of nucleic acid within the nucleolus, while the reticulum itself and all the other granules within the vesicle suffer a decrease in their percentage of phosphorus.

The condition of the germinative vesicle shown in Figure 48 (Plate 6) is found in ova about 150 μ in diameter, in which the yolk bodies are just beginning to be formed. During all of the subsequent growth of the ovum, while it doubles its diameter, the germinative vesicle *decreases* in size, usually diminishing to a little less than half its former diameter (see Table, p. 100). During this shrinking, the vesicle exhibits the wavy and stellate outline characteristic of the stages preceding the maturation of ova (Plate 6, Figs. 49, 50); here, however, the shrivelling is associated not with maturation but with yolk formation.

This shrinking of the germinative vesicle and the formation of the maturation nucleus from it have been studied by Davidoff (pp. 156–159), according to whom the process is very complex and quite unique. First, the membrane disappears, and the major portion of the contents of the germinative vesicle forms the "ergoplasma," or active cytoplasm, which gradually becomes disseminated between the yolk bodies. The nucleolus is the only structural element that remains behind, and it undergoes the most complex modifications. It takes a deep stain, and becomes shrivelled so that its outline is irregular and at times stellate. He says he believes that there is an actual decrease in the volume of the nucleolus accompanying these morphological changes, but his figures do not bear him out in that statement. The next change is, that within the shrivelled nucleolus small chromatic granules are differentiated, which soon aggregate to form a compact chromatic body. This itself subsequently becomes vesicular and contains a central granule. A few of the chromatic granules do not take part in the formation of the compact chromatic body, but initiate the formation of a dense chromatic network, with which the whole nucleolus becomes filled. At the same time a membrane is distinctly differentiated about the periphery of the nucleolus and we have developed from it a nucleus which is neither germinative vesicle nor nucleolus, but the maturation nucleus or "Polkern."

In Distaplia occidentalis, most of the stages discussed by Davidoff are abundantly represented; but I must differ from him in their interpretation and in the order of their sequence. I will first describe the process as I conceive it to be, and then compare my results with those of Davidoff.

At the time when the first yolk is being formed, the germinative vesicle has a full rounded outline and its maximum diameter of about 45 μ (Plate 6, Fig 48). As the formation of the yolk continues, and the ovum grows, the germinative vesicle shrinks, its membrane becomes wavy, and before all of the cytoplasmic reticulum has become transformed into yolk, the vesicle has shrunk to a diameter of about 30 or 35 μ. In the next stage (Fig. 49), the yolk extends up to the membrane of the germinative vesicle, but the central yolk clump is not distinctly separated into the yolk elements. In ova of this stage the germinative vesicle has an average diameter of about 25 μ. Finally (Plate 6, Fig. 50), when the ovum is larger still and the central clump of undivided yolk has broken up, the germinative vesicle has shrivelled to a diameter of about 20 μ (see Table, p. 100).

During the whole of this process, the methyl green and acid fuchsin stain differentiates the nucleolus within the shrivelling germinative vesicle. With some other stains however it cannot be seen, for the germinative vesicle is so deeply stained that no structure at all can be distinguished within it. Iron hæmatoxylin usually has this effect, and the stain is so intense that excessive decoloration does not differentiate a vesicle, but works from the periphery inward, removing all the stain from around the edges, while in the centre it persists with undiminished intensity. Occasionally, however, colonies are encountered in which the stain does not work this way, but differentiates a vesicle, and in these cases (Plate 6, Figs. 49, 50) the nucleolus and the remains of the reticulum are plainly seen.

In order to make perfectly sure that the sequence noted above is correct, I established four classes, based upon the sequence mentioned, and then measured all the eggs in these stages contained in several series, placing each egg in the class to which it belonged according to the structure of the yolk, and germinative vesicle. If my sequence is correct, by this means I should get a progressive increase in the size of the ova in the successive classes, and when passing from one class to the next, and corresponding to this a diminution in the size of the germinative vesicle. This condition is actually what I did obtain.

The classes were: —

1. Yolk bodies formed at the periphery only. Germinative vesicle with a full rounded outline.

2. Central part of the reticular cytoplasm not yet differentiated into yolk. Germinative vesicle with a wavy outline.

3. Yolk extends from the periphery to the germinative vesicle, but

the central clump has not yet broken up into yolk bodies. Germinative vesicle stellate.

4. Central yolk clump has broken up into yolk bodies. Germinative vesicle stellate.

Out of 48 eggs measured, the various sizes, expressed in micra (μ), were distributed as follows : —

Class.	No. of Ova in each Class.	Smallest Ovum.		Largest Ovum.		Average.	
		Size of Ovum.	Dimensions of Germ. Ves.	Size of Ovum.	Dimensions of Germ. Ves.	Size of Ovum.	Dimensions of Germ. Ves.
1	10	133	56 × 50	173	52 × 42	151	47 × 37
2	6	134	46 × 26	191	33 × 25	161	36 × 28
3	15	170	31 × 30	243	28 × 15	205	28 × 20
4	17	230	28 × 25	326	20 × 19	287	23 × 17
Total	48						

From this table, it is seen that the classes established on morphological grounds contain groups of similar ova, and hence represent the actual sequence of events. The column of averages especially shows well how the germinative vesicle diminishes with the growth of the ovum.

Among the fifty-two ova examined, four exceptions were encountered that would not fit well into any of the classes. Two of these were small ova, about on the transition line between the second and third classes, but in which the cytoplasmic conditions were very indistinct. The other two belong to an entirely different category, and from their rare occurrence in my early series, from which the above data were taken, as well as in the later series, they must be considered abnormal. In them the yolk bodies were completely differentiated in all regions, but the contents of the germinative vesicle was finely granular and not separated by a membrane from the yolk.

From this account it follows that the shrinking of the germinative vesicle is a continuous process, and much simpler than Davidoff considered it. In attempting to interpret his results in the light of these investigations, there is but one point that offers any obstacle. That is his initial stage in the shrinking, in which the membrane of the vesicle disappears and its contents penetrate between the neighboring yolk bodies; while the nucleolus remains behind (Davidoff's Figures 18, 19, Taf. V.). It will be seen, however, that this condition is exactly what I have found in the two abnormal ova mentioned above. It may be that this appearance is more common in the species studied by Davidoff than in the one with which I am familiar, and this stage may possibly have some place in the normal series of events in that species, but the close similarity of his other stages to mine does not favor this view.

Davidoff's ergoplasm that in some stages surrounds what he takes to be the nucleolus, but finally penetrates between all the yolk bodies, is, I think, the central clump of yolk surrounding the germinative vesicle in class three. When stained faintly, it sometimes looks slightly granular. But so far as the penetration of the yolk by this substance is concerned, I cannot confirm his results; for in the later stages, as in the earlier, I find no interstitial substance whatever between the yolk bodies.

The body that Davidoff takes to be the nucleolus in the later stages is undoubtedly the shrunken germinative vesicle. In size, shape, and in all other respects, the two objects are entirely similar. Curiously enough Davidoff follows quite a number of these stages backwards, in spite of the fact that he thinks that his " nucleolus " is *shrinking*, and that his figures show the size of that structure to be increasing in the successive stages. The central body which he finds developed within his nucleolus is nothing but the true nucleolus of the vesicle, which I have traced through all the stages, but which would often be obscured by the stain he used. His main trouble consists in not having had before him any of the first stages in the shrinking of the vesicle when its membrane and nucleolus are easily seen. On this account also he missed the entire process of the transformation of the cytoplasmic reticulum into yolk, which occurs at the same period.

That this shrivelling of the germinative vesicle is closely associated with the formation of the yolk, is suggested by the synchronism of the two events, and it is interesting to note that the intense activity of the nucleus, of which this shrinking is probably the result, begins shortly after degenerative changes have commenced in the test cells. It seems, then, that the test cells are particularly active in conveying nourishment to the ovum in the early stages, whereas the nucleus exerts its principal activity in the later stages in converting this material into yolk.

3. Nucleolus.

The nucleolus was left at the time when it had just assumed a nearly spherical shape, but was still attached to the membrane of the germinal vesicle. It progressively assumes a more central position, but remains attached to the membrane for a considerable period by means of a stalk (Plate 3, Figs. 20–22). This stalk is at first quite large, but becomes smaller as the nucleolus increases in size, and finally disappears altogether, never being encountered during the later stages. It cannot be seen in all the young vesicles, and would of course be invisible except in a profile view; but from the generality of its occurrence I believe it is a normal structure serving to attach the nucleolus to the membrane from which it has been derived. Floderus (pp. 214–215) has described nucleoli with similar projections attached to them, and believes that he has in them stages in the formation of "nebennucleoli," but the fact that the largest stalks are attached to the smallest nucleoli, which is also brought out by his figures (Taf. X., Figs. 19, 20, 21), has no significance according to this view.

When first differentiated, the nucleolus appears homogeneous with all the stains used; soon, however, this condition changes and a central medullary mass and an enclosing membrane can be distinguished. In the most favorable hæmatoxylin preparations (Plate 6, Fig. 51) the membrane takes a deep stain, the medulla (*med.*) appears granular and more refractive, and outside of the membrane a faintly staining cortex (*ctx.*) can be distinguished. With methyl green and acid fuchsin the medulla is stained red, and is surrounded by a blue rim that is probably composed of both the membrane and the cortex seen in the hæmatoxylin preparations. The next changes consist in simple growth, the medulla, surrounded by its membrane, coming to occupy an excentric position within the cortex, which is increasing more rapidly than the medulla (Plate 6, Figs. 52, 53). Next we have developed within the medulla, and often very close to its membrane, a variable number of very highly refractive bodies (*cp. ref.*). At the same time the rest of the medulla becomes less refractive and more finely granular (Plate 6, Figs. 54, 55). With the methyl green and acid fuchsin combination, the cortex and medulla are with difficulty distinguishable, both taking a pale bluish green stain; but the refractive bodies are colored a very bright pure green. They are therefore chromatin and apparently pure nucleic acid. At this stage, and for some time later, they are the only structures in the nucleus that take a decided chromatic stain.

After further increase in size, hæmatoxylin stains the cortex deeper and deeper, until it is barely possible to see the medulla and the refractive bodies (Plate **6**, Fig. 56). Later this deep staining is still more pronounced, so that both medulla and refractive bodies are entirely obscured and only a faint lighter central area perceived (Plate **6**, Fig. 48). During the earlier stages also iron hæmatoxylin usually stains the nucleolus so strongly that no structure can be detected within it; and only exceptionally are the conditions illustrated in Figures 51 to 56 (Plate **6**) to be made out. In such instances, however, they may be brought out most distinctly. But with methyl green and acid fuchsin, medulla and cortex are usually differentiated, though not so clearly as with a favorable hæmatoxylin stain.

For the further history of the nucleolus I have depended almost entirely upon the methyl green and acid fuchsin combination. All of the structures increase in volume, the refractive bodies probably most rapidly, until at the time when the yolk bodies are being formed some are considerably over 1 μ in diameter. They still stain a bright green, and are very refractive, but the largest are no longer homogeneous, appearing to be filled with many refractive granules (Plate **6**, Fig. 58). Though usually located in the medulla, some are occasionally found within the cortex (Fig. 58). The cortex itself appears perfectly homogeneous, while the medulla is finely granular, but both take the same bluish tint. The medulla is no longer spherical, but flattened on one side.

From now on, while the germinative vesicle is shrinking, and after the yolk is formed, both cortex and medulla take a fainter and fainter stain, until finally they can no longer be distinguished with the use of this stain. During this process they usually are of a diffuse green color, and sometimes the vicinity of the refractive bodies, which remain with unimpaired distinctness, has a faint suffusion of green, which is probably an indication of the presence of what is left of the nucleolus, though its outlines cannot be seen. After the central yolk clump has broken up, this stain has never shown anything of the nucleolus except the refractive bodies; but I think that the other portions are still there, for in the occasional well-stained hæmatoxylin preparations of this stage it is still seen (Plate **6**, Fig. 50), though in this case too it is fainter than in the stages immediately preceding.

In addition to the stains already mentioned, I also tried List's

('96, pp. 480–487) potassium ferrocyanide methods in order to determine whether any of the structures in the nucleolus were composed of the paranuclein demonstrated by these methods. List says (p. 488), " Werden die Schnitte eine halbe Stunde lang in eine ganz schwache, mit Salzsäure angesäuerte Eisenchloridlösung gestellt (zu 50 ccm destillirtem Wasser gebe man 10 Tropfen einer 0,5% igen Eisenchloridlösung und 5 resp. 15 Tropfen einer 1% igen Salzsäure), und wird dann die Berlinerblaureaction ausgeführt, so bleiben Nucleïn und die verwandten Stoffe farblos, die Substanz des Nebennucleolus dagegen wird blau. Der name Paranucleïn, gleichsam als Gegensatz zu Nucleïn, ist chemisch daher vollkommen gerechtfertigt." Both his first method, which consists in treating the sections directly with two drops of 1.5% potassium ferrocyanide, followed by one or two drops of hydrochloric acid, and his second method, in which the sections are treated first with the mordant mentioned in the quotation above, were employed, and similar results obtained. The refractive bodies were the only structures that took a decided blue stain, and hence would be called paranuclein, according to List. However, not all the refractive bodies in the same section would be colored blue, but usually only the smaller homogeneous ones. After treatment with potassium ferrocyanide, the sections were stained in Mayer's hydrochloric acid carmine, and the principal result of the cyanide method was to prevent the nucleoli taking the carmine stain. The cortex was acted upon least, and usually took a light, but sometimes a rather deep, stain; but in the nucleoli in which medulla and refractive bodies were differentiated, neither had a red color. They were usually greenish yellow. In the younger ova, with nuclei about 20 μ in diameter, the nucleoli were almost entirely colorless, having but a faint bluish or greenish yellow coloration. The principal effect, then, of List's method is to prevent subsequent coloration of the nucleoli by carmine; but it also stains a few and sometimes all of the refractive bodies blue. These bodies, then, are paranuclein, but we have already seen that, with methyl green and acid fuchsin, they are often the only structure in the nucleus that stains bright green, and hence they are nuclein or nucleic acid. Which is correct? It may be that the refractive bodies represent some chemical substance that has not yet been tested by these reagents, and does not belong in the same category as the nucleins and paranuclein. This, however, is hardly probable, and I think that of the two methods the methyl green and fuchsin is much more reliable on account of the chemical tests to which it has been subjected; and believe that the refractive bodies are really composed of nuclein or nucleic acid.

Of course the most interesting problem connected with the nucleolus is whether the refractive bodies contain any of the chromatin that goes to form the chromosomes of the maturation nucleus, but on account of the small number of ova that I have found in the oviduct, and the difficulty experienced in making perfect series of sections, I am unable to offer any direct evidence on the subject. One series from an ovum within the oviduct showed three of these bodies situated within the remains of the disintegrated germinative vesicle, but no other distinct structural elements were detected; and when the ovum has reached the pouch, the tetrads (Plate 6, Figs. 60, 61) are already formed, and no trace of the nucleolus remains. On the whole, it seems rather improbable that the refractive bodies should form the chromosomes, and in the latest ovarian stages there is other chromatic material in the germinative vesicle. Occasionally the whole vesicle will be suffused with a faint green coloration, and sometimes very minute green microsomes are seen on the projections of the shrivelled vesicle. Accordingly, at this stage, there is not the entire absence of other chromatic material that is encountered earlier.

4. Maturation.

The condition obtaining among the ova of Class 4, where the yolk bodies are completely formed and the germinative vesicle much shrivelled, stellate, and about 20 μ in diameter, is the last stage that I have observed in the ovary. The next changes take place in the passage through the oviduct, during which the tetrads are formed.

A few observations have been made on these and subsequent stages, but, owing to the difficulty of obtaining perfect series, they are so scattered that they cannot be easily interpreted, and a discussion of them would be unprofitable. Enough, however, has been seen to show that the number of tetrads in the maturation nucleus is probably twelve, and that two polar bodies are formed. No centrosome or achromatic fibres of any kind have been detected either during maturation or the first cleavage of the ovum, although I have several good preparations of these stages. But, as before mentioned, the number of figures is so small, and the variability in their appearance so great, that as yet no connected history of the processes can be made out.

Cambridge, May, 1898.

POSTSCRIPT.

Since the above was written, Professor Salensky has had the kindness to afford me an opportunity of examining his sections of the embryos of Distaplia magnilarva. As these preparations show a class of facts, not observed in mine, which is of much importance in considering the origin of the cells in the test, their consideration is imperative. But before I proceed to discuss the differences, I will mention two points in which our preparations agree.

1. What I have said about the flattening of the test cells against the ectoderm (p. 86) applies equally well to those of Salensky's preparations that I have seen. The flattening appears to be entirely due to the pressure of the embryonal membranes. Wherever the test cells were flattened and the follicular membrane could be made out at all, the membrane was seen to be pressed against the surface of the embryo; and, conversely, wherever the follicular membrane was seen to lie at some distance from the ectoderm, as where it passes over the tail, the test cells were *never* seen flattened against the ectoderm.

2. The granular substance sometimes found between the test cells in D. occidentalis is also present in D. magnilarva. It seems, in this case also, to be an artifact, being likewise found within the cavities of the embryo, and principally on one side of the embryo. But it is more finely granular and less one-sided in its distribution in D. magnilarva than in D. occidentalis.

The differences between Salensky's preparations and mine are connected with cells situated entirely outside the test-matrix, but having a structure intermediate between that of the cells in the test and the "test cells" (Salensky's kalymmocytes). Whereas, in my preparations, I could find no intermediate stages, in Salensky's quite a perfect transition could be traced from cells that could not be distinguished with certainty from typical kalymmocytes to those looking just like the characteristic vacuolated cells of the test. But among the cells on the outside of the test-matrix the series may be traced even farther, even to the characteristic undifferentiated mesoderm cells with large nuclei and very scanty compact cytoplasm. These facts, and others to be mentioned presently, have forced upon me the conclusion that in *D. magnilarva* the mesoderm cells wander through the ectoderm, not only into the test, but also *on to the surface of the embryo, and there undergo a degenerative vacuolation, the final result of which cannot be dis-*

tinguished from a kalymmocyte. The facts for and against this interpretation may be briefly stated as follows: —

1. The fact that, among the cells entirely outside the embryo, the series may be traced not only to the typical vacuolated cell of the test, but also to the undifferentiated mesoderm cell, tells against Salensky's view that the kalymmocytes become rejuvenated and help to form the test. For, if his view were correct, one would expect that the rejuvenation of the kalymmocytes would cease as soon as they had reached the structure of the typical cell of the test, and that the concentration of the cytoplasm would not go farther, and produce cells not to be distinguished from undifferentiated mesoderm cells. Undifferentiated mesoderm cells are found in the test in comparatively small numbers; and, as it is certain that at least some of them wander through the ectoderm in the undifferentiated condition, and later undergo vacuolation to form the typical cells of the test, it seems probable that sooner or later all the undifferentiated mesoderm cells within the test do the same. If this is true, then the undifferentiated mesoderm cells found on the outside of the test are, according to Salensky's theory, destined to reverse their development once more and become again moderately vacuolated, after having already passed through that stage twice. Of course the considerations adduced in this paragraph do not prove my point, for it may be replied that, as the participation of the kalymmocytes in the building up of the test implies a rejuvenation, it is not at all surprising that some of the cells should become more rejuvenated than is necessary. The above considerations, however, show that the presence of undifferentiated cells on the outside of the test adds a further complication to Salensky's theory.

2. These undifferentiated mesoderm cells are found in such positions, and associated with each other in such a way, that it is difficult to see how they can have been formed from kalymmocytes. Thus, in one case, in an embryo in which none of the cellulose test-matrix had been secreted, an undifferentiated mesoderm cell was found *within* the cytoplasm of a typical kalymmocyte, whose shrivelled nucleus was still distinctly visible. Near by, but still imbedded in the *ectoderm*, was another mesoderm cell of exactly the same appearance, as if to show the course which the first cell had traversed.

In several other places on the surface of the same embryo isolated undifferentiated mesoderm cells were found. The majority, however, of the mesoderm cells thus situated were aggregated into groups. In one case a group of three was encountered, and in another a group of eight or nine, a part of which was contained in each of two sections. If these undifferentiated mesoderm cells had been developed from kalymmocytes, we should not expect to find them thus massed together, but, instead, distributed at intervals approximately corresponding to the distribution of the kalymmocytes about the embryo. Nor should we expect to find them penetrating other kalymmocytes. It must be admitted, however, that neither of these facts is wholly inconsistent with Salensky's theory.

3. Undifferentiated mesoderm cells were found on the surface of younger embryos, such as had not yet secreted any test-matrix, as well as on the surface of older ones possessing a test of considerable thickness. But while in these older embryos there were transitions to cells that were highly vacuolated, like the kalymmocytes, in the younger ones these transitions were entirely absent. This is exactly what should be expected according to my interpretation, for the cells on the younger embryos have just wandered out through the ectoderm, and have not yet had time to become vacuolated, as they have in the older embryos. I do not see how, according to Salensky's view, these facts can be explained, for if the undifferentiated mesoderm cells have been derived from the kalymmocytes, the transition stages should be present in both cases.

4. The strongest objection to my theory, and one that will immediately present itself to every one, is the great improbability that cells which have had such a different history as typical mesoderm cells and kalymmocytes should both end in structures that cannot be distinguished from each other. It must be remembered, however, that both are of mesodermic origin, and that both are subjected to the same environment. Improbable as such a convergence may seem, it does, however, occur in D. magnilarva; for, in Professor Salensky's sections, I have seen in the body cavity cells, certainly not displaced by the knife in sectioning, which were vacuolated in such a way that only with difficulty could they be distinguished from kalymmocytes, — one, indeed, that had exactly the appearance of a kalymmocyte. The a priori improbability of such a convergence in development is thus shown to be without weight. On the whole, then, I think it must be said that, in spite of the series of transitions from kalymmocytes to cells resembling those in the test (D. magnilarva), this series does not prove that the kalymmocytes participate in the formation of the test.

Berlin, March, 1899.

BIBLIOGRAPHY.

Auerbach, L.
'96. Untersuchungen über die Spermatogenese von Paludina vivipara. Jena. Zeitschr. Naturwiss., Bd. 30, Heft 4, pp. 405–554, Taf. XXI., XXII.

Beneden, E. van, et C. Julin.
'85. Recherches sur la morphologie des Tuniciers. Arch. Biol., Tom. 6, Fasc. 2, pp. 237–476, Pl. VII.–XVI.

Calman, W. T.
'94. On Julinia; a new Genus of Compound Ascidians from the Antarctic Ocean. Quart. Jour. Micr. Sci., Vol. 37, Pt. 1, pp. 1–17, Pl. I.–III.

Caullery, M.
'94. Sur les Ascidies composées du genre Distaplia. Comp. Rend. Acad. Sci. Paris, Tom. 118, No. 11, pp. 598–600.

Caullery, M.
'95. Contributions à l'étude des Ascidies composées. Bull. Sci. Fr. Belg., Tom. 27, Fasc. 1, pp. 1–158, Pl. I.–VII.

Dall, W. H.
'71. Descriptions of sixty new forms of Mollusks from the West Coast of North America and the North Pacific Ocean, with notes on others already described. Amer. Jour. Conch., Vol. 7, pp. 93–160, Pl. XIII.–XVI.

Davidoff, M. von.
'89. Untersuchungen zur Entwicklungsgeschichte der Distaplia magnilarva Delle Valle, I. Die Reifung des Eies. Mitth. Zool. Stat. Neapel, Bd. 9, Heft 1, pp. 113–178, Taf. V., VI.

Drasche, R. von.
'83. Die Synascidien der Bucht von Rovigno (Istrien). Ein Beitrag zur Fauna der Adria. Wien, 1883.

Delle Valle, M. A.
'81. Nuove contribuzioni alla Storia naturale delle Ascidie composte del Golfo di Napoli. Mem. Accad. Lincei, (3) Vol. 10, pp. 431–498, Tav. I.–X.

Delle Valle, M. A.
'82. Distaplia, nouveau genre de Synascidie. Arch. Ital. Biol., Tom. 1, Fasc. 2, pp. 193–203, 1 Pl.

Fewkes, J. W.
'89. New Invertebrata from the Coast of California. Bull. Essex Inst., Vol. 21, Nos. 7–9, pp. 99–146, Pl. I.–VII.

Floderus, M.
'96. Ueber die Bildung der Follikelhüllen bei den Ascidien. Zeitschr. f. wiss. Zool., Bd. 61, Heft 2, pp. 163–260, Taf. X.

Fol, H.
'83. Sur l'œuf et ses enveloppes chez les Tuniciers. Rec. Zool. Suisse, Tom. 1, Fasc. 1, pp. 91–160, Pl. VII., VIII.

Heiden, H.
'93. Ascidiæ aggregatæ und Ascidiæ compositæ von der Insel Menorca. Zool. Jahrb., Abth. f. System., Bd. 7, Heft 3, pp. 341–364, Taf. XIII.

Herdman, W. A.
'86. Report on the Tunicata. II Ascidiæ Compositæ. Challenger Rep., Zool., Vol. 14, pp. 1–432, Pl. I.–XLIX.

Hertwig, O.
'72. Untersuchungen über den Bau und die Entwickelung des Cellulosemantels der Tunicaten. Jena. Zeitschr. Naturwiss. Bd. 7, pp. 46–73, Taf. IV.–VI.

Huitfeld-Kaas, H.
'96. Synascidiæ. Norwegian N.-Atl. Exped., Vol. 23, Zool., Tunicata, pp. 1–27, Pl. I., II.

Julin, C.
'93. Structure et développement des glandes sexuelles; ovo-genèse, spermatogenèse, et fécondation chez *Styelopsis grossularia.* Bull. Sci. Fr. Belg., Tom. 25, Fasc. 1, pp. 93–154.

Kupffer, C.
'70. Die Stammverwandschaft zwischen Ascidien und Wirbelthieren. Arch. mikr. Anat., Bd. 6, pp. 115–172, Pl. VIII.–X.

Lahille, F.
'90. Recherches sur les Tuniciers. Toulouse, pp. 1–130.

List, T.
'96. Beiträge zur Chemie der Zelle und Gewebe. I. Ueber die Färbung thierischer Gewebe mit Berlinerblau. Mitt. Zool. Stat. Neapel, Bd. 12, Heft 3, pp. 477–493, Taf. XXII.

Malfatti, H.
'91. Beiträge zur Kenntniss der Nucleine. Zeitschr. Physiol. Chem., Bd. 16, Heft 1 u. 2, pp. 68–86.

Maurice, C.
'88. Étude monographique d'une espèce d'ascidie composée (Fragaroides aurantiacum n. sp.). Arch. Biol., Tom. 8, Fasc. 2, pp. 205–495, Pl. XVI.–XIX.

Morgan, T. H.
'90. The Origin of the Test-cells of Ascidians. Jour. Morph., Vol. 4, No. 2, pp. 195–204, Pl. VIII.

Pizon, A.
'92–'93. Histoire de la blasotogénèse chez les Botryllidés. Ann. Sci. Nat. Zool., Tom. 14, Nos. 1–4, pp. 1–386, Pl. I.–IX.

Ritter, W. E.
'93. Tunicata of the Pacific Coast of North America. I, Perophora annectens n. sp. Proc. Cal. Acad. Sci. (2), Vol. 4, pp. 37–85, Pl. I.–III.

Roule, L.
'85. Sur le développement des enveloppes ovulaires chez les Tuniciers. Rec. Zool. Suisse, Tom. 2, Fasc. 1, pp. 195–202.

Sabatier, A.
'84. Sur les cellules du follicule et les cellules granuleuses chez les Tuniciers. Rec. Zool. Suisse, Tom. 1, Fasc. 3, pp. 423–458, Pl. XXII., XXIII.

Salensky, W.
'92. Ueber die Thätigkeit der Kalymmocyten (Testazellen) bei der Entwicklung einiger Synascidien. Festschrift f. Leuckart, pp. 109–120.

Salensky, W.
'94. Beiträge zur Entwicklungsgeschichte der Synascidien. I. Ueber die Entwicklung von *Diplosoma Listeri.* Mitt. Zool. Stat. Neapel, Bd. 11, Heft 3, pp. 368–474, Taf. XVII.–XX.

Salensky, W.
'95. Beiträge zur Entwicklungsgeschichte der Synascidien. II. Ueber die Entwicklung von *Didemnum niveum.* III. Allgemeiner Theil. Mitt. Zool. Stat. Neapel, Bd. 11, Heft 4, pp. 488–630, Pl. XXI.–XXIV.

Stimpson, W.
'64. Descriptions of new species of Marine Invertebrata from Puget Sound, collected by the Naturalists of the Northwest Boundary Commission, A. H. Campbell, Esq., Commissioner. Proc. Ac. Nat. Sci. Philad., Vol. 1864, pp. 153–161.

EXPLANATION OF PLATES.

All the drawings were outlined with a camera lucida; tube length, 160 mm. projection on the table. Zeiss lenses were used, except where especially specified. *Distaplia occidentalis* is figured in all cases where the name of the species is not mentioned. All the figures were drawn from sections, except where the contrary is stated. The combination of lenses oftenest used was a $\frac{1}{18}$ immersion objective and No. 2 ocular, and these, together with the camera, gave a magnification of 1300 diameters. Where no lenses and magnifications are mentioned this is the combination used.

LIST OF ABBREVIATIONS.

a.	Space due to shrinkage.
brs. ov'dt.	Oviducal part of incubabatory pouch.
brs. pi'brn.	Peribranchial part of incubatory pouch.
cl. con't. tis.	Connective-tissue cell.
cl. fol.	Follicle cell.
cl. fol. pr.	Primordial follicle cell.
cl. ms'drm.	Mesoderm cell.
cl. sp. pr.	Primordial sperm cell.
cl. tst.	Test cell.
cp. c.	Central corpuscle.
cp. ia'll.	Intralamellar body.
cp. ia'vac.	Intravacuolar body.
cp. ia'vt.	Intravitelline body.
cp. lut.	Corpus luteum.
cp. ref.	Refractive body.
cp. vt.	Yolk body.
ctx.	Cortex.
cyt'pl.	Cytoplasm.
ec'drm.	Ectoderm.
en'drm.	Endoderm.
e'th. fol.	Follicular epithelium.
e'th fol. ex.	Outer follicular epithelium.
e'th. fol. i.	Inner follicular epithelium.
e'th. g.	Germinative epithelium.
fun. con't. tis.	Connective tissue strand.
fun. cyt'pl.	Cytoplasmic strand.
fun. gen.	Genital strand.
gra. chr.	Chromatin granules.
in.	Intestine.
lac.	Lacuna.
ll.	Lamella.
lu. oa.	Lumen of the ovary proper.
lu. pd.	Lumen of the stalk tissue.
mb. prp.	Membrana propria.
med.	Medulla.
nl.	Nucleus.
nl. e'th. fol. i.	Nucleus of a cell in the inner follicular epithelium.
nll.	Nucleolus.
oa.	Ovary.
oa-te.	Ovotestis.
ov.	Ovum.
ov'dt.	Oviduct.
ov'go.	Oögonium.
pd.	Stalk or peduncle.
par′.	Superficial wall of the ovary.
par″.	Deep wall of the ovary.
sac. brn.	Branchial sac.
sac. pi'brn. d.	Right peribranchial sac.
sac. pi'brn. s.	Left peribranchial sac.
stg.	Stigmata.
te.	Testis.
tis. pd.	Stalk tissue.
tst.	Test.
vac.	Vacuole.
va. df.	Vas deferens.
vs.	Vesicle.
vs. ex.	Outer vesicle.
vs. i.	Inner vesicle.

PLATE 1.

Fig. 1. Undifferentiated bud.

Fig. 2. Ovotestis of a young bud, showing ovary and testis separated, and the beginnings of a peripheral epithelium about the latter.

Fig. 3. Section immediately anterior to Fig. 2. Ovary and testis are united.

Fig. 4. Sagittal section of a medium sized bud. Ovary and testis differentiated, and both attached to the genital strand.

Fig. 5. Cross-section near the posterior end of the abdomen of an adult zoöid, showing the ovary with its lumen proper, and the lumen of the stalk tissue, and a corpus luteum. D, 3; × 530.

Fig. 6. Same, from another zoöid, showing the ovary. D, 3; × 530.

Fig. 7. Part of the germinative epithelium of an adult zoöid, showing a young oögonium projecting into the lumen of the ovary.

BANCROFT-OVOGENESIS DISTAPLIA PLATE 1

F.W.B. del

E. Meisel lith Boston

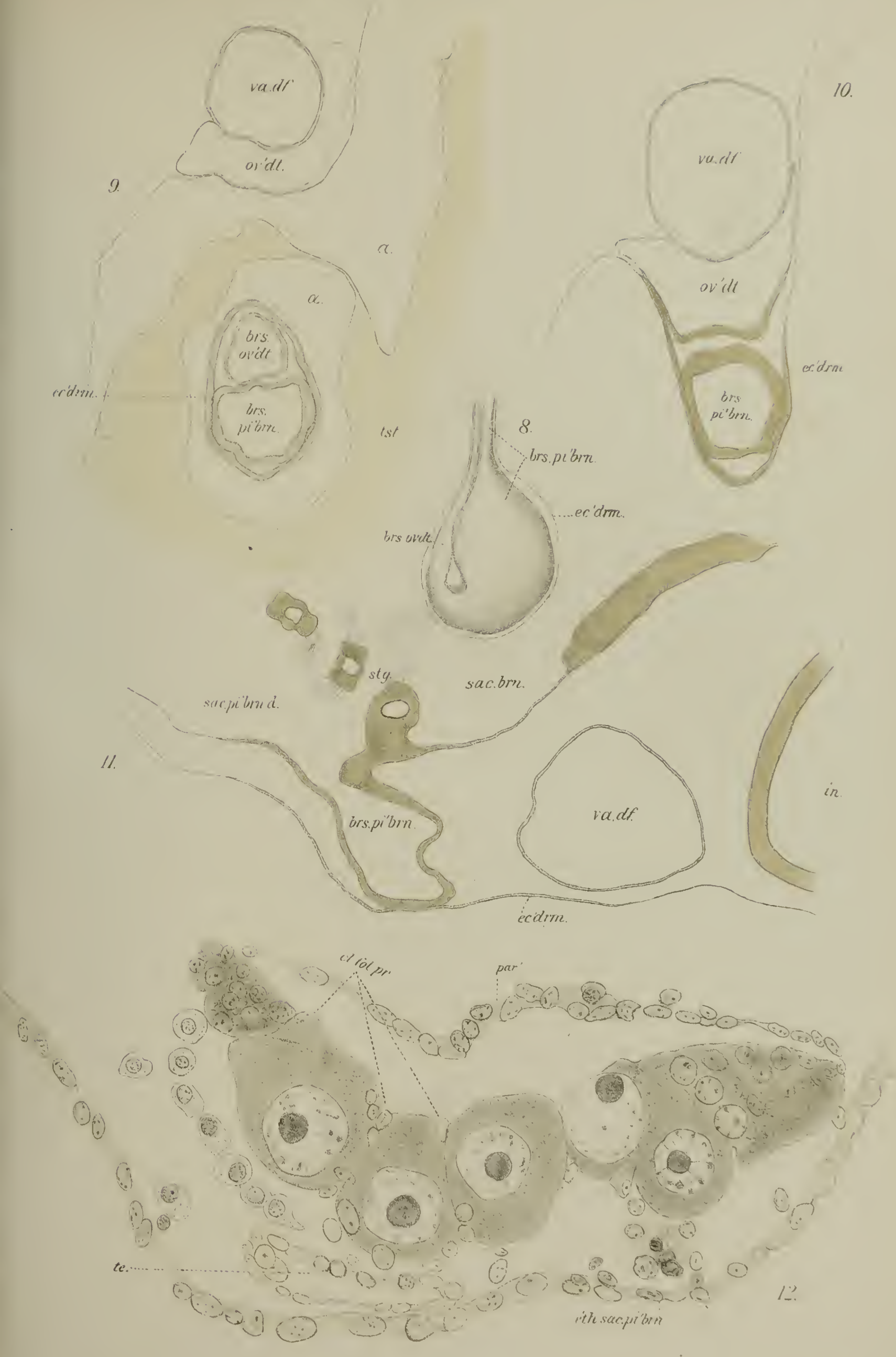
PLATE 2.

Fig. 8. Whole preparation of a young incubatory pouch, about $\frac{1}{4}$ adult size. A, 2; × 91.

Figs. 9, 10. Cross-sections of the posterior end of the thorax of a zoöid that had nearly reached maturity, showing the region where the stalk of the incubatory pouch joins the zoöid. Fig. 10 is the more anterior section. D, 2; × 380.

Fig. 11. From another zoöid of the same age as that figured in Figs. 9, 10, showing the opening of the pouch into the peribranchial sac. D, 2; × 380.

Fig. 12. Cross-section of the ovary and testis of a young *Styela montereyensis.* Powell and Leland $\frac{1}{12}$ immers.; × 850.



FWB. del.   B Meisel lith Boston.

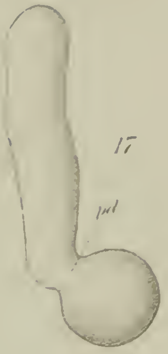
PLATE 3.

Fig. 13. Oögonium from an adult zoöid. The test cells are just forming.
Fig. 14. Part of the wall of the ovary, showing an ovum projecting beyond the ovary and just beginning to form a stalk.
Fig. 15. Same; ovum is much older, with a well-formed stalk containing differentiated stalk tissue.
Fig. 16. Whole preparation of ovum, showing maximum size attained in the ovary. Bausch & Lomb 2 in., Zeiss 2; × 40.
Fig. 17. Same; ovum partly extruded from ovary into oviduct. Bausch & Lomb 2 in., Zeiss 2; × 40.
Fig. 18. Same; ovum has not quite completely entered the pouch. Bausch & Lomb 2 in., Zeiss 2; × 40.
Fig. 19. Section through a medium-sized ovum, showing bends in the nuclear membrane and cytoplasmic vacuoles.
Fig. 20. Germinative vesicle of an ovum in a medium-sized bud.
Fig. 21. Ovum in a medium-sized bud.
Fig. 22. Young ovum from an old bud.
Fig. 23. Same; ovum a little older.
Fig. 24. Follicle and periphery of an ovum a little larger than that in Fig. 13. Test cells are being formed.
Fig. 25. Test cell and follicle cell from the same ovum.
Fig. 26. Follicle and test cells of a medium-sized ovum. A much smaller ovum is enclosed within the thickness of the follicle.

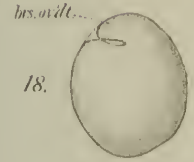
13.

16.

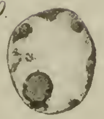
17.



18.



20.

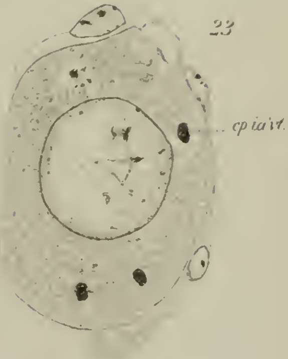


19.

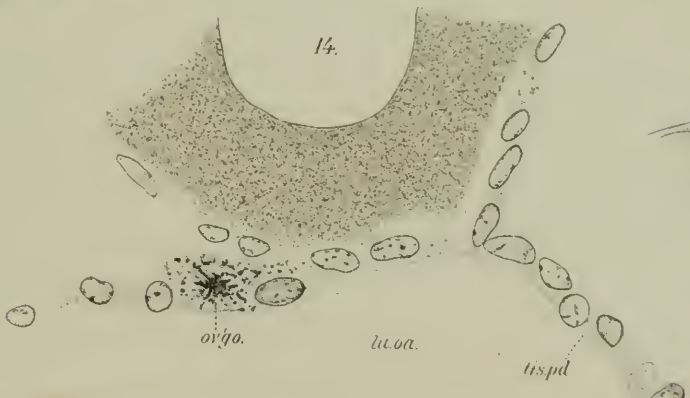
21.

22.

23.



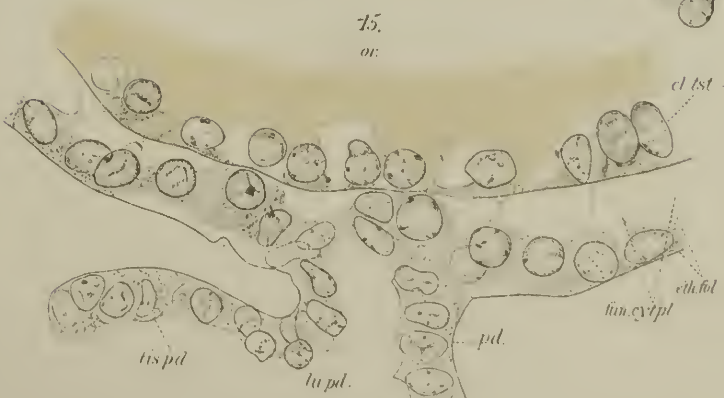
14.



25.

24.

15.



26.

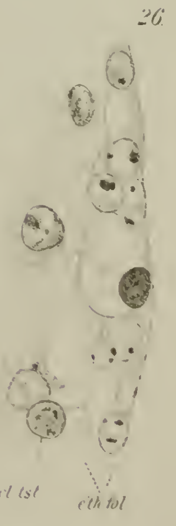


PLATE 4.

Fig. 27. Ovum in which the test cells and secondary follicular epithelium have just become differentiated. Reichert $\frac{1}{12}$ immers., Zeiss 3; × 1240.

Fig. 28. Part of a half grown ovum (173 × 150 μ), showing the formation of the yolk, follicle, and test cells.

Fig. 29. Selected test cells from the same ovum.

F.W.B. del.

B. Meisel lith Boston

PLATE 5.

Fig. 30. Periphery of an old ovum and its follicle.

Fig. 31. Periphery and follicular envelope of an ovum that has just reached the pouch.

Fig. 32. Ectoderm and test at an early stage in the formation of the test.

Fig. 33. Section of the test when a little more developed.

Fig. 34. Test, still farther developed.

Figs. 35–46. Various stages in the degeneration of the test cells of *Styela montereyensis.*

Fig. 35. Ovum containing the test cell is 84 × 65 μ. Test cell shows vacuoles and intravacuolar bodies.

Fig. 36. Ovum 92 × 69 μ.

Fig. 37. Ovum 108 × 69 μ.

Fig. 38. Test cell from the same ovum.

Figs. 39, 40. Test cells, from another ovum, showing the formation of the central corpuscle within the intravacuolar bodies.

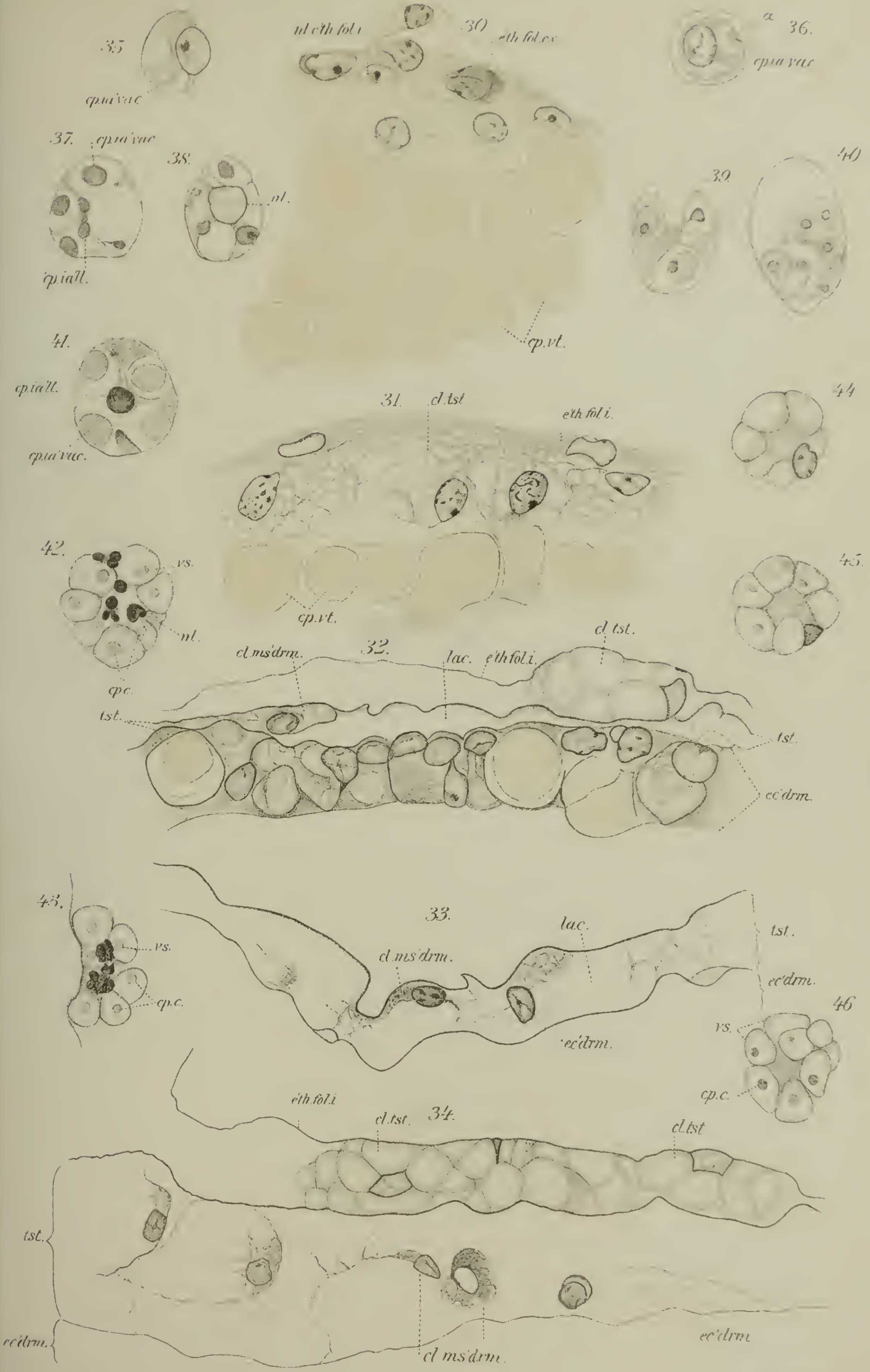
Fig. 41. Ovum 96 × 80 μ.

Figs. 42, 43. From an ovum measuring 134 × 111 μ.

Fig. 44. Ovum 92 × 76 μ.

Fig. 45. Ovum 169 × 80 μ.

Fig. 46. Ovum, nearly mature, measuring 108 × 92 μ.


35
cp.ia'vac.
30
nl.e'th.fol.i.
e'th.fol.ex.
cp.vt.
36.
a
cp.ia'vac.
37.
cp.ia'vac.
cp.ia'll.
38.
nl.
39.
40
41.
cp.ia'll.
cp.ia'vac.
31.
cl.tst
e'th.fol.i.
cp.vt.
44
42.
vs.
nl.
cp.c.
45.
32.
cl.ms'drm.
lac.
e'th.fol.i.
cl.tst.
tst.
tst.
ec'drm.
43.
vs.
cp.c.
33.
cl.ms'drm.
lac.
tst.
ec'drm.
ec'drm.
46
vs.
cp.c.
34.
e'th.fol.i.
cl.tst.
cl.tst
tst.
ec'drm.
cl.ms'drm.
ec'drm.

F.W.B. del

B. [illegible]

PLATE 6.

Fig. 47. Part of the wall of a corpus luteum from which the ovum has just passed out.

Fig. 48. Germinative vesicle just as it is beginning to shrink. From the same ovum as that in Fig. 28, measuring 173 × 150 μ. Reichert $\frac{1}{12}$ immers., Zeiss 2; × 890.

Fig. 49. Germinative vesicle and yolk-clump in an ovum of 190 μ diameter. Reichert $\frac{1}{12}$ immers., Zeiss 2; × 890.

Fig. 50. Germinative vesicle and central yolk bodies at a later stage. Ovum is 254 μ in diameter. Zeiss $\frac{1}{18}$ immers., 2; × 1300.

Figs. 51–59. Nucleoli in various stages of development. The measurements are in μ.

	Dimensions of the Ovum.	Dimensions of the Germinative Vesicle.
Fig. 51.	indistinct	15 × 11
Fig. 52.	23 × 13	13 × 11
Fig. 53.	indistinct	13 × 10
Fig. 54.	46 × 38	25 × 19
Fig. 55.	43 × 34	22 × 18
Fig. 56.	45 × 35	23 × 17
Fig. 57.	191 × ?	33 × 25
Fig. 58.	152 × 113	49 × 30
Fig. 59.	207 × 190	32 × 22

Figs. 60, 61. Two successive sections through the group of tetrads formed just before the formation of the first polar cell. The ovum has just reached the pouch.

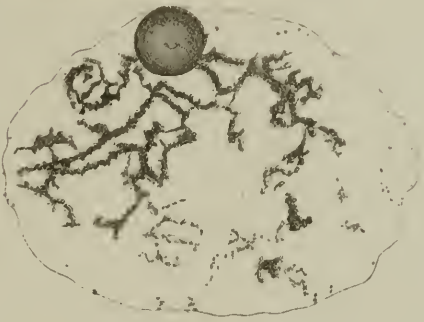
47.

51.

52.

53.

48.



54.

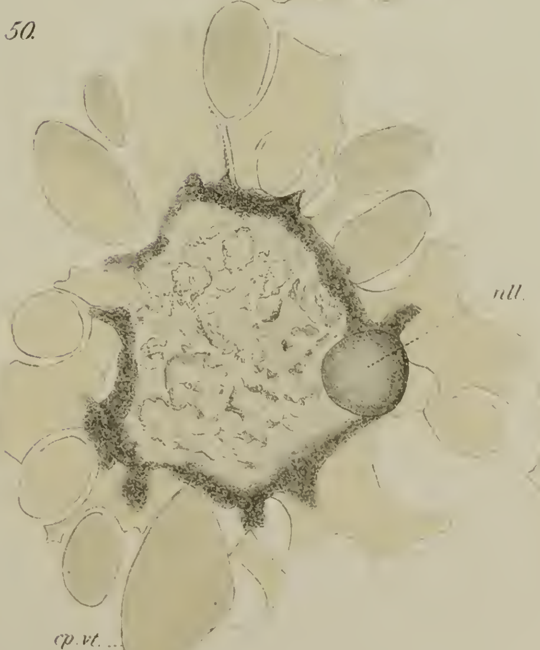
55.

49.

56.

57.

50.



58.

59.

60.

61.

F.W.B. del. B. Meisel lith. Boston

No. 5. — *Observations on Non-sexual Reproduction in Dero vaga.*[1]

By T. W. Galloway.

CONTENTS.

1. Introduction.

The worm upon which the present study is made was originally described by Leidy ('80) as Aulophorus vagus. A more complete account of the anatomy and histology by Reighard ('84) makes it apparent that its divergence from the species of Dero is not sufficient to warrant the establishment of a new genus. The sexual features which I have recently had the fortune to observe confirm this view.

The excellent work of von Bock ('97) on budding in Chætogaster diaphanus, in which there is a review of the work of preceding authors upon non-sexual reproduction in worms, renders it unnecessary for me to summarize previous accounts here. His interpretations are, however, in some respects so diverse from those of earlier authors as to make it desirable that they should be tested in another group. Dero is one of the most specialized of the Naidiform Oligochæta, and for this reason presents certain interesting variations from the conditions encountered in the forms that have been previously studied.

In the autumn, from September to November, Dero vaga is found abundantly in tubes formed of Lemna leaves, or other small light objects, at the surface of water in the ponds and ditches in the environs of

---

[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College, under the direction of E. L. Mark, No. XCIX.

Cambridge. At this time it usually occurs as single individuals or with only two zoöids in a chain. These, collected and placed in a suitable aquarium, will thrive and multiply asexually throughout the winter. The rate of division depends upon the food supply, by the regulation of which certain interesting variants from the normal may be had.

2. Structure of the non-dividing Animal and the Formation of Segments.

In individuals not sexually active and not in process of budding, the following regions may be distinguished: (1) prostomium; (2) four cephalic segments bearing ventral bristles only; (3) twenty to twenty-five well developed body segments, with both dorsal and ventral bristle bundles; (4) a region of incompletely formed segments passing posteriorly into an undifferentiated region or zone, — all of which may equal two or three adult body segments in length; and (5) a completely developed, complex structure, — representing probably at least one segment (anal segment), — which bears the anal orifice, the respiratory lobes (pavilion), and the digitiform appendages.

The formation of new segments in such a worm is a process which presents so many points of similarity to that of budding, that I wish to give a brief description of it before proceeding to the consideration of the latter phenomenon. New segments are invariably formed immediately in front of the anal segment, and always from the anterior portion of the undifferentiated zone. The length of this preanal zone is greater in well nourished than in poorly nourished individuals. In this part of the body all the structures which characterize segments in the more mature regions are less and less differentiated as one proceeds posteriorly. Even the organs which pass through this region in a functionally complete condition, such as the intestine, the blood-vessels, and, in part, the nerve cord, present simpler conditions than they do farther forward. The nerve chain, for example, is represented chiefly by non-fibrous elements, only a few fibres passing through to innervate the pavilion. The ventral and lateral portions of the body cavity are shown, by transverse sections, to be filled with a mass of indifferent tissue derived from cell multiplications in the ectoderm, the products of which break through the muscular layers at definite places and then fuse together, much as in the budding process (Plate **2**, Figs. 8, 9, Plate **3**, Fig. 15) described later. These ectodermal ingrowths are arranged serially in the long axis of the worm, and afford the earliest signs of segmentation.

3. Position of the Bud-zone: Primary and Secondary.

In such a worm, if the food supply be normal, a budding zone is formed some distance anterior to the preanal or segment-forming zone. Bourne ('91) has suggested that the segment at which bud formation takes place is probably constant for each species. This is certainly not the case here, at least not for the asexually produced zoöids. I am not yet able to say what may be true of the sexually derived individuals, for I have not as yet discovered how, if at all, the sexually produced zoöid may be certainly distinguished from the non-sexually produced forms. That probably can be settled satisfactorily only by rearing young worms from fertilized eggs.

The cellular activity accompanying budding, it is to be observed, involves only one segment, and the plane of separation is always midway between dissepiments. The position of this budding segment in the individuals which I have examined is variable within certain narrow limits. It may occur as far forward as the 16th and as far backward as the 21st setigerous segment. The following table, representing observations upon about three hundred individuals, gives in percentages the frequency of occurrence in these two and the intervening segments.

TABLE I.

Setigerous Segment	16th	17th	18th	19th	20th	21st
Percentage of Occurrence	7.6	15.3	38.2	26.7	7.6	4.6

Table II. is a record of observations upon the position of the budding segment in successive generations.

TABLE II.

Primary Division occurs in		Secondary Division occurs			
		Anterior Zoöid, in		Posterior Zoöid, in	
Segment No.	No. of Cases.	Segment No.	No. of Cases.	Segment No.	No. of Cases.
20	1	20	1	20	1
19	4	19	4	19	2
				18	1
				17	1
18	4	18	4	19	1
				18	1
				17	1
				16	1
16	1	16	1	17	1

It will be observed from this table that, when the anterior zoöid again buds, the zone of budding occurs at the same distance from the anterior end as in the first instance, i. e. in the same body segment. This is not true, however, for the posterior zoöid. There may be either an increase

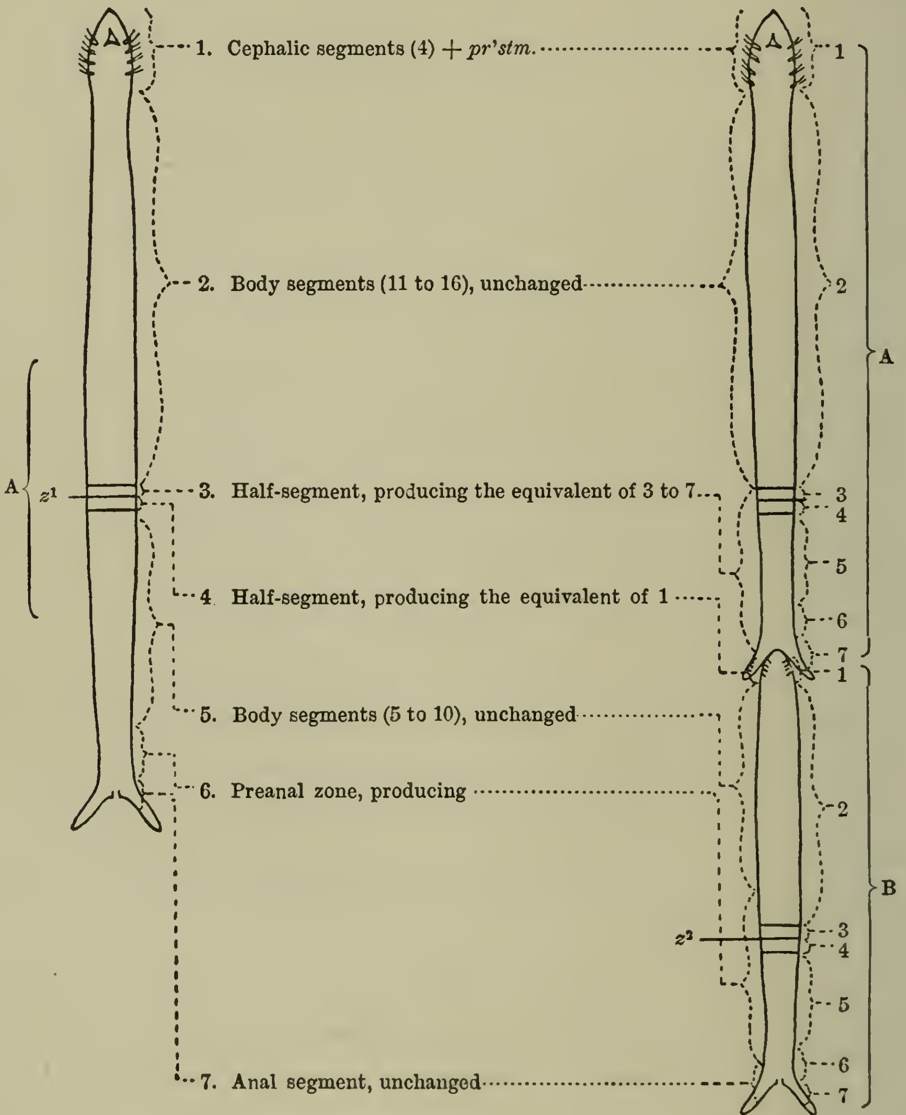


FIG. I. FIG. II.

or a decrease in the number of segments in front of the budding zone as compared with the condition in the parent. This variability is perhaps correlated with the rate of growth as dependent upon food, etc.

It will be seen from the accompanying diagram (Figures I. and II.) that the half-segment *A*, 3 (Fig. I.) produces *A*, 3–7 (Fig. II.), which simulates the condition of *A*, 3–7 (Fig. I.), and consequently that the second new individual, which is thus to be produced at the posterior end of *A* (Fig. I.), arises from a region which was undifferentiated during the first budding. The half-segment 4 (Fig. I.) produces a prostomium and four cephalic segments, *B*, 1 (Fig. II.). At the same time, the indifferent preanal zone, 6 (Fig. I.) is adding segments to the region 5, which before these additions embraces a small but variable (5–10) number of body segments. Since the budding in no case takes place in a segment so near the head as the tenth body segment, it follows that this must occur in the undifferentiated region 6 (Fig. I.), and consequently it is true for the posterior as well as the anterior zoöid that, when a new budding takes place, it occurs in a zone that was undifferentiated during the preceding process of budding.

4. Relation of Budding to Formation of Segments.

If the worms are well nourished, the secondary divisions often commence before the first is completed. A condition of this sort is shown in Plate **1**, Fig. 3. In such instances the secondary bud (z^2) in each zoöid lies within the limits, either of the indifferent zone (anterior zoöid), or of still incompletely differentiated segments (a condition more usually found in the posterior zoöid).

There is thus shown to be a close relation between the process of budding and that of forming new segments. For the material which is destined to subserve the process of budding is at one time an indisguishable part of the zone (preanal) the posterior part of which is a continuous source of new segments. In every case the budding zone, on its part, gives rise to two segment forming regions: a posterior, which is normally limited to the production of four segments beside the cephalic lobe; and an anterior, which never loses the power of forming new segments, since some of the segments thus produced, or at least one of them, retain the capacity of forming a new bud, by which the process is repeated and the power perpetuated indefinitely. In other words, the relation of the two processes in this worm is such as to lend support to the view that here budding is a specialized form of normal segmentation. The cycle of procedure occurs just as if, in the formation of segments from the indifferent preanal zone, there were deposited at a certain stage, in one or several segments, materials which are capable under appropriate circumstances of giving rise to indifferent tissue and to new segments.

This fact allies itself with what is known of regeneration of lost parts.

As several authors have shown, the likelihood of the regeneration of a given portion is decreased proportionally to the distance of the regenerating region from the part whose reproduction is expected. For example, the head segments in the earthworm are much more likely to be regenerated from anterior segments than from middle or posterior ones. In this case, too, the behavior suggests, one might say, a diminution of head-producing material posteriorly.

In addition to this normally recurrent relation between these two regenerative processes in Dero, I have found in two cases that, if a large number of posterior segments are removed from a worm in which the budding zone has just begun, the process of budding continues, without any effort being made to regenerate the lost tail piece. In such cases, however, the budding departs from the normal course, since the proliferations in what should become the head of the posterior zoöid are amorphous, none of the normal structures being produced; but the anterior half of the budding segment produces an indifferent zone and an anal segment in the customary way, with, however, minor imperfections. Here the behavior is as if the regenerative process had been transferred, as a matter of economy, to the budding region instead of taking place where the injury existed. In a case where only a small number of segments were removed, the cut being immediately in front of the indifferent preanal zone, regeneration occurred at the point of cutting, and the ectodermal thickening of the budding zone disappeared. After the regeneration of the tail piece was completed, the animal formed again the budding zone in the original segment (in this instance the 18th setigerous) and ultimately divided.

It is a suggestive fact, that, furthermore, in the sexual individuals, *some* of which are known to be asexually produced, I have found that the testes are formed upon the posterior face of dissepiment iii/iv, i. e. on a new dissepiment produced in the process of budding, in a region which was of course located in the parent individual much posterior to the usual place of production of gonads. The ovaries arise likewise upon the posterior wall of the dissepiment between setigerous segments iv/v. Although this is one of the original dissepiments, the new tissues are closely related to it in their origin and development.

5. Experiments on the Rate of Budding.

In the effort to secure an abundance of budding material, there appeared certain facts of practical and perhaps theoretical importance relative to the rate of division. Two classes of culture solutions were used in rearing the worms. Algæ and other organic substances native to pond water were supplied in the first; the second consisted of an infusion of boiled corn-meal in water in the proportion of 1 : 1000. Of the first, three grades were roughly distinguished: (1) that in which the organic matter was in such excess that striking evidence of decomposition was sure to occur; (2) that in which the organic matter was present in such quantities that no conspicuous impurity arose from its decomposition; and (3) that in which the organic material was reduced to a small per cent of what could have been employed without signs of decomposition. In the first solution, bacteria, paramœcia, and stentors appeared in great abundance, and it became necessary from time to time to pour a part of this away and renew the water. In the other two cases the water was not disturbed except as evaporation made renewal necessary. In the corn-meal solution frequent changing was necessary on account of rapid fermentation.

The following tabulated statement represents the results, but gives of course only rough quantitative data as to the effect of the food supply in influencing growth, as measured by the rate of germination. In each experiment, at the outset, ten individuals were taken approximately at the same (an early) stage of division. The figures in the columns of "days" indicate the number of separate worms at the end of the time

10 Individuals in each Culture.	Pond-water, with Algæ and other organic Food Supply.						Corn-meal in Water.	
	A. In Excess.		B. Medium.		C. Minimum.		D. 1 : 1000 parts.	
	15 days.	30 days.	15 days.	30 days.	15 days.	30 days.	10 days.	20 days.
Exper. 1	18	23	15	28	13	15	18	25
Exper. 2	22	19	18	30	12	14	20	22
Exper. 3	21	22	14	26	15	16		
Average	20.3	21.3	15.6	28	13 3	15	19	23.5
	1st 15 days.	2d 15 days.	1st 15 days.	2d 15 days.	1st 15 days.	2d 15 days.	1st 10 days.	2d 10 days.
Percentage Increase	103%	5%	56%	80%	33%	13%	90%	23 5%

indicated. The "30 days" columns take no cognizance of the stages of division of the individuals occurring at the end of the "15 days" periods, and for this reason the two columns of each culture are perhaps not strictly comparable. The horizontal line of percentages is reckoned upon the number of individuals existing at the beginning of the period in question.

It will be seen that during the first fifteen days solution "A" was productive of the most rapid division, in some instances the second division being accomplished; but during the second period the worms scarcely more than held their own. This is seemingly due to the prevalence of bacteria. Culture "D" presents somewhat similar phenomena. In "C" the falling off in the second period is probably caused by the disappearance of food from the water and from the tissues of the body. "B" is the control culture, and more nearly represents the ordinary rate of reproduction under favorable conditions. These are winter cultures. Propagation would doubtless be more rapid with fresh worms in summer or fall.

6. Methods.

Dero does not present any special technical difficulties except that, in the later stages of budding, separation of the zoöids is likely to occur in the process of killing, whereby control of the material is lost. I used as killing and fixing reagents with about equal success (1) a saturated aqueous solution of corrosive sublimate plus 1% acetic acid (hot), and (2) a solution of hot picro-sulphuric acid (Kleinenberg's). Staining of excellent quality was secured by Heidenhain's iron-hæmatoxylin method. Sections were made from 6 to 12 μ in thickness.

7. Histological Features of the Budding Process.

In the discussion of the rôle played by the different embryonic layers in the production of the new organs made necessary by budding, I shall first treat in a general way of the changes occurring in each layer, and the organs which are wholly developed therefrom. Afterward, at the risk of some repetition, I shall correlate the share of each layer in the formation of the mouth, and such other structures as involve more than one germinal layer.

a. Ectoderm.

The first evidence of the bud-zone, as seen in optical sections of the living worm, is a slight thickening of the ectodermal elements of the dermo-muscular wall (Plate **1**, Fig. 2, z'; Plate **2**, Figs. 11, 12). The thickening is first manifest on the ventral aspect, extending ultimately as a girdle around the segment. It is interseptal in position, and about equally distant from the nearest dissepiments. That this thickening is a matter of growth and not of local contraction is shown both by the increased number of cells and the increased length of the segment. The peripheral margins of the dissepiments bounding the bud-zone are crowded apart, as indicated in Figure 2. The bristle bundles belonging to the involved segment are forced backward into contact with the following dissepiment. They become the bundles of the 5th setigerous segment of the posterior zoöid. An external groove (Plate **1**, Figs. 4, 5, *sul.*) is next formed in the ectodermal thickening, and persists as the outward demarcation between the zoöids, indicating the place of ultimate separation. This groove deepens gradually but unequally at different points of its circumference. The activity of the tissue is strictly confined to one segment, the segments in front of and behind this one undergoing no appreciable changes. Hence, it is possible to affirm that the tissues of the active segment posterior to the plane of the groove furnish the material out of which are formed the prostomium, four new segments, and the anterior portion of the fifth segment, with their contained structures. Similarly, from the anterior half of the segment spring the whole set of structures appropriate to the tail end of the worm. It is possible to locate the fundaments of these organs from the beginning of the process.

The division of ectodermal cells may continue until a thickness of three or four cells is reached in the dermal layer. In the mean time, as may be seen in transverse sections, the proliferating ectodermal tissue breaks through the muscular layer into the body cavity, especially in the spaces between the longitudinal muscle bands (Figs. 8–10). These invading elements on either side the median plane coalesce with each other and with proliferations of the cells from the ventral nerve cord, filling the ventral and lateral portions of the body cavity in a very characteristic way (Plate **1**, Figs. 6, 7). In a sagittal section, a differentiation of this internal cell-mass into an anterior and posterior portion is apparent at a relatively early stage (Fig. 5). The cells on the contiguous faces of these masses become arranged into bounding surfaces, which are ultimately continuous with the external layer, and become, in part, the boundaries of the deepening groove. Thus the latter is supplemented in its deeper portion by an internal delamination, and the two together produce deep invaginations, especially from the latero-ventral regions (Plate **3**, Figs. 16, 17, *sul.*), which are paired and contribute to the formation of the mouth. The apparent depth of the ectodermic depression is increased by a pair of growths (directed backward and outward) of the thickened ectoderm anterior to the groove in the latero-ventral regions, to form the digitiform appendages (Figs. 16, 17, *pr'c. dg.*).

The process of ectodermic ingrowths between and through the muscle bands, referred to above, is kept up both anterior and posterior to the plane of separation of the zoöids.

In the *posterior* zoöid there are five distinct regions of cellular activity in the ventral part of the body, namely: (1) the ectoderm in the spaces between the lateral and ventral bands of longitudinal muscles (Plate **1**, Figs. 6, 7; Plate **2**, Figs. 8, 9); (2) the ectoderm invading the ventral muscle band and cutting off certain fibres (Plate **1**, Figs. 6, 7, *mu. v.* and *mu. v'.*) at either margin; and (3) the cellular elements of the ventral nerve cord itself. More dorsally, in the spaces between the dorsal and lateral longitudinal muscles, there is likewise an ingrowth of ectoderm on either side of the body, which in some measure supplements and fuses with the masses already described. More dorsal still, approximately at a level with the dorsal wall of the gut, is seen (Fig. 7) another irruption of ectoderm so located as to cut off a strand from the ventral margin of the dorsal muscle. This ingrowth differs from the former ones in the very important fact that its extent in an antero-posterior direction is extremely limited. The former proliferations occur one after another in longitudinal series, one of each series to every segment. The ingrowth through the dorsal muscle band, on the contrary, is limited to a single pair of cell masses situated well forward toward the plane of division. The cells from this pair of ingrowths move dorsally and toward the median plane until they rest upon the digestive tract, and finally meet each other, forming the brain ganglia, whose elements later produce a connective (Plate **1**, Fig. 6, *con't. crc'œ.*). The detached portion of the dorsal muscle band approximately equals in dimensions the whole lateral band. The pair of irruptions through the marginal portions of the ventral muscle, in conjunction with elements from the ventral nerve cord itself, furnishes the material for the cord in the newly forming segments of the anterior zoöid and the infra-pharyngeal enlargements of the nerve cord in the posterior zoöid. In the posterior worm there is a degeneration of that part of the old nerve tract which lies in front of the place to be occupied by the infra-pharyngeal ganglia, only a few fibres remaining to preserve connection between the individuals until separation is accomplished.

The ingrowths between the ventral and lateral muscle bands give rise, in each of the four cephalic segments of the posterior individual, to a pair of ventral bristle sacs, and to the ectodermal part of the nephridial organs. There are no dorsal bristle bundles formed in the cephalic segments of the posterior zoöid.

The fate of the proliferation between the dorsal and lateral longitudinal muscle bands is more obscure. The circumœsophageal connective, in running from the brain ventrally, passes, as has been said, between the main portion of the dorsal muscle band and the lateral part of it, which is thereby split off from the main band. In its further course ventrad, the connective again returns to a position inside the longitudinal muscles. This it does by running inward between the split off portion of the dorsal band and the lateral band of muscles, so that no part of the lateral muscle band ever lies inside the connective. It is perhaps significant that the cells of the lateral line make their appearance in the same space between the dorsal and lateral muscle bands (Plate **1**, Figs. 6, 7; Plate **2**, Fig. 10, *prf.* and *cl. ln. l.*). The two sets of nervous structures, — the circumœsophageal connective and the lateral line cells, — if the latter are really nervous, are thus apparently in relationship by their proximity. It is, furthermore, possible that the cells which push in and go to form the brain do so here rather than at the more dorsal position previously noted. The fact that the whole ectodermal arc peripheral to the detached portion of the dorsal band is very much thickened would seem to support this view. In this event, we should be compelled to admit that the future nervous elements produced at this place grow dorsally in a position peripheral to the cut off portion of the dorsal longitudinal muscle band, between which and the rest of the dorsal band they pass into the body cavity. This would help to explain the course taken by the fibres of the connective in uniting the brain and subpharyngeal ganglion. It would also connect the brain in its origin with the lateral line system, rather than with the ventral chain, the connection with the latter being an altogether secondary one. However this may be, the course of the nervous connective is associated with the position of the lateral line cells in a very suggestive way. I am as yet unable to state what, histologically, the origin of the connective fibres may be. From analogy with other annelids we should expect them to arise from the cells of the brain, or possibly from the subœsophageal ganglia, or both. The course of the connective is shown semi-diagrammatically in Figure 10, *con't. crc'œ.*

In the *anterior* zoöid the course of development is somewhat different.

The ectodermic invasions occur in the same way as in the posterior zoöid and in corresponding positions, but the one which cuts off a lateral portion of the dorsal muscle band is ultimately repeated here for each new segment, and occurs at the place where subsequently the dorsal bristle bundles are found. In fact, these ingrowing elements constitute the bristle forming organs. It is further to be noted that, at the time of separation of the zoöids, the bristle bundles of the anterior worm are in a much less advanced state of development than those of the posterior worm. Another point of difference is found in the fact that there is a much more intimate fusion of the several ectodermic ingrowths of the ventral and lateral regions with each other and with mesodermic elements in the anterior than in the posterior zoöid. In this manner is produced an indifferent zone, similar in all particulars to the undifferentiated segment-forming zone previously mentioned as characteristic of the preanal region. From the ectoderm comes, as in the posterior zoöid, the mass of tissue from which ventral nerve chain, ventral bristle sacs, etc., are developed. All stages in the differentiation of these structures may be found in a rapidly growing worm, as one passes forward. Immediately in front of the anal segment, where the tissue is least differentiated and the ventral nerve cord is to be developed almost *de novo*, an ectodermic ingrowth in a mid-ventral position divides the ventral longitudinal muscle and contributes to the ventral cells of the cord (Plate **3**, Fig. 15; Plate **4**, Fig. 23). Proliferations which are lateral, but still penetrate the ventral muscle, add cellular elements to the margins of the cord (Plate **2**, Fig. 8; Plate **5**, Fig. 24, *gn. v.*). Thus in the formative region the cord can be resolved into a median and two lateral constituents. It was the latter which Semper ('76) regarded as mesodermal. The fibres of the nerve oord naturally become less numerous posteriorly. The more dorsal, i. e. the deeper fibres, are the first to appear; this produces the condition figured in Plate **3**, Fig. 15, in which the fibrous tract appears to occupy a more and more dorsal position as one proceeds toward the tail. The ectoderm on the ventral side of the body in this region is especially thickened, being four or five layers of cells deep (Figs. 15, 16, 22, 23, 24).

b. Entoderm.

It is to be borne in mind that before the beginning of division the digestive tract in the region affected by that process is a simple tube with interseptal enlargements. The wall of the intestine, reckoning from the lumen outward, here consists of (1) a layer of ciliated epithelium, in which the free ends of the cells form a wavy contour; (2) scattered sub-epithelial cells lying in the basal portion of this epithelium (Plate **2**, Fig. 13); and (3), surrounding all, a distinct basement membrane. Outside the basement membrane is an investment of connective tissue, occasional muscle fibres, and chlorogogue cells. The pharynx, on the contrary, is a more highly specialized structure. Its wall is seen in cross section (Plate **4**, Fig. 18) to consist of a dorsal arched portion with a very thick wall, a nearly flat ventral floor, and much thinner latero-ventral connecting regions. The thin latero-ventral portions of the wall may be evaginated to form a pair of longitudinal grooves (*sul.*). The flexibility of this region allows considerable variability in the form of the tube, for the floor may be infolded into the arched dorsal portion so as nearly to obliterate the lumen, or it may be depressed until the lumen is nearly circular in cross section. Strongly ciliated, long columnar epithelial cells form the dorsal wall, and extend ventrally somewhat more than half way down the sides (Fig. 18, *phy. d.*). The ventral floor (*phy. v.*) is similarly formed of ciliated cells, but these are not so long as those of the dorsal wall, while the wall of the groove is formed of cubical non-ciliated epithelial cells. The new pharynx, formed as it is during budding, is derived exclusively from material lying anterior to the dissepiment which originally marks the posterior boundary of the budding zone. This shows that it must be either a modification of the posterior half of the intestine of the segment which is involved in the budding process, or a new structure, the material for which is supplied from other growth centres within the half-segment.

In a budding worm, while the body wall of the bud zone increases in length by the rapid multiplication of the elements making up that wall, there seems to be no corresponding growth on the part of the cells of the intestine. The digestive tube is thus mechanically stretched; this tends to obliterate the inequalities of its calibre. (Compare Fig. 5 with Fig. 16.) By the continuation of this stretching, the individual cells are transformed from their original columnar character into relatively thin pavement-like elements. I have no evidence that these ciliated epithelial cells divide during the budding process.

The first signs of cellular activity in the entoderm are seen in the small, indifferent, sub-epithelial cells (Plate **2**, Fig. 13). These become more and more numerous, first in the ventral part of the gut, and later in its lateral and dorsal walls; they form at length a sheath of cells around the epithelial layer which extends through the larger part of the active segment, and is especially well marked in its posterior half (Plate **3**, Fig. 16). This cell multiplication may continue in certain places until the layer *en'drm.*^{2} becomes five or six cells deep (Figs. 7–9). The cytoplasm of the older layer (*en'drm.*^{1}) stains feebly and diffusely, while that of the new layer (*en'drm.*^{2}) takes a very deep stain. The new entodermal layer attains a greater thickness in the posterior than in the anterior zoöid. The dorsal portion of the digestive tube of the posterior zoöid, beginning just behind the brain and extending to the posterior limit of the budding zone, is the region of greatest thickening. The thickness diminishes gradually from the dorsal to the ventral side of the tube. Later a separation of the old from the new entoderm occurs, and a cavity — crescent-shaped in cross section, the lumen of the new pharynx — appears (*phy. lu.*, Figs. 9, 16). The new entodermal cells next take on the typical columnar form and then become ciliated (Plate **3**, Fig. 17 ; Plate **4**, Fig. 19). The action of the cilia is manifest before the separation of the zoöids, and before the rudimentary lumen of the pharynx has any connection with either the old lumen or the outside world. The old entodermal lining finally becomes detached throughout the pharyngeal tract (Plate **2**, Fig. 14, *en'drm.*^{1}) and is swallowed or ejected through the mouth.

It is important to note that the entodermal cells are even more completely separated into two functionally different regions, corresponding to the two zoöids, than are the cells of the ectoderm. There is a distinct neutral zone between them, embracing the plane of division. This interruption is most conspicuous dorsally and laterally, being only slight ventrally (Plate **3**, Fig. 16).

In the anterior zoöid, immediately in front of the future plane of separation, two pairs of thickenings arise in a manner entirely analogous to that just described for the pharynx of the posterior zoöid (Plate **3**, Figs. 16, 17 ; Plate **4**, Fig. 23 ; Plate **5**, Figs. 24, 25, *pav.*), and in these thickenings spaces are formed, as in the case of the pharynx. Ultimately the dorsal and ventral cavities on the same side coalesce, and likewise the right and left communicate across the median plane, both dorsally and ventrally, thus forming a complete annular space of varying calibre around the old tube. These new entodermal cells, like those of the pharyngeal wall, bear cilia ; they constitute the lining of the pavilion. The ectoderm has no part in forming the inner face of the pavilion, the concrescence of the free margins of the two layers, ectoderm and entoderm, taking place at the margin of the pavilion. The digitiform process, however, is wholly covered with ectoderm, the boundary between ectoderm and entoderm being at the base of the inner side of that appendage.

It is only in the region of the pavilion that the entoderm of the anterior zoöid becomes especially active during budding, but anterior to this the sub-epithelial cells form a more or less continuous layer beneath the ciliated epithelium, in a manner characteristic of the indifferent preanal zone of the mature worm. As the digestive tube lengthens in the formation of new segments, these sub-epithelial cells, in my opinion, become interpolated between the ciliate cells, and thus help to form the lining of the tube, for I find no evidence that the ciliate cells in this region are undergoing division.

Summarizing the facts concerning the growth regions in the entoderm, we may distinguish the following in the anterior zoöid: (1) the antepavilion region, where a single layer of sub-epithelial cells reinforces the digestive cells, the latter not being sloughed; (2) the pavilion thickening, from which the old entoderm is lost; and in the posterior zoöid, (3) the pharyngeal region, of somewhat irregular shape, surrounding the gut and extending posteriorly to the old dissepiment; from this region also the original entodermic lining is cast off. Between (2) and (3) is a neutral zone, more extensive dorsally, narrowing below, in which the old layer alone exists.

I shall deal more fully with this in discussing the mouth.

The old entoderm in the budding zone does not lose continuity until the zoöids separate; thus there is no functional mouth nor anus until separation. The cells of the original lining of the digestive tract show signs of degeneration long before separation. The cell boundaries become less distinct, the cytoplasm stains more diffusely and less intensely, and vacuoles occur in the cytoplasm.

c. MESODERM.

The general arrangement of muscle fibres is the same in Dero as in other Oligochæta. The circular muscles lie beneath the dermis, and beneath these the longitudinal fibres are grouped in four bands: (1) the dorsal band occupies slightly more than one half the circumference of the body; (2) the narrow lateral band on either side is perhaps equal to one eighth of the circumference, and is separated by a space from the dorsal muscle; and (3) the ventral band, which is somewhat broader than the lateral bands, from which it is separated by a space.

In the formation of the budding zone the lateral bands are little interfered with until the zoöids separate, when their broken ends become spread out and attached to the lateral walls of the pavilion in the anterior zoöid, and to the prostomium in the posterior individual. The dorsal and ventral muscle bands, on the contrary, are both split, it will be remembered, by ectodermic invasions which penetrate between their fibres. Two symmetrically located series of ingrowths penetrate the ventral muscle, so that this band throughout the bud zone is made to consist of a median (*mu. v.*) and two lateral portions (*mu. v'.*). During the ingrowth of the indifferent ectoderm tissue, the lateral parts are pushed inward much more than the median, and in the posterior zoöid they come to lie inside the circle of the newly formed pharyngeal nerve ring (Plate **1**, Fig. 6; Plate **4**, Fig. 21, *mu. v'.*). These lateral fibres of the ventral band, on account of their deeper position, are less interfered with by the formation of the ventral groove than is the median strand. As a result, they constitute the muscular connection on the ventral side of the zoöids which persists longest. Thus the mid-ventral strand is sooner free to form new attachments in connection with the mouth and head of the new individual; its fibres are in fact seen to be distributed to the lower lip, to the sides of the mouth, and to the pharynx, persisting as the principal ventral muscle. The lateral portion of the ventral band, which passes within the nerve ring, becomes attached to the deeper portion of the ectodermal constituent of the ventral surface of the mouth (Plate **5**, Fig. 26, *mu. v'.*).

In the budding zone of the anterior individual the *old* median band is superficial even to the newly forming circular muscle fibres; the band becomes broken up into smaller groups of fibres by the penetration of ectodermal elements. The deeper lateral strands of the ventral muscle band become more conspicuous, and a *new* median constituent is formed between them; in this way is reproduced the typical single ventral muscle. Anterior and posterior to the region of ectodermal ingrowth the strands merge into a normally continuous sheet.

The dorsal muscle band is likewise separated into a median and lateral portions by the development of the nerve ring, which passes exterior to the extreme lateral portions of the band (Plate **2**, Fig. 10, *mu. d'.*), but interior to the dorsal (median) part of it. Thus, while the zoöids remain connected, the brain is supported by a sling, as it were, composed of the lateral strands of the dorsal muscle bands (Plate **2**, Fig. 10; Plate **3**, Figs. 16, 17, *mu d'.*). In this position, some of the fibres become attached to the brain capsule (Plate **5**, Fig. 28); others remain attached to the dermo-muscular wall at the anterior dorsal boundary of the posterior zoöid. The contraction of the latter fibres, when separation of the zoöids takes place, in connection with the action of the circular muscles to be described in detail later, pulls the ectodermal margin downward and backward into connection with the median-dorsal entodermal and dorso-lateral ectodermal elements previously mentioned. The median dorsal fibres are distributed to the prostomium (Plate **5**, Fig. 28, *mu. d.*).

New circular muscles are formed among the pre-existing fibres as the bud-zone increases in length. The chief special modification occurs in the immediate vicinity of the future separation. In connection with the ectodermic ingrowths contributing to the formation of the mouth, circular fibres are carried inward in such a way as to constitute an investment of the new epithelium which forms the floor of the mouth (Plate **3**, Figs. 16, 17, *mu. crc'œ.*, fibres cut crosswise).

Before separation of the zoöids, these circular fibres (Plate **5**, Fig. 25, *mu. crc'œ.*) pass, like the circumœsophageal nerve ring, between the separated strands of the ventral muscle band, a lie for and part of their course within the nerve ring. Another interesting fact concerning the circular muscle fibres of this region is that they do not constitute a complete circular band. The ends of the fibres, instead of meeting in the mid-dorsal line, pass forward as well as upward, and are inserted into the sides of the prostomium (Plate **5**, Figs. 26, 29, *mu. crc'œ.*) ; they aid in pulling the prostomium downward into its normal position when the posterior individual becomes detached from the anterior one. The fibres of this semicircular band (Figs. 16, 17, *mu. crc'œ.*) are coextensive, on the ventral floor of the mouth, with the latero-ventral ectodermal invaginations, and thus contribute to the buccal wall.

The radial fibres from the dermo-muscular sac to the pharynx represent longitudinal fibres, which have been diverted from their ordinary course of growth, and have become attached to the wall of the newly formed pharynx. Similarly, the fibres moving the bristle bundles are apparently derived from the muscle bands in their immediate vicinity. This is clearly true of those moving the setæ in the plane parallel with the axis of the body (i. e. the longitudinal fibres). There are also setal muscles in the transverse plane, but I am not certain as to their origin.

The dissepiments in the undifferentiated region of the anterior zoöid seem to be formed in a somewhat mechanical way. The cell proliferations of the ectoderm are, from the beginning, discontinuous. They are practically successive pairs of buds or ingrowths, which force before them the portions of the peritomal lining and its connective tissue investment which lie immediately opposite them. Between successive buds, i. e. in the septal planes, the mesodermic elements remain attached to the permanent ectoderm. The ectodermic buds in their further growth continue to carry the connective-tissue mesoderm before them until they come into contact with the wall of the digestive tube. The connective-tissue partition between the successive masses of ectodermic cells may be clearly seen in longitudinal sections of stages as advanced as that of Figure 16 (Plate 3), the anterior masses being more clearly separated than the posterior ones.

The blood-vessels undergo considerable branching and anastomosis in the anterior and posterior ends of the mature animal. In the part of the adult worm where budding is to take place, the dorsal and ventral vessels are not connected by conspicuous circumintestinal loops; but in the budding zone, long before separation of the zoöids, a complete vascular loop is formed in each zoöid close to the plane of division (Plate 3, Fig. 17, *vas. sng. crc.*). The complex anastomosis is not, so far as I can determine, completed until the animals become independent. The loops are of very small calibre until this occurs.

d. SUMMARY OF CHANGES IN THE FORMATION OF THE MOUTH AND PHARYNX.

In concluding this part of the subject, it is perhaps desirable to summarize under a separate heading the chief features connected with the rather complex processes involved in the formation of the structures appropriate to the anterior end of the digestive tract. This is rendered desirable from the fact that each of the germ layers contributes to its production.

The wall of the new pharynx is formed around the old gut by a proliferation of the cells occupying the base of the original epithelium, and a delamination of the layer thus formed. The lumen of the pharynx exists, as a lacuna dorsal to the gut, between the old and new entoderm before the separation of the zoöids. Dorsally, the new entodermal wall does not reach forward beyond the position of the brain. Laterally, its anterior margin passes downward and somewhat backward, but turns forward again in the middle of the ventral side of the worm. To the curved lateral margin of this new wall is applied a pair of ectodermal ingrowths, whose history is as follows.

The groove marking the region of separation of the zoöids, relatively shallow in other regions, becomes specially deepened at two points, symmetrical to the median plane, and corresponding to the space between the ventral and lateral longitudinal muscles. The axis of these depressions lies in the plane of the groove, which inclines forward, and dorsally. The direction of the plane of the groove is shown in Figure 3. The depth of the two infoldings is enhanced by the outgrowing digitiform appendages of the anterior zoöid. When the depressions have reached a considerable depth, they turn somewhat abruptly upward and backward on either side of the digestive tract (Plate **3**, Figs. 16, 17; Plate **4**, Fig. 22, *sul.*). The ectodermal wall bounding this lumen applies itself to the lateral wall of the old gut, but does not reach its mid-dorsal line. Posteriorly these ingrowths become continuous with the new pharyngeal wall described above, and ultimately, after the separation of the zoöids, their lumina, by the breaking through of the tip of the invagination, are put in communication with the lumen of the new pharynx (Fig. 19). This represents the condition attained before the zoöids separate; the condition of the tissues involved is shown in Figures 19–24. At the moment of separation, the contraction of the semicircular muscles (Plate **3**, Fig. 17; Plate **5**, Fig. 26, *mu. crc'œ.*) and other muscles, both circular and longitudinal, in the posterior zoöid, pulls the whole prostomium downward, closing up the communication of the body cavity with the outside world which otherwise would result, bringing the aperture of the gut into a ventral, instead of a terminal position. Simultaneously, the lateral fibres of the dorsal muscle which lie inside the circumœsophageal commissure mechanically draw the ectoderm of the free anterior portion of the dorsal wall inward and backward, under the brain, into the space left by the failure of the lateral ectodermal ingrowths to meet in the mid-dorsal line; thus is formed the roof of the buccal cavity. A similar service in the formation of the floor of the mouth is performed by the detached constituents of the ventral muscle, in the mid-ventral line.

The buccal cavity is thus lined with ectoderm from two sources: (1) the floor and roof are produced by a simple infolding of already formed ectoderm, unaccompanied by a process of growth; (2) the sides, which extend farther posteriorly, by the latero-ventral ingrowths. The deep groove in the ectoderm (Plate **3**, Fig. 16, *sul.*; Plate **4**, Fig. 23) persists as a lateral furrow at either side of the mouth (Plate **5**, Fig. 26, *i'vag. os. l.*).

When the zoöids separate, and the lumina of the lateral ectodermal invaginations become continuous with the lumen of the pharynx, there is seen in this structure a pair of grooves (Plate **4**, Fig. 18, *sul.*) which are directly continuous with the ectodermal grooves of the mouth and buccal cavity. By muscular contractions the old gut is loosened from its remaining points of attachment to the new, chiefly on the ventral aspect, and the mouth and pharynx are functionally and structurally complete.

8. Conclusions.

1. Two normal regenerative processes are to be distinguished in Dero (1) that by which new segments are formed, limited to the region immediately in front of the anal segment, and (2) the formation of the budding zone in segments which have been derived from (1). The first process gives rise to undifferentiated materials from which the bud-zone is produced; the bud-zone, in turn, produces a segment-forming zone. These two processes are so related in this species that budding may be looked upon as a specialized method of segment formation.

2. The sexual gonads in Dero vaga arise upon the posterior walls of dissepiments iii/iv and iv/v, in individuals known to be produced asexually. The dissepiment iii/iv, on which the testes occur, is produced *de novo* in the budding process, and dissepiment iv/v is the bounding dissepiment of the budding segment. These facts show a close relation between the sexual elements and the new structures formed from the indifferent cell masses during the budding process, and suggest that both are referable to the preanal segment-forming region as their source.

3. The budding zone in Dero is formed, and division takes place midway between dissepiments, i. e. in the middle of the segment, if the dissepiments mark the boundaries of segments. Semper ('76) states that in Nais barbata and Nais proboscidea budding occurs between two old segments. Von Kennel ('82) says that the bud is formed immediately behind a dissepiment in Ctenodrilus pardalis. Von Bock ('97) describes the bud as forming between segments in Chætogaster. His Fig. 14, Taf. VI. illustrates this and shows the dissepiment splitting. It appears to me, however, desirable that the method of the formation of new segments in Chætogaster be more fully made out. It seems to me that the splitting of the dissepiment may possibly be a part of the process of the formation of *new segments* rather than of the immediate production of the more specialized bud-zone, and that the separation occurs, after all, in the middle of this newly formed segment. The appearance of the gut in Figure 14 would suggest this interpretation. We know that new segments are formed in these regions in Chætogaster, and it is not clear how much of this precedes and how much follows the budding process.

4. The histological steps of bud formation in Dero agree for the most part with those described for Chætogaster by von Bock. This is true of the origin of the brain from paired ectodermic ingrowths, the reinforcement of the ventral nerve cord by serial ectodermic invasions between the longitudinal muscle bands, the ectodermic origin of the bristle sacs in the newly formed segments, the origin of the pharynx from the entodermal cells of the old gut, the paired ectodermic invaginations concerned in the formation of the mouth, and the absence of a proctodæum in the anterior individual. The chief points of difference which should be noted are as follows.

(*a.*) In Chætogaster the old entoderm and the wall of the body cavity unite directly in the anal segment. In Dero there is an outgrowth of newly formed ciliated entoderm which unites the old entoderm with the body wall. This new entoderm lines the pavilion. The anus is at the place of union of the old and new entoderm. According to von Kennel (82), there is a proctodæum in Ctenodrilus pardalis.

(*b.*) While the mouth and pharynx of Dero and Chætogaster present certain common features in their mode of origin, there are important differences between the two worms in each region. In Chætogaster the paired ectodermal invaginations ultimately run together across the median plane to the mouth, and they secure union with the new pharynx before the separation of the zoöids. The ectodermic invaginations in Dero, on the other hand, never meet, producing merely the buccal sinus at either lateral angle of the mouth cavity. The floor and roof of the mouth are formed by mechanical infolding of the appropriate portions of the anterior margin of the body wall around the old gut. This old ectoderm is brought into contact with the new entoderm and with the new ectoderm of the invaginations mentioned above, *after* the separation of the zoöids. The pharynx is formed in Chætogaster by an outgrowth of the entodermal cells on the floor of the old gut. This cell mass comes to be occupied by a lumen, single behind but continued forward as a pair of curved branches which come to communicate with the ectodermal invaginations which are the beginnings of the mouth. The old gut becomes constricted, and, together with the nerve cord and the ventral body wall lying between the fundaments of the mouth, is resorbed. In Dero the pharynx is formed around the old gut, especially well developed on the dorsal side, and the cavity of the gut becomes the lumen of the pharynx, the old wall being split away from the new entoderm, but not losing its continuity until the zoöids separate, whereupon the old wall is entirely broken down and lost. The differences cited above are perhaps to be correlated in part with the fact that the zoöids of Dero are much less inclined than those of Chætogaster to remain associated after the development of the bud zone has gone so far as to render them capable of independent existence.

(*c*.) For Chætogaster von Bock ('97, Taf. VI. Figs. 9, 13) figures the connective as passing superficial to the lateral longitudinal muscle bands, and describes the brain as arising by the fusion of the ectodermic contributions from the spaces between the dorsal and lateral (" obere Muskellücken"), and from those between the lateral and ventral muscle bands (" untere Muskellücken "). These cell masses grow dorsad, overarching the gut, and fuse with the corresponding masses of the other side to form the brain. According to my observations on Dero, the brain is formed wholly by cells which break through the dorsal longitudinal muscle band. When the connective is formed, it lies superficial to a detached lateral portion of the dorsal muscle and returns to the body cavity between this and the lateral muscle (the region at which the cells of the lateral line occur). The regions of ectodermal activity responsible for the elements of the brain and connective are thus seen to lie immediately superficial to the lower margins of the dorsal muscle band. From this place there is an upward growth to form the brain, and a ventral growth which marks the course of the connective as it passes toward the ventral cord. The position of the mature connective external to certain longitudinal muscle fibres is thus rendered intelligible. In a similar way the region from which nervous cells spring on the ventral side, being superficial to the lateral fibres of the ventral muscle, gives rise to elements, a part of which penetrate the ventral muscle band (cutting off a lateral portion of it) to fuse with the ventral nerve chain, while others pass into the body cavity between the ventral and lateral muscles. The position of the connective in its course from the brain to the ventral ganglia is thus determined, and, as in the dorsal region, is superficial to the lateral portion of the ventral longitudinal muscle.

While it is entirely possible that the differences in the families studied may account for the apparent differences in the origin of the nervous elements, the course of the connective as figured by von Bock would suggest that the region superficial to the *lateral* muscle band is the place at which the nervous elements in this case arise, and that the more dorsal ingrowth is chiefly, if not wholly, the source of the brain, — the one between the lateral and ventral bands marking the course of the connective, rather than contributing directly to form the brain. Otherwise, it is very difficult to see why the connective should not follow the line of least resistance along the *inside* of the body wall, rather than penetrate the body wall, as its course actually indicates. I am aware that this suggestion is based upon general considerations and upon analogy merely, while the care shown throughout von Bock's paper gives abundant ground for the trustworthiness of his results.

I have great pleasure, finally, in expressing the sense of obligation I feel to Dr. E. L. Mark, under whose direction this work has been done, for his advice and assistance throughout its prosecution.

BIBLIOGRAPHY.

Beddard, F. E.

'95. A Monograph of the Order Oligochæta. Oxford. xii + 769 pp., 5 Plates.

Bock, M. von.

'97. Ueber die Knospung von Chætogaster diaphanus. Jena. Zeitschr., Bd. 31, Heft 2, pp. 105–552, Taf. 6–8.

Bourne, A. G.

'86. On Budding in Oligochæta. Report of Brit. Assoc., pp. 1096, 1097.

Bourne, A. G.

'91. Notes on the Naidiform Oligochæta. Quart. Jour. Micr. Sci., Vol. 32. pp. 335–356, Plates 26, 27.

Bulow, C.

'83. Die Keimschichten des wachsenden Schwanzendes von Lumbriculus variegatus, nebst Beiträgen zur Anatomie und Histologie dieses Wurmes, Zeitschr. f. wiss. Zool., Bd. 39, pp. 64–96, Taf. 5.

Bulow, C.

'83ª. Ueber Theilungs- u. Regenerations vorgänge bei Würmern (Lumbriculus variegatus, Gr.). Arch. f. Naturg., Jahrg. 49, Bd. 1, pp. 1–96.

Hatschek, B.

'58. Studien über Entwickelungsgeschichte der Anneliden. Arbeit. a. d. Zool. Inst. Wien, pp. 277–404, Taf. 23–30.

Hepke, P.

'96. Zur Regeneration der Naiden. Zool. Anzeiger, Bd. 19, No. 520, p. 514.

Hepke, P.

'97. Ueber histo- und organogenetische Vorgänge bei Regenerations-processen der Naiden. Zeitschr. f. wiss. Zool., Bd. 63, pp. 263–291, Taf. 14 und 15.

Hescheler, K.

'96. Ueber Regenerations Vorgänge bei Lumbriciden. Jena. Zeitschr., Bd. 30, pp. 177–290; Bd. 31, pp. 521–604, Taf. 21–26.

Keller, J.

'94. Die Ungeschlechtliche Fortpflanzung der Süsswasserturbellarien. Jena. Zeitschr., Bd. 28, pp. 370–407.

Kennel, J. von.

'82. Ueber Ctenodrilus pardalis. Arbeit. a. d. Zool. Inst. Würzburg, Bd. 5, pp. 373–429, Taf. 16.

Leidy, J.
'80. Notice of some Aquatic Worms of the Family Naides. Amer. Nat., Vol. 14, pp. 421–425.

Leuckart, F. S.
'51. Ueber die ungeschlechtliche Vermehrung bei Nais proboscidea. Arch. f. Naturg., Jahrg. 17, Bd. 1, pp. 134–138, Taf. 2.

Perrier, E.
'70. Sur la reproduction scissipare des Naidines. Compt. Rend., Tom. 70, p. 1304.

Randolph, H.
'92. Regeneration of the Tail in Lumbriculus. Journ. Morph., Vol. 7, pp. 317–344, Plate 19.

Reighard, J.
'84. On the Anatomy and Histology of Aulophorus vagus. Proc. Amer. Acad. Arts and Sci., Vol. 20, pp. 88–106, Plates 1–3.

Rievel, H. von.
'96. Ueber die Regeneration des Vorderdarmes und Enddarmes bei einigen Anneliden. Zeitschr. f. wiss. Zool., Bd. 62, pp. 289–341, Taf. 12–14.

Schultze, M.
'49. Ueber die Fortpflanzung durch Theilung bei Nais proboscidea. Arch. f. Naturg., Jahrg. 15, Bd. 1, pp. 293–304.

Schultze, M.
'52. Noch ein Wort über die ungeschlechtliche Vermehrung bei Nais proboscidea. Arch. f. Naturg., Jahrg. 18, Bd. 1, pp. 3–7, Taf. 1.

Seeliger, O.
'96. Natur u. allgemeine Auffassung der Knospenfortpflanzung der Metazoen. Verhandl. der Deutsch. Zool. Gesellsch., pp. 25–58.

Semper, C.
'76. Ueber die Verwandtschaftsbeziehungen der gegliederten Thiere. Arbeit. a. d. Zool. Inst. Würzburg., Bd. 3, pp. 115–404, Taf. 5–15.

Vejdowsky, F.
'84. System und Morphologie der Oligochæten. Prag. 166 pp., 16 Taf.

Wagner, F. von.
'90. Zur Kenntniss der ungeschlechtlichen Fortpflanzung von Microstoma. Zool. Jahrb., Abth. f. Anat. u. Ontog., Bd. 4, pp. 349–423, Taf. 22–25.

Wagner, F. von.
'93. Einige Bemerkungen über das Verhältniss von Ontogenie und Regeneration (Vorläufiger Bericht). Biol. Centralb., Bd. 13, pp. 287–296.

Wagner, F. von.
'97. Zwei Wort zur Kenntniss der Regeneration des Vorderdarmes bei Lumbriculus. Zool. Anzeiger, Jahrg. 20, No. 526, p. 69.

Zeppelin, Graf M.
'83. Ueber den Bau und die Teilungsvorgänge des Ctenodrilus monostylus, nov. sp. Zeitschr. f. wiss. Zool., Bd. 39, pp. 615–652, Taf. 36, 37.

EXPLANATION OF PLATES.

ABBREVIATIONS.

a.	Anterior.
an.	Anus.
cl. gn.	Ganglion cells.
cl. ln. l.	Cells of the lateral line.
con't. crc'œ.	Circumœsophageal connective.
con't. tis.	Connective tissue.
d.	Dorsal.
di'sep.	Dissepiment.
ec'drm.^{1}	Old ectoderm.
ec'drm.^{2}	New ectoderm.
en'drm.^{1}	Old entoderm.
en'drm.^{2}	New entoderm.
e'th.	Epithelium.
f'br. n.	Fibrous elements of nervous system.
gn. su'œ.	Brain.
gn. v.	Ventral nerve ganglion.
in.	Intestine.
i'vag.	Invagination.
i'vag. os. l.	Lateral groove of mouth.
lu.^{1}	Old lumen.
lu.^{2}	New lumen.
mb. ba.	Basement membrane.
ms'drm.	Mesoderm.
mu.	Muscles.
mu. crc.	Circular muscles of body wall.
mu. crc'œ.	Circumœsophageal muscles.
mu.d.	Dorsal muscles (longitudinal).
mu.d'.	Portion of dorsal muscle detached by ectodermal ingrowth.
mu. l.	Lateral muscles (longitudinal).
mu. r.	Radial muscles.
mu. v.	Ventral muscles (longitudinal).
mu. v'.	Portion of ventral muscle detached by ectodermal ingrowth.
nph.	Nephridium.
œ.	Œsophagus.
os.	Mouth.
p.	Posterior.
pav.	Pavilion.
pav. lu.	Lumen of pavilion.
phy.	Pharynx.
phy. d.	Dorsal wall of pharynx.
phy. ec'drm.	Ectoderm of pharynx.
phy. en'drm.	Entoderm of pharynx.
phy. lu.	Lumen of pharynx.
phy. v.	Ventral wall of pharynx.
pr'c. dg.	Digitiform process.
pr'f.	Proliferation.
pr'stm.	Prostomium.
sac. drm-mu.	Dermo-muscular sac.
sb-e'th.	Sub-epithelium.
set. d.	Dorsal bristle sacs.
set. v.	Ventral bristle sacs.
sul.	Groove.
v.	Ventral.
vas. sng. d.	Dorsal blood-vessel.
vas. sng. crc.	Vascular loops.
vas. sng. v.	Ventral blood-vessel.
z.	Undifferentiated preanal zone.
z.^{1}	Primary bud zone.
z.^{2}	Secondary bud zone.
zo'd. a.	Anterior zoöid.
zo'd. p.	Posterior zoöid.

PLATE 1.

Fig. 1. Optical sagittal section of posterior portion of a worm not in process of budding, showing undifferentiated preanal zone (*z.*). × 30.

Fig. 2. Similar view of portion of an individual in which the bud zone ($z.^1$) is already distinguishable. × 30.

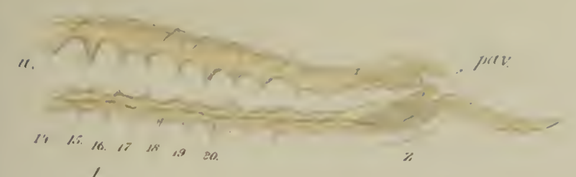
Fig. 3. Budding worm in which the secondary bud zone ($z.^2$) is recognizable. The Roman numerals indicate the number of the segment behind the prostomium of the original worm; the Arabic, those of the zoöids. The accented Arabic numerals, 1′–4′, denote the zone of undifferentiated materials out of which are to be formed the cephalic segments of the individual produced by the *second* budding. × 100.

Fig. 4. Parasagittal section of a budding segment showing ectodermal thickening and ingrowth on ventral surface only, at a fairly advanced stage. Section considerably to one side of the median plane. × 655.

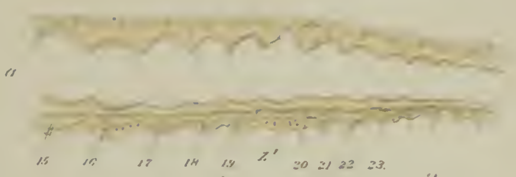
Fig. 5. Parasagittal section of the whole segment at a later stage. × 218.

Fig. 6. Cross section of a stage much more advanced than the preceding, through the posterior zoöid, showing the position of the brain (*gn. su'œ.*). × 218.

Fig. 7. Transverse section of a similar stage, posterior to position of the brain, showing the regions where the ectoderm grows in between the muscle bands. × 218.



1.



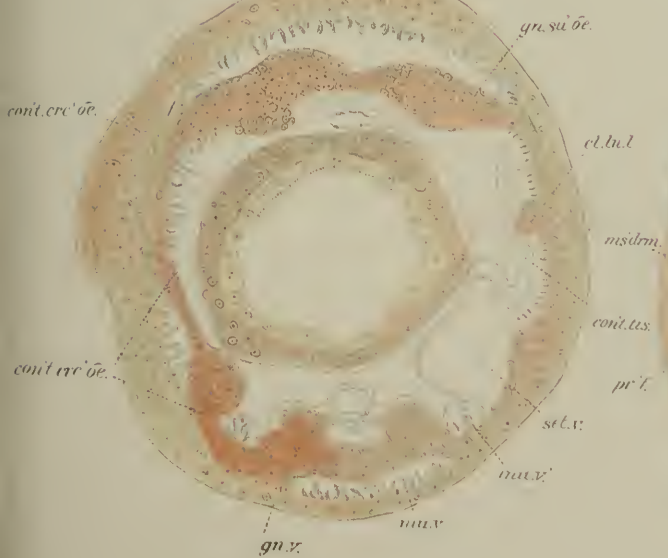
2.

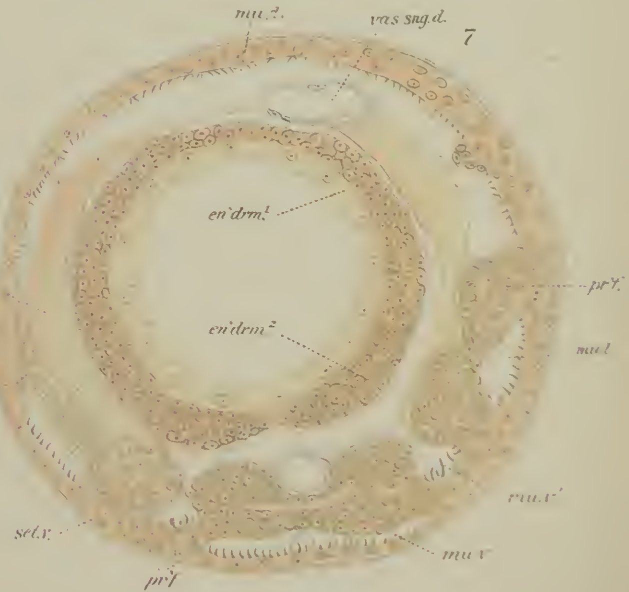
3.

4.

5.

6.





TWG del

PLATE 2.

Fig. 8. Transverse section of the same worm as that from which Figure 7 is drawn, but anterior to the plane of separation. × 218.

Fig. 9. Transverse section of posterior zoöid in the region of the pharynx (*phy.*). The stage is later than that represented in Figures 6-8. The lumen appears as a cavity formed by the splitting of the old entoderm (*en'drm.*^{1}) from the new (*en'drm.*^{2}).

Fig. 10. Semi-diagrammatic representation of the course of the circumœsophageal connective (*con't. crc'œ.*) in its relation to the ganglia, the muscles, and the lateral line cells (*cl. ln. l.*). × 200.

Fig. 11. Parasagittal section showing the ectodermal thickening on the ventral surface of the budding segment, at a very early stage. × 500.

Fig. 12. Similar section at a later stage. × 500. (Figures 11, 12, are to be compared with Figures 4 and 5.)

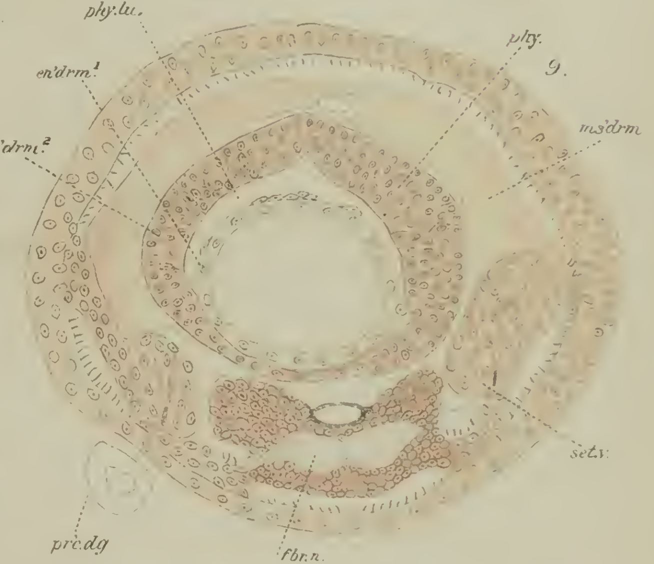
Fig. 13. Part of longitudinal section of normal entodermal layer of intestine, showing sub-epithelial cells (*sb-e'th.*). × 800.

Fig. 14. Sagittal section of head of posterior zoöid which has been separated from anterior zoöid one hour, showing the extent of ectoderm and entoderm in the formation of the mouth and pharynx, in the median plane *Ec'drm.*^{2} marks the boundary between new ectoderm and new entoderm; *ec'drm.*^{1}, the boundary between the newly formed ectoderm and the old ectoderm of the mechanically infolded edge of the prostomium, formerly attached to the anterior zoöid. × 218.

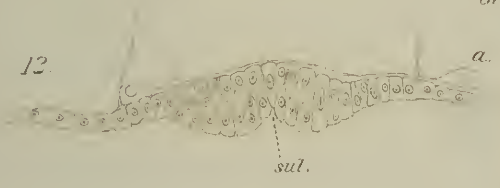
8.

10.

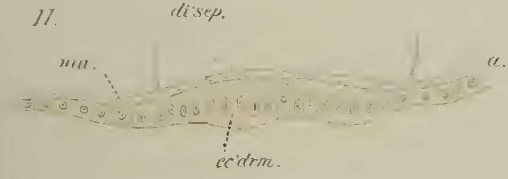
9.



12.



11.



13.

14.

T.W.G. del

B. Meisel lith.

PLATE 3.

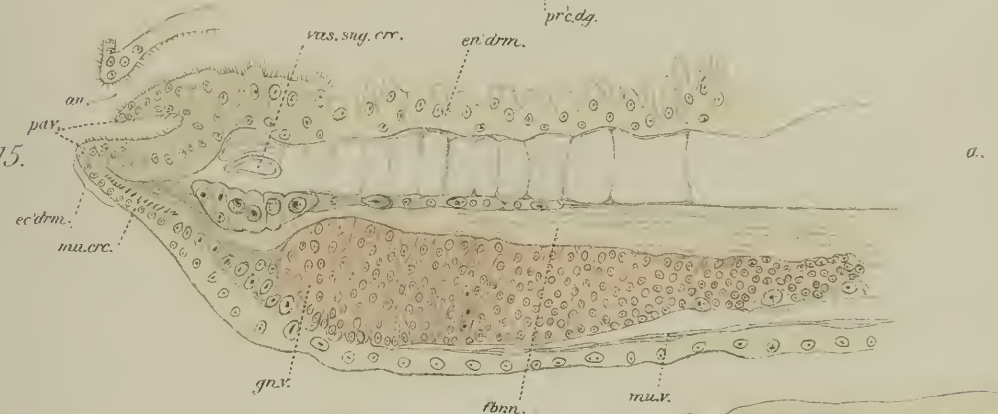
Fig. 15. Sagittal section showing development of the ventral nerve chain in the preanal zone of a recently separated zoöid. × 312.

Fig. 16. Parasagittal section, considerably to one side of median plane; stage about the same as that represented in Fig. 9. × 218.

Fig. 17. Similar section, later stage. × 375.

16.

15.



17.

T.W.G. del

B. Meisel lith. Boston

PLATE 4.

Fig. 18. Cross section of the pharynx of a mature worm. × 312.

Figs. 19–24. Posterior face of cross sections from a single series through a bud-zone in which separation is imminent. × 312. The higher the number, the farther forward the section is in the series. Figures 19–21 belong entirely to the posterior zoöid. Figures 22–24 show parts of both zoöids. Sections 10 μ thick.

Fig. 19. Section through pharynx of posterior zoöid; dorsal lumen conspicuous.

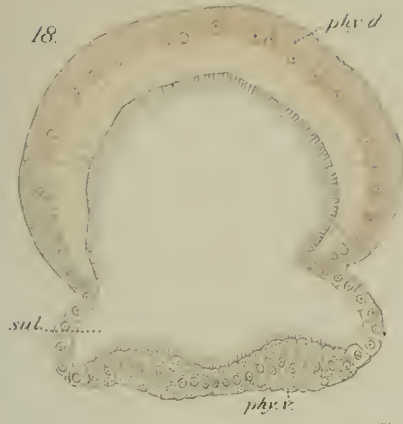
Fig. 20. Next section in front of that of Figure 19 showing anterior portion of dorsal pharyngeal lumen.

Fig. 21. Same series, two sections anterior to the preceding.

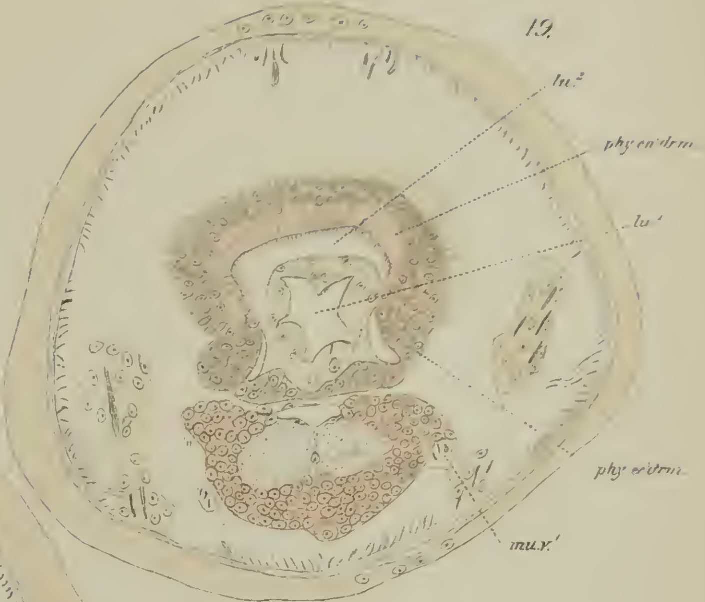
Fig. 22. Section (3rd in front of that of Figure 21) passing through ectodermal invagination (*sul.*) between the zoöids. The entodermal wall of pavilion (*en'drm.*) is seen below the gut.

Fig. 23. The section immediately in front of the last, showing that on the left side the plane of section is farther cephalad than on the right side.

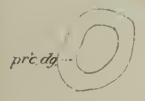
18.



19.

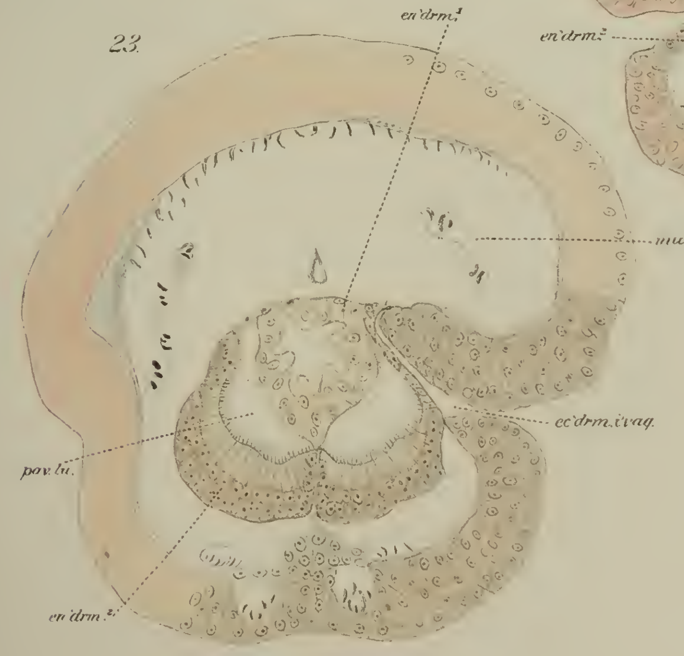


21.



22.

23.



20.

PLATE **5**.

Fig. 24. Only the margin of the prostomium of posterior zoöid appears in this section, which is three sections anterior to that of Fig. 23. The ventral part of the section passes through the undifferentiated segment-forming zone of the anterior individual. (Compare Fig. 15, Plate **3**, which represents a more advanced stage in longitudinal section.)

Fig. 25. Frontal section through stage of about the same age as that shown in Fig. 16, Plate **3**. × 218.

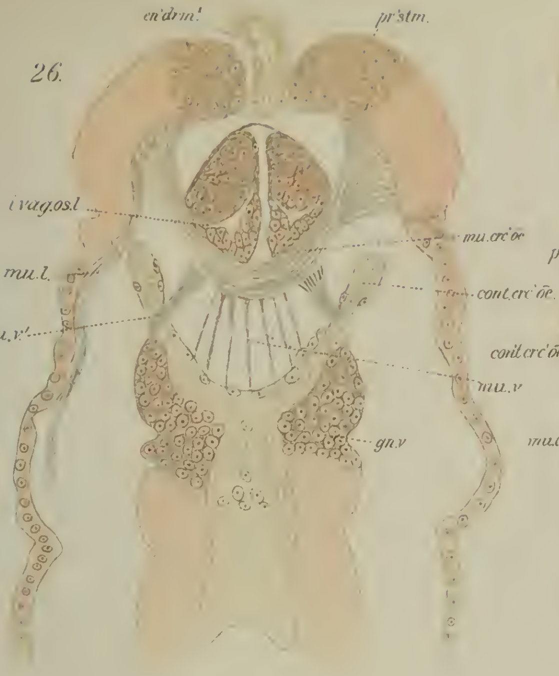
Fig. 26. Frontal section through head of posterior zoöid which has been separated from the anterior zoöid two hours. × 166.

Fig. 27. Section of same series, four sections ventral to the preceding. The lateral grooves of the mouth are shown (*i'vag. os. l.*). × 166.

Fig. 28. Parasagittal section, nearly median, through the head of a posterior zoöid, showing distribution of muscles. Ventral nerve cord is not shown. × 166.

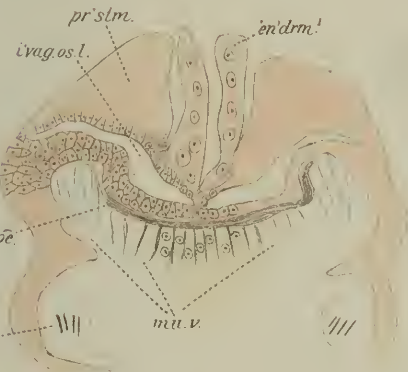
Fig. 29. Parasagittal, but more lateral, section from the same series. × 166.

26.



25

27.



24

28.

29.

T.W.G. del.

E. Meisel lith Boston.

No. 6. — *The Photomechanical Changes in the Retinal Pigment of Gammarus.*[1] By G. H. Parker.

The following studies were made with the intention of comparing the photomechanical changes in the retina of one of the simpler crustaceans with those already known in the decapods. In this respect, very few of the simpler forms have been studied, and almost all that has been done is contained in a single paper by Szczawinska ('91). This paper appeared shortly before Exner's ('91) well known monograph, in which the photomechanical changes of the compound eye first received a consistent physiological interpretation, and consequently it does not touch several important questions raised by Exner's work.

The lower crustaceans studied by Szczawinska were Gammarus, Phronima, and Branchipus, and of these, judging from the figures given, Gammarus has the most pronounced photomechanical changes. I have therefore studied the common American form, Gammarus ornatus Milne-Edwards. Vigorous individuals of this species were kept, some in the dark and some in the light, for six hours, and were then killed by being momentarily immersed in hot water (85° C.). They were afterwards cut in sections, and their eyes studied and compared.

The structure of the eye in Gammarus ornatus has already been described (cf. Parker, '91, p. 68), and agrees almost exactly with that of G. pulex as given by Carrière ('85, p. 156). Szczawinska's ('91, p. 534) description of the eye in G. roeselii is so different from the accounts given for the other two species that I am persuaded it must be in part erroneous.

In G. ornatus the corneal cuticula (Fig. 1, *crn.*), which is not facetted, is covered internally by a corneal hypodermis (*cl. crn.*) the cells of which are not regularly grouped with reference to the ommatidia. The axis of each ommatidium is occupied distally by a two-celled cone (*con.*) and proximally by a slender rhabdome (*rhb.*). These two structures are entirely distinct from each other and not continuous, as described by

---

[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College. E. L. Mark, Director. No. C.

Szczawinska ('91, p. 536). The transparent axis thus formed is sheathed laterally by five elongated pigment cells, the retinular cells (*cl. rtn.'*). Each retinular cell consists of three parts: a flattened distal portion applied to the side of the cone; a middle rod-like portion (Fig. 2, *cl. rtn.'*) lying against the rabdome; and an enlarged basal portion proximal to the basement membrane (*mb. ba.*) and containing the nucleus. The proximal end of this last part becomes attenuated and forms a retinal nerve fibre (*fbr. r.*) which passes to the optic ganglion. All parts of these cells except the nucleus may contain more or less blackish pigment. The space between the ommatidia is filled with a coarse granular pigment, whitish by reflected light and containing nuclei (*nl. sn.*). This material is made up of the accessory pigment cells, the boundaries of which are not easily discernible.

In Szczawinska's description of the eye in Gammarus roeselii, the three parts of the retinular cells described above are stated to be each a separate cell containing its nucleus. She correctly identified the nucleus in the proximal portion. What she believed to be the nuclei of the middle parts (Planche XVI. Fig. 4, *n.²pg.*) are without question the nuclei of the accessory pigment cells, which she failed to recognize as such. In the distal portions of the retinular cells of Gammarus ornatus nothing resembling nuclei could be discovered, and I am of opinion that she was mistaken in attributing such bodies to the corresponding parts in G. roeselii. The continuity of the three parts of the retinular cells in G. ornatus can be clearly demonstrated in serial transverse sections, in longitudinal sections, and in isolation preparations, and I therefore believe that these three portions are only parts of one cell. If this is true of G. ornatus, it is probably also true of G. roeselii, and I am strengthened in this belief as Szczawinska's own figures (Planche XVI. Figs. 4, 5) admit more readily of this interpretation than they do of her own. In these respects, then, her account is probably at fault.

In an eye of G. ornatus that had been subjected to light for some six hours (Fig. 1), a considerable amount of black pigment was found uniformly distributed through the distal and middle portions of the retinular cells, thus sheathing the cone and rhabdome laterally (Fig. 2). The proximal portion of each cell contained a few irregularly scattered pigment granules except near the nucleus, where the pigment was more abundant.

In an eye from an animal kept some six hours in the dark (Fig. 3), the pigment in the distal portions of the retinular cells presented the same condition as in the eyes exposed to light. The middle portions, however, were almost entirely devoid of pigment, while the proximal portions were as densely filled with pigment as the distal portions.

Obviously the changes induced by the presence or absence of light affect the pigment of only the middle and proximal parts. When an animal that has been kept in the dark is exposed to the light, the pigment that is massed in the proximal parts of the retinular cells (Fig. 3) migrates distally and fills the middle portions, without however entirely abandoning the proximal parts, especially around the nucleus (Fig. 1). When an animal that has been kept in the light is placed in the dark, the pigment in the middle portions (Fig. 1) migrates into the proximal parts till almost no pigment is left in the middle portions. In other words, the presence of light induces a distal migration of much of the pigment from the proximal parts and the absence of light brings about a proximal migration of almost all the pigment in the middle parts.

In none of my observations was there any evidence of photomechanical changes in the accessory pigment cells.

Aside from the disparity due to the different anatomical descriptions of the eyes, the physiological results given in this paper confirm in the main those given by Szczawinska ('91, p. 548). In one respect only is there a significant difference. Szczawinska claims that in G. roeselii the pigment in what I have called the distal parts of the retinular cells shows photomechanical changes. In G. ornatus no evidence of such changes could be found, and since in G. roeselii, according to the figures given by Szczawinska (Planche XVI. Figs. 1, 2), the supposed evidence of these changes may be entirely the result of a slight difference in the planes at which the sections have been cut, it may fairly be doubted if these changes occur at all.

The relations that the photomechanical changes, described above, bear to the physiology of the eye in G. ornatus are not far to seek. Light passing through the axis of any cone in the eye of this animal would be conducted directly to the rhabdome under the given cone. Light entering a cone obliquely to its axis would fall upon one of its pigmented sides, where, if not absorbed, the light would suffer reflection. As the sides of the cone are not parallel but approach proximally, the light would not undergo simple internal reflection as in a cylinder, but would be so turned at each reflection that it would eventually be discharged from the end of the cone at which it entered. Thus oblique light would not reach the underlying rhabdome at all. This action, by which the axial light of the cone is conducted to the rhabdome and the oblique light is discharged, has been called by Exner ('91, p. 59) the catoptric action of the cone, and has been fully described by him. In accordance with this relation, then, the rhabdome of each ommatidium would receive light from an external region corresponding to the outward projection of the axis of the cone distal to it.

As the pigment which surrounds the cone is merely concerned with the absorption of the lateral rays, and as these rays would be equally disturbing whether the animal were in bright light or dim light, it follows that no photomechanical changes in correspondence with changes in the intensity of the light should be expected in this pigment, and as a matter of fact in G. ornatus no such changes have been observed.

The axial light, which according to the foregoing account finds its way into the rhabdome, must have a certain degree of intensity in order to stimulate that organ. Ordinary daylight is presumably more than sufficient to call forth this stimulation, and such superfluous light as may pass to the edges of the rhabdome or through it is probably absorbed by the black pigment that in bright light (Figs. 1, 2) surrounds that body. In dim light, however, there must be times when the light which enters the rhabdome is scarcely intense enough to stimulate that organ. Under such circumstances the more oblique rays, which ordinarily would be absorbed by the black pigment on the sides of the rhabdome, would materially aid in stimulating it if they were turned back into the rhabdome. That these rays are probably thus turned back is shown by the fact that in dim light the black pigment is removed from the rhabdome and the surrounding whitish reflecting pigment of the accessory pigment cells is exposed (compare Figs. 2, 4).

Changes exactly comparable with these have been described in the proximal retinular cells of the higher crustaceans. The changes in the distal retinular cells, the iris pigment of Exner, which are connected with the formation of superposition images, find no representatives in the eyes of Gammarus ornatus. As this eye is in many respects primitive, it is likely that the ancestral crustacean ommatidium possessed a catoptric cone and a retinula provided with a reflecting apparatus for use in dim light. In the differentiation of the higher type of crustacean ommatidium the reflecting mechanism was retained, but the catoptric cone gave way to a second type of cone provided with special pigment cells whose movements were associated with the superposition images formed by this type of cone.

SUMMARY.

1. In Gammarus ornatus photomechanical changes in the retinal pigment are not observable in the accessory pigment cells or in the distal parts of the retinular cells, but are limited to the black pigment in the middle and proximal portions of the retinular cells.

2. In the light the middle portion of each retinular cell is well filled with pigment, thus enclosing the rhabdome in a black sheath; the proximal portion contains scattered grains except near the nucleus, where the pigment is more massed.

3. In the dark the middle portion of each cell is almost free from pigment, which now fills the proximal part.

4. In the dark the removal of the black pigment from around the rhabdome exposes the accessory pigment cells, which probably act as reflecting organs, and in very dim light turn such rays as have escaped laterally from the rhabdome back into that structure, thus aiding in an effective stimulation of this organ.

CAMBRIDGE, December 15, 1898.

PAPERS CITED.

Carrière, J.
'85. Die Sehorgane der Thiere vergleichend-anatomisch dargestellt. R. Oldenbourg. München und Leipzig. 6 + 205 pp., 147 Abbildungen und 1 Tafel.

Exner, S.
'91. Die Physiologie der facettirten Augen von Krebsen und Insecten. Deuticke, Leipzig und Wien. vi + 206 pp., 7 Taf.

Parker, G. H.
'91. The Compound Eyes in Crustaceans. Bull. Mus. Comp. Zoöl. Harvard Coll., Vol. XXI. pp. 45–140, Plates I.–X.

Szczawinska, W.
'91. Contribution à l'étude des yeux de quelques Crustacés et Recherches expérimentales sur les mouvements du pigment granuleux et des cellules pigmentaires sous l'influence de la lumière et de l'obscurité dans les yeux des Crustacés et des Arachnides. Arch. de Biol., Tom. X. pp. 523–566, Planches XVI., XVII.

EXPLANATION OF THE PLATE.

All the figures were taken from preparations of the eyes of Gammarus ornatus M.-Edw. They were drawn with the aid of an Abbé camera, and are magnified 570 diameters.

ABBREVIATIONS.

cl. crn.	Corneal hypodermis.
cl. rtn.′	Retinular cell.
cl. sn.	Accessory pigment cell.
con.	Cone.
crn.	Corneal cuticula.
fbr. r.	Retinal nerve fibre.
mb. ba.	Basement membrane.
nl. rtn.′	Nucleus of retinular cell.
nl. sn.	Nucleus of accessory pigment cell.
rhb.	Rhabdome.

Fig. 1. Longitudinal section of an ommatidium, showing the arrangement of pigment due to exposure to bright light.

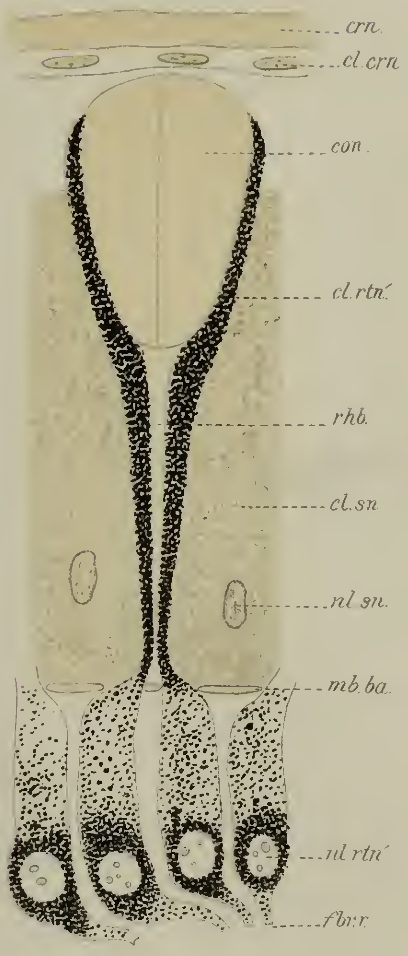
Fig. 2. Transverse section of a retinula from such a preparation as that shown in Figure 1, and taken near the level marked *rhb.* in that figure.

Fig. 3. Longitudinal section of an ommatidium showing the arrangement of pigment due to the absence of light.

Fig. 4. Transverse section of a retinula from such a preparation as that shown in Figure 3, and taken near the level marked *rhb.* in Figure 1.

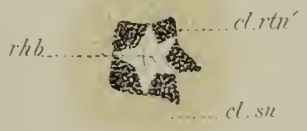
LIGHT.

DARK.



1

3



2.

4.

G.H.P. del.

B. Meisel, lith. Boston.

No. 7. — *The Structure and Development of the Antennal Glands in Homarus americanus Milne-Edwards.*[1] By Frederick C. Waite.

CONTENTS.

Introduction.

The antennal glands of Crustacea have been the subject of much discussion ever since the first discovery [illegible] them in Astacus by Rösel von Rosenhof (1755, p. 321). The true relation of the parts of the organ was for a long time overlooked, and the gland proper was considered as distinct from the storage reservoir and duct to the exterior. The former was supposed to be connected with the digestive tract, either as a salivary gland or as the source of the gastroliths, while the latter was taken for a sense organ, first as auditory, later as olfactory. Brandt ('33, p. 64) showed that the parts which had been considered as two organs of different functions really constituted a single structure. To this was ascribed the function of hearing.

All observations were confined to Astacus until Semper ('61) extended his work to Lucifer. Shortly afterward Claus ('63) added observations

---

[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College, under the direction of E. L. Mark, No. 105.

upon a few other forms. The first extensive comparative work was that of Grobben ('80), who studied these organs in a number of Entomostraca and Malacostraca, and sought to prove them homologous in the two groups.

The earliest evidence of the excretory function of these organs was afforded by Will und Gorup-Besanez ('48), who made the following statement (column 828): ". . . in der That haben wir im sogenannten grünen Organ des Flusskrebses (Astacus fluviatilis) und im Bojanus'-schen Organ des Teichmuschel (Anodonta) einen Stoff aufgefunden, der Reaktionserscheinungen zeigte, die mit der grössten Wahrscheinlichkeit auf Guanin hinweisen, doch gebrach es uns bisher an dem nöthigen Material, um entscheidende Versuche damit anzustellen." Similar chemical experiments were carried on by several later investigators, but the most conclusive evidence of the excretory activity of these organs rests upon extensive experiments in *intra vitam* injection and feeding which were inaugurated by Kowalevsky ('89), and extended in subsequent papers by him and by other authors, especially by Cuénot ('94).

By far the most comprehensive work on excretion in Crustacea is that of Marchal ('92). Until the publication of this work, the major part of the literature, especially as regards histology, was on Astacus, with additions on some of the Carididæ (Grobben '80, Kowalevsky '89, and Weldon '89 and '91). Marchal in his memoir gives the results of a careful research on the morphology, histology, and physiology of a long series of species representing all the typical genera of the Decapoda. The work was carried on by the methods of modern technique, including the *intra vitam* method of Kowalevsky ('89).

This is the only paper that deals with the antennal gland in Homarus. The species studied by Marchal (H. vulgaris), however, was not the same as that of the present paper. In H. vulgaris, according to Marchal (pp. 156–163), the gland presents an entirely different appearance from that seen in Astacus, although the main divisions into gland proper, vesicle, and duct are found in both. In H. vulgaris the gland as seen from above is triangular in shape, the antero-posterior axis being the longest. The posterior tip is curved mediad, and the periphery is more or less notched. The dorsal face is slightly concave, the ventral markedly convex.

The structure is much less complex than in Astacus, and there are two distinct regions besides the duct, — the saccule and the labyrinth. The former is thin and flattened out over the dorsal face of the gland, covering it except for a narrow projecting margin. The saccule has a large central cavity, from which radiate ramifying culs-de-sac. The labyrinth is three times as thick as the saccule and forms the greater bulk of the gland. It is divided by an antero-posterior fissure on the ventral face, so as to be U-shaped, the arms of the U pointing anteriorly. The connection with the overlying saccule is at the end of the lateral arm, that with the excretory duct at the end of the median arm. In the latter case, this is by means of several parallel canaliculi, which open as pores in the wall of the duct. The vesicle is a dorsal outpocketing from the duct, and is not in direct connection with the gland. The labyrinth consists of a spongy tissue formed by the walls of innumerable canals, which anastomose with one another without any determinable system.

The cells of the saccule are narrow, crowded, with rounded free ends, and without cuticula, while in the labyrinth the cells are markedly striate, and surmounted often by clear vesicles. A cuticuloid covering is sometimes present.

The present state of opinion as to the function of the antennal glands in Decapoda is not one of complete accord. It needs but a superficial examination of the epithelium in these organs to convince one of their glandular nature. The *intra vitam* experiments of Kowalevsky ('89) and Cuénot ('94) show conclusively that the cells take up grains of coloring matter introduced into the circulation and eliminate them. Moreover, with the exception of the ductless branchial glands and certain cells of the liver, this function is confined, as far as we at present know, to these antennal glands. The glandular secreting cells of the intestine perform no such function. Conclusions like those of Will und Gorup-Besanez ('48), who asserted the presence of guanin, have been reached by H. Dohrn ('61),[1] by Kirch ('86), and especially by Griffiths ('85). Griffiths got definite tests for uric acid, and he carefully describes the chemical analysis by the murexid method; further, he obtained small traces of the base guanin. Szigethy ('84) also found what he believed to be uric acid crystals. In each of these cases the analysis was upon the gland in Astacus.

Marchal ('92, pp. 237–245), on the other hand, made analyses of the excremental fluid of Maia squinado, and could get no traces of urea or uric acid, but did obtain nitrogen. He however obtained an acid somewhat analogous to uric acid, which he terms carcinuric acid. This be-

---

[1] I quote Dohrn and Kirch on the authority of Gerstaecker ('95, p. 1000), as the original papers are inaccessible to me.

longs to the series of the carbopyridic acids. There is also found a base, leucomaine, which is analogous to the vegetable alkaloids. He denies that the gland in Astacus contains uric acid.

It is difficult to reconcile these diverse results. It is undoubtedly true that the antennal glands eliminate certain ammonia compounds, and it is also shown by Marchal ('92, p. 243), that one of their functions is to rid the organism of the excess of mineral salts present in the blood, and Kirch ('86) has found that in Astacus these organs contain glycogen. Gerstaecker ('95, pp. 1009, 1010) concludes that, in view of all these results, we must consider the antennal glands of Decapoda not as closely analogous to a kidney, but as excretory organs important in the general metabolism; and, by reason of recent work, that we must concede the physiology of the antennal glands to be in many respects an open question, the solution of which will require much research, and that it is not wholly improbable that these glands, like the liver, are subject to temporarily changing functions.

This seems a fair and conservative statement, which expresses the present state of our knowledge in regard to the function of these organs.

The work represented by this paper was done during the years 1896–97 and 1897–98 in the Zoölogical Laboratory of Harvard University. During the year 1896–97 my work was aided by privileges afforded by a Morgan Fellowship in that University. I wish here to express my indebtedness to Prof. E. L. Mark, Director of the Laboratory, for his kindness in many ways, and for his supervision and able criticism of the work during its progress. I am also indebted to Mr. Alexander Agassiz for the opportunity of working at his Newport Laboratory during part of the summer of 1897, and for appointment to a table at the United States Fish Commission Laboratory at Wood's Hole during the summer of 1896; to Hon. J. J. Brice, formerly United States Commissioner of Fish and Fisheries, for courtesies extended at various times at the Wood's Hole and Gloucester stations of the United States Fish Commission; and to Prof. F. H. Herrick and Dr. G. H. Parker for the use of embryonic material of certain stages.

Methods.

The methods employed were different in the embryonic, larval, and adult stages.

In studying the finer anatomy of the adult organ, I have had recourse to maceration, teasing, and serial sections. For sectioning, the most serviceable fixing reagents were, in the order named, the chrom-osmo-picro-acetic mixture of vom Rath followed by pyroligneous acid, Perenyi's fluid, and corrosive sublimate. For staining the material fixed in Perenyi's fluid and corrosive sublimate, I have used Heidenhain's iron hæmatoxylin, Delafield's hæmatoxylin, and Ehrlich's acetic acid-alum hæmatoxylin. For a double stain orange G of Grübler after either of the last two is of value. In general the carmines are not serviceable in this connection, but picro-lithium carminate has afforded very good results on the wall of the vesicle.

Both surface preparations and serial sections were used in studying embryos. The yolk was sometimes dissected away before sectioning, but at other times it was sectioned with the embryo. The selection of the killing agent to be used depends in a measure upon which of these two methods is to be followed in sectioning. The specimens to be used for examination by transmitted light must necessarily be separated from the yolk. This was accomplished with fine needles and a small stream of fluid from a pipette, the work being done under a dissecting microscope and in alcohol of a lower grade than that in which the embryos had been kept. This change in the grade of alcohol distends the egg membrane so that it may easily be shelled off. The difficulty of the separation of the yolk depends upon its friability and the age of the embryo.

I have used for killing the following: (1) water, heated to boiling and then quickly poured over the embryos; (2) saturated aqueous solution of corrosive sublimate, used either hot or cold; (3) Perenyi's fluid; (4) Kleinenberg's picro-sulphuric mixture; (5) Flemming's fluid, — weaker mixture. Of these the hot water and the corrosive sublimate treatment render the yolk granular and friable, so that it is easily separated from the embryo; at the same time the yolk particles are so loosely united that it is impracticable to section embryos with the yolk attached. On the other hand, treatment with Perenyi's fluid makes the yolk so firm and tough that it is almost impossible to dissect off the embryo without serious injury to it. Treatment with picro-sulphuric mixture, if of short duration (15 to 30 minutes), allows the yolk to be removed in large masses, and completely, without injury. Longer treatment (60 to 90 minutes) interferes with such removal, but solidifies the yolk so that it can be easily sectioned with the embryo. The weaker Flemming's fluid when used for a short time (20 to 30 minutes) gives a tenacious rind enclosing the embryo, which is easily separable from the coarsely granular central part of the yolk. A longer treatment (45 to 90 minutes) gives the best condition I have obtained for sectioning entire the yolk and embryo. The time of exposure to any killing fluid should vary with the age of the embryo.

I have tried a variety of stains. Of the many carmine combinations used, I have found Grenacher's aqueous alum carmine the most serviceable. The best results are gained from material killed with hot water. Of the hæmatoxylins, I have found Ehrlich's acetic acid-alum mixture as good as any, and the most reliable. It stains material fixed by any of the methods mentioned, the best results being obtained after fixing with Perenyi's fluid or with Flemming's weaker mixture. I have found, however, that the staining is much better if the hæmatoxylin is followed by an aniline dye. Of several tried I have found orange G of Grübler much the best; consequently I have used this excellent combination in most of my work. The results are precise and clear, and the manipulation of staining is very simple. Sections 6⅔, 10, or 13⅓ micra in thickness are stained on the slide in Ehrlich's mixture from 20 to 30 minutes, then washed in acidulated alcohol until they are very pale, next neutralized in a two per cent solution of bicarbonate of soda, then thoroughly washed in distilled water and put into a saturated aqueous solution of orange G. This is allowed to act from 10 to 20 minutes, the time being determined by watching the action of the stain. The slide, after draining, is transferred directly to absolute alcohol, which sets the stain and at the same time washes out the excess. After clearing in xylol, the sections are mounted in xylol balsam, the stain being thoroughly permanent.

In studying the larval organ I have depended entirely upon serial sections, for the gland is too small to permit satisfactory dissections, and the shell of the appendage does not clear readily enough to permit study of the entire organ *in situ.* The first larva was obtainable in abundance, so that various methods could be tried, but the older larvæ are more difficult to get, and as a matter of fact all of the older larvæ which I had were already preserved when they came into my hands.

The most successful results with the first larva were obtained with the weaker Flemming's mixture, Perenyi's fluid, corrosive sublimate, or Kleinenberg's picro-sulphuric mixture. I give these reagents preference in the order named; the last, however, is not available in the older larval or the adolescent stages, when the shell comes to contain considerable quantities of lime salts.

For this stage several stains have been used. I finally settled upon Ehrlich's acetic acid-alum hæmatoxylin, however, as the most reliable stain for the gland. For a double stain I have used this followed by acid fuchsin or orange G, the latter being, in my opinion, preferable.

The paraffin method of embedding has been used exclusively. The cuticular shell in the larval stages is rather resistant, and soon dulls the knife, but with a sharp knife good series 6⅔ micra in thickness were obtained.

I. Structure in the Adult.

The structure of the adult antennal gland in the genus Homarus has been described by only one writer, Marchal ('92, pp. 156–163, Plate VII. Fig. 1), who gives an account of the organ in H. vulgaris. There is no published account of this gland in H. americanus except a short abstract of this paper (Waite, '98).

A. Gross Anatomy.

The gland, with its accessory structures, is situated at the base of the second antenna, and the most of it is within the cephalothorax. It occupies the greater part of the space beneath, and on the side of the masticatory stomach, anterior to the voluminous hepato-pancreas. The organ as a whole may be divided roughly into three parts, which are easily recognized and sharply separated, namely: (1) the gland proper, often referred to hereafter simply as the gland; (2) the overlying vesicle, or storage reservoir; and (3) the duct leading to the exterior, together with the tubercle upon which it opens.

The *gland proper* lies almost entirely on the ventral floor of the cephalothorax, but its anterior median lobe extends into the base of the antenna. It lies close to the sagittal plane, the median edges of the two glands being but about five millimetres apart.[1] None of the principal axes of the gland proper are parallel to the principal axes of the body. The dorsal face is so inclined to the frontal plane of the animal that its anterior edge is 20° or 30° more dorsal than its posterior edge, and its lateral border 25° or 30° more dorsal than its median. The chief axis of the gland as viewed from above runs from the anterior notch or hilus to the most distant point of the posterior edge (Plate **1**, Fig. 1). This axis makes an angle of about 30° with the sagittal plane of the animal, its anterior end being nearer that plane.

The general shape of the gland proper as seen from above resembles that of a cordate leaf with a blunt point, the notch being anterior (Plate **1**, Fig. 1). The dorsal face is irregularly concave. This concavity is filled

---

[1] All measurements given for the adult gland are for an average adult nine inches (= 23 cm.) in length from tip of rostrum to tip of telson.

by the ventral part of the overlying vesicle, the wall of which is closely applied to the smooth dorsal surface of the gland (Plate **1**, Fig. 2, *par. vs.*). The ventral face of the gland is in general convex, but has in it depressions which conform to the underlying hard parts of the endophragmal system and shell, and to the muscles upon which the gland rests. The ventral surface differs much in appearance from the smooth dorsal surface. It is uneven, being thrown into numerous ridges and furrows, resembling to some extent the gyri and sulci of the cerebral hemispheres in higher mammals. All these furrows radiate in a general way from a region of the gland lying near the bottom of the hilus, but the individual furrows are comparatively short, and separated by ridges from other furrows in the same radius. The furrow lying in the main axis of the gland is the most prominent and deepest one. It is a direct continuation of the hilus. The dorso-ventral diameter varies, but is greatest in the centre of the organ, and thins out to a translucent edge on the borders. The outline of the border of the gland is irregular. In the middle of the anterior edge there is a sharp V-shaped hilus extending posteriorly 2 to 3 millimetres (Plate **1**, Fig. 1, *hi.*). The bottom of the hilus marks very nearly the centre of the gland. The median edge of the gland presents a simple curve convex toward the median plane of the body, and having a radius of about a centimetre. The lateral edge is S-shaped, the posterior bend of the S giving the gland the appearance of being notched to accommodate the flexor antennarius muscle, on which it does in part rest. This notch is 2.5 or 3 mm. deep and 5 or 6 mm. broad. The edge of the gland for the most of its extent is bluntly toothed or lobed, so that the outline is more or less sinuous.

For purposes of description the gland proper may be said to present three lobes: a median anterior (*lob. m-a.*, Plate **1**, Fig. 1), a lateral anterior (*lob. l-a.*), and a posterior one (*lob. p.*).

The gland measures in its longest diameter, from the edge of the median anterior lobe to the posterior apex, 13 to 15 mm.; from the bottom of the lateral notch to the middle of the median border, 9 to 10 mm. Its greatest dorso-ventral thickness is about 3 mm. It is thus evident that the gland is much flattened.

In color the gland is a light olive, the ventral face being of a darker shade than the dorsal; the latter in some individuals approaches yellowish brown. The light dorsal surface is surrounded by a narrow border of the darker shade from 1 to 2 mm. in width (Plate **1**, Fig. 1, *marg.*), which is left without tint in the figure. This border widens to quite a broad band on the median anterior lobe. The area of lighter color corresponds with the extent of the endsac; that of the darker border, with that part of the dorsal face of the labyrinth which is not covered by the endsac, or which shows through the attenuated edge of the endsac.

From the median anterior lobe there is given off a smaller lobe 2.5 to 3 mm. in diameter and 5 to 6 mm. in length. This is directed caudad and ventrad, and tapers to a point. Its general shape is conical. In color it is so distinct from the other parts of the gland that Marchal ('92, p. 159) has called it the white lobe. The tapering point opens into the excretory duct in a region ventral to the centre of the gland. This opening is not single, but consists of several minute pores, to each of which there leads one of a series of converging tubules which are in turn formed by the confluence of other smaller tubules in the basal part of the white lobe. These pores are on the dorso-median wall of the duct, 2 to 3 mm. from its external orifice. By these the products of the gland are discharged into the duct. *This is the only communication which the gland proper has with its accessory structures,* there being no direct communication between the gland and the vesicle, as there is in Astacus. Therefore the vesicle must be filled by the backing up of the secreted products in the duct from the point where the pores open, a process which is presumably effected by closure of the external opening of the duct.

The *vesicle* is situated in the cephalothorax at the side of the masticatory stomach. Its anterior end lies against the muscles of the body wall. On its median face it presses against the stomach, while posteriorly it reaches the hepato-pancreas and extends between its lobes. Ventrally, it is in part closely and firmly attached to the dorsal face of the gland (Plate 1, Figs. 1, 2, *par. vs.*). Posterior to the gland it lies free upon the floor of the cephalothorax. Its shape is roughly oval, its long axis lying in a parasagittal plane. Usually the posterior end is slightly divided into two blunt lobes. Since the thin elastic walls easily conform to the surrounding organs, its actual shape in detail is irregular, depending upon the state of its own distention and that of the stomach, hepato-pancreas, and reproductive organs, and the contraction or relaxation of the muscles in this region. In some individuals it seems to fill every niche of unoccupied space; in others there are considerable spaces between it and the body wall.

I have found no ligamentous attachments for holding the vesicle in place other than that to the dorsal surface of the gland, already noted, and those to the blood-vessels and nerves which come to its surface.

The wall of the vesicle is uniformly very thin and transparent in all parts except immediately around the orifice of the duct, where it is somewhat thicker; but there is no muscular sphincter at this point. The histological structure of the wall is described in another connection (pp. 166, 167).

At the anterior end of the vesicle, at a point on a line with the median border of the hilus and a little in front of the anterior edge of the gland, there is an orifice which opens into the duct leading to the exterior (Plate 1, Fig. 1, *of. i.*). This orifice is circular, or slightly oval, and 1 to 1.5 mm. in diameter. It is noticeable that it retains its shape when the walls of the vesicle are collapsed.

The *duct* is a thin-walled tube, oval in cross section, — being slightly flattened dorso-ventrally, — and lies wholly within the antenna. From the orifice in the vesicle it extends downward and slightly forward and outward for a distance of 5 to 7 mm. Its average diameter through this region is 2 mm. At the level of the coxo-basal joint the duct turns abruptly through an arc of about 45° in a parasagittal plane of the body, and runs downward and backward to the tubercle on the ventral face of the coxopodite, through which it opens to the exterior. Its diameter through this second part of its course is somewhat greater than in the first part, but diminishes noticeably as it enters the tubercle. There is a slight dilatation at the point where the tubules from the white lobe enter. The entire length of the duct is not over 1.5 cm., and its average diameter is perhaps 2.5 mm.

I find no sphincters or other muscular structures in or around the wall of the duct, other than the muscles of the antenna, among which it runs. It seems, then, that the ejaculatory process, by which the secretion of the gland is sometimes forced out of the external orifice, cannot have its origin in any intrinsic action of the duct. It may arise from concerted action of the muscles of the antenna, but since no especially active movement of the antenna has been noted in connection with this function, it is probable that the force producing such ejaculation has its seat in the muscular walls of the vesicle, the duct being passive.

The *external orifice* of the duct is situated at the apex of a truncate conical tubercle, which rises from the general ventral surface of the coxopodite of the second antenna. This tubercle is nearly in the midventral line of the appendage. It does not stand perpendicular to the general surface, but its axis is inclined slightly forward and medianward, so that if the antennæ were at rest in the horizontal position, the axes of the two tubercles prolonged would intersect at a point in the sagittal plane about 2.5 cm. in front of, and 4 cm. ventral to, the bases of the first antennæ. The posterior and median sides of the tubercle are more elevated from the general surface than are the anterior and lateral sides. The truncated face of the tubercle is a circle with a diameter of about 1 mm., and is covered with a membrane which has concentric markings. The actual orifice is situated in the centre of this membranous area, and is less than 0.1 mm. in diameter. The opening into the tubercle from the main cavity of the appendage, as may be seen by inspecting the inside of a moulted shell, is semicircular, the anterior edge being straight; from this edge a toothed process of the shell, serving for the attachment of muscles, projects backward.

The *blood supply* of the antennal gland is mainly from two sources: (*a*) the antennal artery (arteria lateralis of Gerstaecker); (*b*) the sternal artery. The antennal artery arises directly from the heart, and passes obliquely forward and downward close to the dorsal body wall. In that part of its course where it runs near the vesicle, it gives off several small branches, which are distributed to the lateral wall of this organ. This artery sends branches into the gland proper at three regions: (1.) As the artery passes ventrad along the anterior face of the antennal flexor muscle, a large branch is given off, which goes on the lateral and ventral side of this muscle (i. e. outside of the muscle), and enters the lateral region of the posterior lobe of the gland on its ventral face, to which region it is distributed. (2.) As the antennal artery passes ventral to the lateral anterior lobe of the gland it sends several small branches into the ventral face of this lobe; and one large branch to the bottom of the hilus, whence it passes dorsad to be distributed to the endsac (Plate 1, Fig. 1, *art. sac.*). This branch Marchal ('92, p. 162) terms the "artère sacculaire." (3.) From the dorsal branch of the antennal artery a small branch is given off, which runs ventrad and mediad to enter the median anterior lobe of the gland. It enters on the ventral face close to the anterior edge. The antennal artery after giving off the artery to the endsac passes into the second antenna. In the region of the coxo-basal joint of this appendage two small branches are given off to the walls of the duct and to the tissues at the base of the tubercle.

The second source of blood supply is the sternal artery. A branch from this artery comes to the median surface of the posterior lobe, where it divides. The larger of the resulting branches enters the extreme posterior region of the lobe on the ventral face close to the edge; the smaller passes forward along the edge of the gland and enters the ventral face of the median anterior lobe. Other smaller vessels enter the ventral face of the gland at several points, coming from the trunks supplying the tissues upon which the gland rests.

To summarize, the lateral part of the labyrinth, together with all the endsac, is supplied by the antennal artery, while the median part — except the tip of the median anterior lobe — is supplied from the sternal artery.

The *nerve supply* of the gland is from the nerve trunk running to the second antenna. Immediately after this trunk emerges from the superœsophageal ganglion, it gives off a branch which passes outward and backward to enter the median anterior lobe of the gland. The point of entrance is on the ventral face near the median edge. The nerve trunk to the second antenna also sends several small branches into the edge of the median anterior lobe; these arise at points more distal than that at which the main branch arises. I have not found any nerve branches entering at the hilus, nor in the posterior region in a position corresponding to the blood supply from the sternal artery.

B. Finer Anatomy.

The gland proper consists of two distinct parts. The relation of the two parts — the endsac (*sac. trm.*) and the labyrinth (*lby.*) — is seen in Figure 2 (Plate 1), which is a transverse section of the gland proper about half a millimetre posterior to the bottom of the hilus. The endsac is dorsal to and covers the whole of the labyrinth except its extreme edges. Its average dorso-ventral depth at this region is about one fourth that of the labyrinth. This ratio is greater than the average for the whole gland.

The *endsac* shows a considerable regularity in the arrangement of its cavities. At the bottom of the hilus there is a single large chamber of irregular shape, from which outpocketings radiate. These are separated from one another by folds of the wall of the endsac, which form complete septa. These outpocketings branch dichotomously many times, and thus produce a system of compartments which become smaller and smaller until the edge of the endsac is reached. In these compartments there are secondary foldings of the wall forming incomplete septa, which are more frequent on the ventral than on the dorsal wall of the compartments. In Figure 2 (Plate 1) the compartments near the edge of the endsac are cut crosswise; those near the centre, lengthwise or diagonally.

The dorsal face of the endsac has attached to it the closely adhering ventral wall (*par. vs.*, Figure 2, Plate 1) of the overlying vesicle. This consists, however, of only the glandular epithelium of the vesicle wall, the muscular layer — to be described later (p. 167) — being in this region absent. Between the basement membrane of the epithelium of the vesicle and the wall of the endsac there is a rich plexus of blood-vessels, — branches of the sacculary artery, — some of which are shown cut across in Figure 2 (*vas. sng.*).

The septa of the endsac, both complete and incomplete, consist each of a fold of the epithelial lining of the sac (Plate 1, Figure 3, *cl. sac. trm.*), embracing a sheet of connective tissue (*tis. con't.*) between its two layers. This connective tissue is highly vascular, being principally formed of the walls of blood vessels and blood lacunæ. The glandular epithelium of the endsac forms of course a continuous layer, lining all compartments and investing all septa. It is everywhere a single layer thick, and its cells have certain distinctive characters. In shape they vary both according to location and to condition of activity. They are most elongated on the dorsal wall (Figure 4) and at the place of junction with the cells of the labyrinth; most rotund on the ventral floor and on the septa which rise from it (Figure 3, *cl. sac. trm.*).

The difference of shape due to the state of activity is more striking. Cells lying side by side (Figure 4) vary much in this respect. Among shorter cells of nearly uniform diameter there are many elongated cells, the free ends of which are expanded into globules often in diameter two or three times that of the basal portion of the cell. The contents of these swollen ends are less dense and stain less deeply than do the basal portions of the cells. The globules become detached and pass to the exterior, the lumen of the endsac being more or less filled with various sized globules of this nature (Figure 4, *glb.*). Each, when detached, — if free from mechanical pressure, — is spherical and contains a granular clot nearly filling it. This clot is not homogenous, but made up of granules of various sizes and degrees of opacity. Various progressive stages in the constricting off of the globules from the cell are seen, so that there can be no doubt that they arise primarily from the cells. These globules seem to be composed of a mass of secretion products enclosed in a capsule, which is part of the cell wall. They are not detached cells, for they never contain a nucleus, nor, so far as I have seen, any chromatin particles. Further, there are no evidences of nuclear division in the glandular epithelium, as would probably be the case if these globules were degenerate cells; for if some cells became degenerate and passed off, division would be necessary in the normal cells to make up the loss.

These glandular cells are crowded with a mass of spherical vacuoles, which are smaller in the attached end of the cell than in its free end (Figure 4), and sometimes are not found at all in its basal part (Figure 5). The cytoplasm also contains granules of various sizes and shapes, which differ widely in refractive powers. These are found throughout the cell, often in compact opaque masses. Such masses are also common in the globules (Figure 4).

In sections prepared by certain methods, namely, in material fixed in saturated aqueous-corrosive sublimate, or in vom Rath's platinic-aceto-osmic mixture, acicular crystals are found in many cells, though not in all. Such crystals are not found in material treated with Perenyi's fluid or with Flemming's weaker mixture, nor in any sections which have been decolorized with alcohol acidulated with 1% HCl. These crystals are all fine and needle-like, but differ in length (Fig. 5, *cry.*, and Fig. 6). It is noticeable that they are confined to the cells of the endsac, none being found either in the lumen of the endsac or in the cells or lumina of labyrinth or vesicle.

Szigethy ('85, p. 109) found in the gland of Astacus crystals which he regarded as uric acid. I have not seen his figures in the original paper, and so cannot compare them with those I have described. In the present case, I think it probable that the crystals are artifacts; at any rate, more detailed investigation is necessary before they can be considered of physiological importance. I have simply made a record of the condition noticed.

The nuclei of the cells of the endsac are oval and usually situated in the basal half of the cell; but in some cases they are crowded toward the free end (Figure 4). The cells rest upon a membrane (*mb. ba.*, Figs. 4 and 5) of appreciable thickness, but without nuclei.

There is *but one region of communication between endsac and labyrinth.* This is in the main axis of the gland immediately posterior to the bottom of the hilus. The section from which Figure 2 is drawn passes through this region. The communication is between the central lumen of the endsac and the lateral anterior lobe of the labyrinth. The median anterior lobe has no direct communication with the endsac, but it will be remembered that it is from the median anterior lobe that the white lobe — which is the direct passage to the exterior — arises (p. 159). Therefore the products of the endsac must pass through the lateral-anterior, the median-anterior, and the white lobes in the order named before reaching the duct to the exterior. The communication between the endsac and the lateral-anterior lobe is about 0.4 millimetre in diameter, and runs obliquely ventrad and laterad. It is short, and soon branches to become continuous with the lumina of the various labyrinth tubules.

At the border of this short channel, as indicated at *a* in Figure 2, there is a sudden transition from the cells of the endsac to those of the labyrinth, there being no cells of intermediate character. The boundary of this opening is the only place where the cells of endsac and labyrinth come into contact. At all other places where endsac and labyrinth come together, the basement membranes of the two are face to face.

The *labyrinth* is not a single pocket with evaginations like the endsac, but is composed of a system of branching tubules; these are not, however, simply coiled tubules, for they undergo anastomosis at frequent intervals, and it is therefore impossible to trace any single tubule for a great distance. Moreover, the tubules are not of uniform calibre, but have numerous outpocketings, which still further complicate the appearances presented in sections. This communicating system of lumina is so complicated that it is impossible to say that it presents a definite plan. It is certain, however, that it does not represent one or a few coiled tubules, as has been described for Astacus. The whole system of labyrinthine passages is lined by a continuous layer of epithelium. The basement membrane (Figs. 7 and 8, *mb. ba.*) of this epithelium is somewhat thicker than that of the epithelium of the endsac. The spaces between the epithelial lining of adjacent tubules is occupied by a vascular connective tissue (Fig. 7, *tis. con't.*), like that described in the septa of the endsac (p. 163). The blood-vessels and lacunæ found in this tissue contain blood corpuscles (Fig. 8, *vas. sng.*).

The epithelial cells in different regions of the labyrinth do not show differences of form, but they are very unlike those of the endsac. The cytoplasm is denser and stains more deeply, and the vacuolated condition so characteristic of the cells of the endsac is not seen. Instead, the cytoplasm contains large numbers of granules of very uniform size and power of refraction, and exhibits a striation which is perpendicular to the basement membrane. The oval nuclei lie near the middle of the cell, and are somewhat larger than those of the epithelium of the endsac. But the distinguishing feature of the epithelium of the labyrinth is its free border. This differs in different glands, and in different parts of the same gland; the extreme conditions may, indeed, be seen even in neighboring regions of the same tubule. In Figures 7 and 8 are shown the extremes of the conditions seen. The free border of the cells shown in Figure 8 appears striate, and there is formed a layer which, though it is not a true cuticula, resembles one. The parallel striæ represent partitions between adjacent vacuoles which form a single superficial layer and are by pressure elongated in the long axis of the cell. In Figure 7 some cells exhibit large globular protrusions from their free ends. The cytoplasm of these protrusions is less dense than that at the base of the cell, and they bear some resemblance to the globules found on the cells of the endsac. Other cells in Figure 7 show two or three small globules, and still other cells might have been shown having a larger number of proportionally smaller globules. I believe that the large globules arise from cells in the condition seen in Figure 8, by the progressive fusion of neighboring small vacuoles at the free ends of the cells, accompanied by an expansion and protrusion of the wall of the free end of the cell. As far as my observations go, I can agree with the main points of Marchal's ('92, pp. 228–230) description of this process, except that I do not find secondary smaller globules *within* the larger ones.

The large terminal globules evidently become detached from the cells, since great numbers of such globules (Fig. 7, *glb.*) of various sizes appear free in the lumina of the tubules. They resemble the globules from the endsac in being spherical, but their contents are much more homogeneous, the granules being nearly alike in size and refractive properties. This production of globular bodies with granular contents characterizes the cells of both endsac and labyrinth, but the manner of their formation differs somewhat in the two cases. There is, then, a typical true secretion by these cells, not merely a filtration of substance through them.

The *vesicle* has a wall without folds or protuberances. It is composed of three layers; the inner one epithelial (Plate **1**, Figs. 10 and 11, *la. e'th.*), the outer one muscular (*la. mu.*), and between these a third layer containing a system of blood vessels (Figure 11).

The epithelium is throughout one layer deep. The cells in surface view (Fig. 9) are seen to be irregularly polygonal. They are often elongated parallel to the axis of an underlying blood vessel. The resemblance to the cells of the labyrinth is close, as is to be expected from their similarity of origin (p. 189). The cytoplasm is granular and striate, but shows more vacuoles (Figs. 9, 10, and 11) than occur in the cells of the labyrinth. The nuclei are oval and situated near the middle of the cell. There is a basement membrane of appreciable thickness, which may be separated from the cells by maceration and teasing. The free border of the epithelium (Figs. 10 and 11) presents the same condition as that seen in Figure 8 from the labyrinth; but I do not find the other extreme condition (Fig. 7), with large globules attached to cells, although some of the earlier intermediate conditions between these two extremes are found.

The muscular layer is more variable in thickness than is the epithelial layer. It is composed of long spindle-shaped cells (Fig. 12) of different lengths, containing centrally located nuclei. The cells and nuclei are much flattened in one plane. The edge of the cell is frequently crinkled so as to produce a sinuous outline (Fig. 13). The cell contents are fibrillar, as is well shown when a cell is frayed out in teasing. The fibrillæ are likewise crinkled. There is usually present an axial bundle (Fig. 13, *fas. ax.*) of fibrillæ, which seem to be more closely bound together than are the others; these stain with hæmatoxylin more deeply than the rest of the cell. The thickness of this muscular layer varies. It may be several cells (Fig. 10, *la. mu.*) or a single cell deep (Fig. 11, *la. mu.*), or it may disappear altogether, as it does where the wall of the vesicle is attached to the dorsal face of the endsac (Fig. 2, *par. vs.*). In any given place in the muscular sheath the cells lie parallel with one another, there being no crossing or formation of meshwork.

Between the basement membrane of the epithelium and the muscular sheath there is a layer of connective tissue containing a plexus of blood-vessels. One of these is seen cut crosswise in Figure 11 (*vas. sng.*). These vessels present the ordinary structure seen in the vessels of other parts of the body, and are readily distinguishable from the two other layers of the wall of the vesicle.

The position and external appearance of the tubercle upon which the duct opens has already been described (p. 160). In Figure 14 (Plate 1) is shown a section in the long axis of the appendage through this tubercle. It is seen that the base is much constricted by an infolding of the integument on the anterior side. This is the toothed process referred to on page 161. As the duct passes through this narrow region, it is constricted, but within the tubercle again enlarges. It opens through the middle of the integumental membrane which covers the face of the tubercle. This opening varies in different specimens from 25 to 40 micra in diameter (Figure 14, *of. ex.*). The tegumental membrane is composed of three layers, which, passing from within outward, are, (1) the thin non-calcified layer of the shell; (2) the non-pigmented calcified layer (Figure 14, *la. cx.*); (3) the cuticula or enamel layer. The pigmented calcified layer (Figure 14, *la. cx'.*) stops abruptly at the edge of the truncate face of the tubercle. The three layers of the membrane are traceable into the duct on the anterior side, but not on the posterior. However, even on the anterior side these rapidly thin out and disappear entirely at a short distance from the outer face of the membrane. This continuation of the integument into the anterior floor of the duct forms a sort of operculum (Figure 14, *op.*). The epidermal cells upon which this rests, and by which of course it has been produced, are much elongated, and their deep ends are attached to a ligament (Figure 14, *lig.*). To this ligament are attached, in turn, other elongated epidermal cells, the basal ends of which are attached to the integument of the "toothed process." I have no evidence that either set of these epidermal cells is contractile, but they are both peculiarly elongated, and if they are contractile we have here a mechanism for opening the external orifice by depressing the operculum. This would allow the escape of the excretory products, they being forced out by contractions of the muscular layer of the wall of the vesicle.

The space between the duct and the wall of the tubercle is filled by the dermis (Figure 14, *drm.*), in which are found tegumental glands (*gl. e'drm.*). At its base are striated muscles (*mu.*) belonging to the antenna, but having no connection with the operculum. On the tubercle, especially around the edge of its truncate face, there are numerous sensory hairs (*set. sns.*).

II. Development.

A. Historical Summary.

The published work on the development of the antennal glands in decapod Crustacea is meagre and lacks both detail and completeness. In most cases, it is only a by-product of researches along some other line, or part of a general consideration of the life history of some species; this may account for the contradictory statements on the subject.

Rathke ('29) in a work much in advance of his time describes (p. 51) for the crayfish embryo, at the time when pigmentation of the optic lobes is well begun, the formation of a slender narrow plate, whose greatest diameter is directed from dorsal-posterior to ventral-anterior. This plate presents a rounded outline dorsally and ventrally; its posterior edge is concave; its anterior convex. The outer surface is in contact with the integument, the inner with the yolk, from which it has its origin "through deposit of plastic material." The duct to the exterior was not made out. These "Speicheldrüsen," while remaining in connection with the yolk, increase in size and become more spherical (p. 60). Just before hatching, there may be seen in these organs small round green spots, the occurrence of which may be assumed to indicate the beginning of secretory activity. When the yolk disappears, they have a discoidal form, are green in color, and lie against the wall of the stomach (p. 64).

This early account is nearly correct as far as it goes, but it deals with only those parts resulting from the ectodermic invagination; the author failed, moreover, to see the connection with the exterior, which would have shown him the relations of the organ and would have prevented the use of the term "Speicheldrüsen" in relation to them.

The next reference to the embryology of the organ is by Lereboullet ('62), who describes (pp. 760, 761), also in the crayfish, the formation of certain glandular bodies of unknown function at the stage when the stomach grows forward to produce the lateral pouches. These bodies are formed of a simple transparent tube, which in one part of its course is coiled, and is directed toward the base of the corresponding external antenna. The green glandular body also formed by coiling of the same tube is not seen until later.

It is difficult to reconcile this last statement with the preceding, but it seems to indicate that the author believed that there were two glands of different kinds arising in this region, but not simultaneously. The part first referred to is probably the duct to the exterior.

A. Dohrn ('70, pp. 253, 254) describes in the basal segment of the antenna, in the early embryonic stages of Scyllarus arctus, a round cell-mass surrounded by a membrane, and outside this by "einer starken Hypodermisschicht." In Palinurus vulgaris, according to Dohrn, the antennal glands lie in the basal segment of the antenna (p. 261). They are surrounded by the hypodermis, but are free from it. The central part is a cavity in which lie rather close together large free cells, while the wall of the gland is continuous by means of the duct with the ventral and inner wall of the base of the antenna. The free cells within the cavity are probably of the same origin as those of the wall, and ultimately all are incorporated into the wall of the gland. I think it probable that the author erred at this point, for the "free cells" are probably of *different* origin from the others, i. e. of mesodermic origin, and are the Anlage of the endsac.

Reichenbach ('77, p. 191) finds that the green glands arise by invagination of the ectoderm at the stage when the maxillipeds begin to appear, but he gives no figures of them.

Grobben ('80, p. 104) says the antennal glands, as well as the shell glands in Moina, arise from the middle germ layer, but he fails to give arguments, descriptive figures, or authority to warrant this conclusion concerning the *antennal* glands, or even to say in what species it occurs. I cannot therefore agree with Kingsley ('89, p. 30) in saying that Grobben "showed that the gland belonged to the mesodermal tissues."

Ishikawa ('85, p. 422, Pl. XXVIII. Figs. 68, 90–94) finds in Atyephira, in the base of the second antenna at the time of the appearance of the first pair of maxillipeds, a circular group of about eight granular ectodermic cells. In these is formed a cup-shaped depression from the exterior, which has a large mouth and grows deeper while the opening narrows. "The cells which are concerned in the formation of it [the antennal gland] are all ectodermic." By the time of hatching, the depression has become a canal having three or four convolutions and filled with granular fluid.

Reichenbach ('86, pp. 97, 98) sees in sections of the embryo of Astacus with well outlined maxillipeds (Stage G) the Anlagen of the glands appearing in the basal segment of the second antennæ as recently formed plugs of ectoderm (Taf. X. Fig. 125 u. 126, *g. D.*). The arrangement of cells shows that a sac is to appear, although no lumen is as yet present. At a slightly older stage (Stage H), with pereiopods marked off, surface views show a crescentic arrangement of cells bordering an involution. The opening of the ectodermic invagination is the permanent mouth of the gland. This invagination grows anteriorly, making a slight turn. The Anlage remains in connection with the ectoderm, and at first does not even approach mesodermic tissue. At later stages (Stage J, with distinct pleopods, and Stage K, with strongly developed eye pigment) flat connective-tissue cells begin to surround and soon envelop the gland (Taf. XIII. Fig. 205).

Thus far, with the exception of the unsupported statement of Grobben ('80), there is a consensus of opinion as to the ectodermal origin of the glands.

With this opinion Kingsley disagrees. He found ('89, p. 29, Plate II. Fig. 49) in Crangon vulgaris a patch of mesoderm stretching into the base of the second antenna as a solid plug at a stage when the eye pigment existed as a crescentic line (Stage G). In a somewhat older embryo (Stage H) "a cavity (Plate II. Fig. 61) appears in this tissue, and the cells lining it take a well marked epithelial character, their boundaries being distinct." At no "stage does the green gland have any connection with any other cavity within the body. . . . The external opening to the gland is not formed until after hatching." By this, I infer, is meant the confluence of the lumina of the endsac and the duct. The mesodermal origin of the antennal gland in Crangon agreed with that for the shell gland of Phyllopods, as already worked out by Grobben ('79, p. 23), and later confirmed by Lebedinsky ('91, p. 152).

Lebedinsky ('89, p. 197, see also '90, p. 184) has found that the "Segmentalorgan" in the first maxilliped of Eriphia is formed from both ectoderm and mesoderm, and from this he concludes ('92, p. 233) that the antennal glands, the shell glands, and "Segmentalorgane" in Crustacea are serially homologous organs.

Allen ('93, p. 338) says that in a larva of Palæmonetes a few days old the green gland consists of an endsac, which communicates by means of a U-shaped tube with a very short ureter opening at the base of the antenna, and that the distal portion of the tube is slightly enlarged and may be termed a bladder. At hatching, the deeper part of the gland is a mass of cells without lumen, but ureter and external opening are present. Very early in larval life the cells of this deeper portion separate from one another, giving rise to the lumen, and the gland probably becomes functional at that time. The development of the organ in the larva consists chiefly in the enlargement of the bladder, which, arising at the elbow of the U-shaped tube, grows mediad and dorsad to a great extent. The shell gland, opening at the base of the second maxilla, is the functional kidney during embryonic life, but it is not found in young adults.

In his later paper Allen ('93^a) gives figures (Plate XXXVI. Figs. 1 and 2) showing that in the young larva the endsac differs histologically from the tubule and bladder, the two last being lined with an epithelium composed of cells which are striated and capped with a cuticular structure. The plexus of tubules between the endsac and the bladder arises from the original tubule in that region "obviously . . . by the splitting up of the single tubule" (p. 406).

Boutchinsky ('95, pp. 78, 79, Tab. II. Fig. 51) found that in Iphinoë the ectodermal part of the gland arises as a true invagination from the exterior, with a lumen at all times connected with the outside world. The deep end of this invagination is surrounded by a mass of mesodermic cells. In Gebia littoralis, at a stage (Tab. IV. Fig. 85) when the telson has grown forward so that it is even with the mandibles, he saw (pp. 169, 170) the first appearance of the antennal gland as a compact ball of mesodermic cells (Tab. VI. Fig. 143) with distinct walls and large granular nuclei. The ectodermic invagination occurs at a later stage (Fig. 153), a lumen meanwhile having formed in the mesodermic part of the gland. The mesodermic part soon elongates and becomes horseshoe-shaped (Fig. 154). He reaches two general conclusions in regard to the embryology of the gland: — (1) that it is formed from an inner mesodermic and an outer ectodermic part; (2) that the formation occurs at a time when the mesoderm shows no regularity in the distribution of its cells, these being scattered without visible order.

I have published (Waite, '98) a short abstract of some of the chief points in the development more fully described hereafter.

B. Development in the Embryo.

In the following account of the development of the antennal glands in Homarus, it should be stated at the outset that it is very difficult to fix definitely the time intervals between successive stages in the embryonic development. The determination of age in hours or even in days is not of much importance. Since the rate of development is known to depend largely upon temperature, the conditions of embryos of the same age must vary with every station, with eggs extruded at different seasons of the year, and also with eggs extruded at the same date in a given locality in different years. Since, then, rate of development is dependent upon many variables, the known intervals between the killing of different embryos in the same series are of only relative value, not being accurately comparable with the intervals of any other series. Further, even in the same series, in which apparently the same conditions have prevailed, there is individual variation.

Notwithstanding these sources of uncertainty, I shall state the approximate age at which the several stages appear, this approximation being arrived at by comparing the several series of my material with one another and with the published figures of Bumpus ('91) and Herrick ('95). I shall give in each case the date of killing, which will indicate the seasonal influences to which the development was subjected.

The earliest embryo which it is necessary to consider in dealing with the development of the antennal gland was killed on August 29, and had reached the late nauplius stage (Plate **2**, Fig. 15). This embryo has the cephalic lobes well marked off, and the first (*at. 1*) and second antennæ (*at. 2*) and the mandibles (*md.*) well defined. The second antennæ are biramous and reach nearly to the posterior limit of the pleonic flexure. Of the post-oral appendages, the buds of the first maxillæ have just begun to appear.[1]

---

[1] This stage is a little further developed than that figured by Herrick ('95) in Cut 32, Plate I., which he estimates by comparison with embryos raised from seg-

In an embryo of this age I find in sections that the basal region of the second antenna is completely filled with cells having certain distinctive characters (Plate **2**, Fig. 18, *ms'drm.*), which serve to differentiate them from the outer wall (*ec'drm.*) of the appendage. These axial cells are oval or slightly elongate, with rounded outlines, and less uniform in size and less densely granular than the rectangular ectoderm cells (*ec'drm.*), which form the outer wall of the appendage. The nuclei of the axial cells are more oval than the nearly spherical nuclei of the ectoderm cells. In some sections it is to be seen that this plug of axial cells is connected with similar plugs of cells in the base of the first antenna and of the mandible by means of a single layer of cells immediately beneath the ectoderm of this region.

According to recent works on the formation of the germ layers and of the appendages in Decapods, — I refer especially to Reichenbach ('86, p. 24, Taf. IX. Fig. 84, and Taf. X. Fig. 121), Bumpus ('91, p. 245, Plate XVIII. Fig. 6), and Herrick ('95, p. 209), — the cells which form the axis of the appendage are clearly mesoderm, in the generally accepted meaning of the word.

In embryos one day older (Plate **2**, Fig. 16), in which the first maxillæ (*mx. 1*) are marked off, a small number of these axial mesodermic cells in the base of the second antennæ have become differentiated from the rest. *They are destined to become the deeper part of the antennal gland.* These cells are nearly on a level with the general surface of the body. They are larger than the remaining mesodermal cells, and have the cytoplasm less densely granular, especially toward the centre of the cell, and their nuclei also are larger and stain much more deeply with hæmatoxylin. The nuclei are likely to be eccentric, and in many cases they are surrounded by a clear zone of non-granular or very sparsely granular cytoplasm (Plate **2**, Figs. 19, 20, 21, 22, *sac. trm.*).

I believe that there is at first only one of these differentiated cells in each antenna, although I have not found this condition in any of my sections. My reason for thinking so is that in several cases in which only two nuclei are present I have found these close together, and with their adjacent sides somewhat flattened (Plate **2**, Fig 19, *sac. trm.*), as if recently divided. I have not found, however, any mitotic phenomena which might serve as proof of a recent division. On the other hand, it

mentation stages (see his Tables 17 and 18, p. 56) as 14 to 16 days old. With this as a basis, the embryo of my Figure 15 would probably be between 15 and 17 days old. It falls between the Stages N and O of Bumpus ('91, p. 248, Plate XIV.), and is a little further developed than Reichenbach's ('86, p. 47, Taf. III. Fig. 10) Stage G of Astacus.

is possible that there are two cells differentiated at the same time. Sections preceding and following the one seen in Figure 19 show that only two of these differentiated cells are present in this appendage at this stage. In three other specimens also I have found only two such cells, so that there is certainly a two-cell stage in the development of this organ. These nuclei divide, but divisions are not necessarily simultaneous, for I have found cases in which there are three, four (Fig. 21), five, six, seven, eight, nine, and twelve nuclei present. In a few cases mitotic phenomena are found in some of the nuclei, but in most cases, even where an odd number of nuclei is present, there are no mitotic figures. These nuclei are distinctly different from those of the ectoderm and of the surrounding mesoderm in the appendage. There can be no doubt about these differentiated cells being of mesodermic origin. In another particular this region differs from the surrounding mesoderm; although the nuclei increase in number, there is not a corresponding increase of distinctly separated cells. There are partial cell walls (Plate **2**, Figs. 19, 21, *par. cl.*), but the cell areas are not fully or sharply defined by cell membranes. This condition is found in individuals which have been treated by one or other of several different methods of killing, hardening, and staining; it does not appear therefore to be due to the influence of particular reagents.[1] The result is a partial syncytium, or cell complex, in which the nuclei are irregularly distributed, but often show a tendency to take a peripheral position (Plate **2**, Figs. 23, 24).

Bergh ('88, p. 228) has found a parallel condition in the nephridia of Criodrilus. My results do not, however, agree with the condition found by Boutchinsky ('95, p. 169, Tab. VI. Fig. 143) in Gebia, in which, as he says, the cells at a similar stage are separated by distinct walls.

In Homarus this syncytial mass has an even oval outline, the longer axis of the oval lying nearly in the transverse plane of the body, but directed obliquely laterad and ventrad at an angle of 20° or 30° with the frontal plane. The evenly rounded outline of the mass is preserved even where it is separated from the mesenchyme by only a thin layer of mesodermic cells. This oval syncytium with its contained nuclei *becomes the endsac of the antennal gland,* and in the further description will be so designated.

---

[1] It should, however, be stated that my material had been in alcohol for some time, which may have caused disintegration of cell walls in this particular region. The cell walls of neighboring regions, and of corresponding positions in other appendages, are however firm and distinct.

In an embryo about 22 to 24 days old (September 5th),[1] represented by Figure 17 (Plate **2**), the spheroidal form of the endsac is well marked (Plate **2**, Fig. 23, *sac. trm.*). At this stage, however, when there are twelve nuclei, it is not visible from the ventral surface of the appendage, nor is there any circular or crescentic arrangement of nuclei and cells at the base of the appendage, such as several authors figure as representing the first trace of the antennal gland. Such an appearance accompanies the ectodermic invagination, of which there is as yet no trace, either in surface view or in sections.

In an embryo from the same brood two days older (September 5th to 7th) there appears in sections a definite vacuole (Plate **2**, Fig. 24, *vac.*) situated centrally in the endsac, which here has only nine nuclei. This vacuole has a smooth distinct outline, which is evidence that it is not an artifact. It is clearly not intercellular, for there are no cell membranes near it. From this stage on there are seen in the endsac of each individual a few well marked vacuoles of various sizes (Plate **2**, Fig. 22, Plate **3**, Fig. 26).

It seems probable that the lumen of the endsac originates by the confluence of the vacuoles of the syncytium. I can therefore agree with Kingsley ('89, p. 29) that the lumen of the endsac is neither an enclosure of part of the body cavity nor in any way connected with it. A process parallel to this is described by Bergh ('88, p. 228) in the formation of the nephridia of Criodrilus.

It is interesting to notice that the formation of the lumen of the endsac begins before there is any trace of the ectodermic invagination, and only eight days (August 30th to September 7th) after the earliest differentiation of the endsac is seen, whereas in Palæmonetes (Allen, '93, p. 338) the lumen of the endsac does not appear until early in larval life and is there intercellular.

The next stage to be noticed is from another series. It is slightly older than that figured by Herrick ('95) in Cut 34, Plate I., and between Stages O and P of Bumpus ('91, Pl. XIV.). The tip of the telson has grown cephalad until it is somewhat in advance of the base of the second antenna; there is no pigment in the eye. There have elapsed since fertilization, to judge from a comparison with Herrick's figures, 23 to 25 days, but the actual interval is greater, — probably 28 to 30 days, — as

---

[1] This embryo was from the same brood as that from which Figure 16 was drawn, showing the earliest recognized condition of the endsac. Since the younger was killed on August 30th, and the older on September 5th, there is an interval of six days between the two.

these embryos were killed in October. In most individuals of this age there is no sign of ectodermic invagination in the region of the endsac. The endsac (Plate **2**, Fig. 25, *sac. trm.*) is oval and contains in different individuals from 18 to 26 nuclei, which are often only partially separated by cell walls, these being evident in the peripheral portions of the organ only. The central area of the endsac is a granular mass with one or more large irregular vacuoles, or several small ones, while the nuclei lie peripherally in compartments between the incomplete cell walls. In some cases the cell walls are completed, and thus a definite boundary to the lumen is formed. This is the condition of the endsac when invagination of the ectoderm begins, but in some individuals, even after invagination is well started, the cell walls of the endsac are incomplete and its interior is still a granular mass with several vacuoles (Plate **3**, Fig. 26, *sac. trm.*, *vac.*).

In some precocious individuals of this batch of embryos I find evidence of the beginning of the invagination, — a slight depression of ectoderm cells. In Figure 25 (Plate **2**) at the median ventral border of the endsac appears a thickening of the ectoderm (*i'vag. ec'drm.*). This represents the beginning of the ectodermic ingrowth.

In sections of the stages succeeding this it is seen that the ectodermic growth extends proximad and dorsad.[1] The axis of this line of growth is not parallel with the antero-posterior axis of the body of the embryo, but in passing proximad trends slightly laterad, so that true parasagittal sections of the embryo cut the invagination obliquely. The ingrowth consists of a plug, or perhaps better, a sheet of cells, the width of the sheet being however small. This sheet grows up around the endsac and lies against its distal and dorsal faces (Plate **3**, Figs. 26, 27, *i'vag. ec'drm.*).

From all the evidence afforded by my sections I believe that this sheet of cells arises by a process of growth which is most active at its free (deep) end. The conclusive evidence must rest upon signs of mitosis in numerous series of stages covering the period of this growth. I have not sufficient material at command to settle the point definitely.

However this may be, this ectodermic ingrowth occupies a narrow space between the distal and dorsal faces of the endsac and the wall of

---

[1] In referring to the embryonic organ I must use designations of direction which seem contradictory. For that face of the second antenna which lies nearest the mandible and is now the dorsal face is ultimately the ventral, and must be so designated. It assumes its normal position at the time of hatching by revolving about its base as a centre through an arc of about 135° in a parasagittal plane.

the appendage. As a result, in a parasagittal section — at this stage a proximo-distal section of the appendage — there is to be seen a single row of cells (Plate 3, Fig. 26, *i'vag. ec'drm.*). Preceding or following sections of the series usually show that there is an accompanying row by the side of this, i. e. the sheet is two cells wide, and one cell deep dorso-ventrally. In a few cases there is evidence in transverse sections that there are three rows through at least part of its course, these being so arranged that the cross section is triangular. These rows are not distinctly separated but interdigitate, so that the dividing line is anything but straight and sharp, as would be the case were this formation an actual invagination. The line — there is no lumen — between these rows may represent a potential lumen derived from the outside world, but I can trace no actual connection. There is, to be sure, in the region of the connection with the ectodermic wall, a slight depression (Plate 3, Fig. 26, *fos.*) in the surface of the ectoderm, but the cellular arrangement does not warrant the conclusion that this is a real invagination. I believe therefore that the *ectodermic ingrowth is a solid plug, and not an invaginated sac.*

As this plug advances along the dorsal (now ventral) face of the endsac and approaches the proximal border, it is subjected to less stress, its proximo-dorsal border being in contact with only the mesenchyme and the fluids of the body cavity. The plug here enlarges; at first there are in this region one or two extra rows of cells (Plate 3, Fig. 26, *i'vag. ec'drm.*), — cross sections often show four rows, — a little later the plug enlarges into a knob-like body in which an intercellular lumen appears (Plate 3, Fig. 27, *i'vag. ec'drm., lu.*). There is no reason to believe that the lumen thus arising is an enclosed part of the body cavity, and there is no evidence to show that it is actually a part of the outside world. I believe that it is a lumen of independent origin, just as is that of the endsac; but in the case of the ectodermic ingrowth it is *inter*-cellular, while in the endsac it begins as an *intra*-cellular space.

This ingrowth of the ectodermic plug and its expansion into a knob containing a lumen is a rapid process. I have found all the stages hitherto noted in the same batch of eggs from a single female, and all killed at the same moment. In September and October this condition is attained in about 30 days, probably in somewhat less time in eggs extruded in the middle of summer.

The condition shown in Figure 27 (Plate 3) progresses distad and ventrad along the ectodermic plug towards the region of its connection with the ectodermic wall of the appendage. The axial line separating the cell rows is now distinct and even, and quite different from the line separating the two interdigitating rows of earlier stages. This axial line represents a potential lumen, and by separation of the apposed walls the lumen is formed here at later stages. Figure 28 (Plate 3) is a parasagittal section from an embryo about 35 days old. The endsac (*sac. trm.*) has its cell walls well marked and the lumen (*lu.*) is sharply bounded. The ectodermic ingrowth (*i'vag. ec'drm.*) shows in longitudinal section two rows (many rows in all) to a point near the distal end of the endsac. The cells are more columnar than in earlier stages. Some of the ectodermic cells of the wall of the appendage are much elongated. They go to form the ligaments seen in this region in later stages.

Figure 29 (Plate 3) is a transverse section at a little later stage (about 40 days, September 10th to October 20th). Here the lumen of the ectodermic plug (*i'vag. ec'drm.*) is evident and can be traced to the exterior (*of. ex.*). This duct has arisen as the outward extension of an intercellular lumen, first appearing in the region of the deep proximo-dorsal end of the ectodermic plug.

There is thus formed in the embryo of about six weeks an endsac with definite lumen, and an ectodermic ingrowth with lumen, and with a duct opening to the outside world, but these two lumina are not in connection. The duct of the ectodermic ingrowth persists as the permanent duct of the adult organ. However, its lumen is not always visible, especially in the deeper regions, for the growth and resulting pressure at times apparently obliterate it by causing a close apposition of the walls, which, however, do not actually fuse, for at all subsequent stages when a section in the region is torn the lumen is reopened.

There are still two important points to be determined in the embryology of the antennal gland. When, and at what point, does the lumen of the endsac become continuous with that of the ectodermic sac? In a series of embryos taken from a female kept in confinement during the winter (see Herrick, '95, No. (3) 18, Table 18, p. 56) I find that in those killed April 1st (estimated age 273 days) the lumina are separate, but in embryos of the same series killed May 1st (estimated age 303 days) the lumina are continuous. The details of the union of the two lumina I am unable to describe, as I have no intermediate stages.

For some time before this last stage is reached, the lumen of each part is seen in sections, but the two lumina are separated by the closely apposed walls of the two sacs (Plate 3, Fig. 31). The break through the two walls occurs on the dorsal face of the proximal region of the endsac and at the terminal end of the ventral part of the forked proximal end of the ectodermic sac (cf. Fig. 30, Plate 3). After communication is established, an abrupt transition in the character of the wall is still noticeable at the point of union. This level may be termed the mes-ectal line, since it is the line of junction of the mesodermic with the ectodermic part of the organ. There is a valve-like flap of cells projecting from the wall of the endsac into the orifice connecting the two cavities. This condition is still evident in the first larva (Plate 6, Fig. 51, *vlv.*).

The brood of this female kept in confinement during the winter was hatched 33 days after the killing of the specimens which showed connecting lumina (about 330 days after fertilization), so that when the endsac comes into communication with the exterior the embryo has already passed through ten elevenths of its embryonic period. It is possible that the establishment of the communication between the two sacs occurs in the earlier part of the period embraced between the ages of 273 and 303 days, but even if it does not occur until the latter part of the period, the lumen of the endsac is in direct communication with the exterior at least a month before the end of embryonic life. The only records that I find of the time when this connection is effected in other Crustacea is that made by Allen ('93, p. 338) for Palæmonetes, and by Kingsley ('89, p. 30) for Crangon. Kingsley states that "the external opening to the gland is not formed until after hatching." Allen says that the formation of the lumen of the endsac and its communication with the exterior occur early in larval life. In Homarus, however, the lumen of the endsac communicates with the outside world late in embryonic life. If, as Allen thinks, the establishment of this condition marks the beginning of functional activity, then the antennal gland in the lobster is functional as an embryonic organ. But I cannot agree with Allen. On *a priori* grounds we may expect an excretory organ in the lobster embryo. Excretion takes place in many yolk-bearing embryos, and special embryonic organs having this function occur in many cases, such as the embryonic nephridia of Annelids and pulmonate Gasteropods, and the shell gland in the embryo of many Crustacea. In some decapod Crustacea the shell gland is functional in the embryo, but atrophies soon after hatching. Whether it is present in Homarus I am unable to say; but I believe it probable that excretion in the embryo is performed by some such special organ rather than by the antennal gland, for in the latter I find no direct evidence of excretory activity during embryonic life. The cavity of the gland contains neither a granular clot nor excretory globules, such as are found in the larval and adult stages, nor have the cells of the wall of the ectodermic sac the marked striation which is seen later when glandular activity certainly exists. It may well be that excretion in the embryo is less abundant than in the predatory larva, because of the less active metabolism and the more perfect food supply of the yolk. The presence or absence of excretion products in the organ during embryonic life might be demonstrated on fresh material by micro-chemical tests, and the question thus definitely settled; but my material is not so preserved as to permit the application of such tests.

After the formation of the ectodermic ingrowth, as shown in Figures 26 and 27 (Plate **3**), the further embryonic development consists, then, in four chief phases: — (*a.*) The line representing its lumen extends to the outside world and so establishes a potential duct. This is a rapid process and is completed shortly after the stage shown in Figure 28 (Plate **3**). The condition previously noted at the deep end of the ectodermic ingrowth — several rows of cells — progresses and finally reaches the exterior near the point where the ectodermic ingrowth first appeared (Fig. 25). This potential duct is open in many cases (Fig. 29). The opening of the duct is on the anterior side of the appendage, somewhat toward its ventral face. The ectodermic duct and sac extend from this external orifice dorsad and proximad, covering the distal and dorsal faces of the endsac, but not until a later stage does it pass ventral to the endsac, nor ever much beyond its proximal border.

(*b.*) The ectodermic sac becomes extended and complicated throughout embryonic life by the formation of evaginations, which begin to appear as soon as the lumen of the duct has been extended to the external world. These outgrowths are flattened, probably by mechanical pressure. There are three regions at which principally these evaginations occur. One of these is proximal, i. e. at the deep end of the ectodermic ingrowth. Here the outgrowth soon becomes forked, there being a ventral portion nearer the endsac and a proximal portion more nearly in line with the axis of the appendage. Figure 30 (Plate **3**) shows these forks, but the proximal one is seen only in cross section. It extends at right angles to the main axis of the appendage and to the plane of the section, approximately parallel to the frontal plane of the embryo. The notch separating these forks never becomes very deep, but it is recognizable from the second month of embryonic life until the late larval stages. On the dorsal face of the ectodermic sac in the region of its sharpest curvature is a second area of evagination. This outgrowth, which is dorsad, does not exist at the stage shown in Figure 30, but it appears slightly later. It has a considerable horizontal extent (Figure 31, Plate **3**), being all that part of the ectodermic sac which later lies distal to the duct. The third region is along the entire length of the ectodermic sac in the dorso-median area. An idea of the position of this region may be gained from Figure 31 (Plate 3), which is a transverse section. It is there represented by the long dorsal tract of the ectodermic sac, extending mediad near the letters "*sac. trm.*"

The complications in the shape of the ectodermic sac arise from the differential growth in these three regions. The ventral fork (Figure 30) grows ventrad around the proximal face of the endsac, and then distad between it and the wall of the appendage, meanwhile extending laterad and mediad in the frontal plane. It is this extension that finally connects with the endsac. The proximal fork has grown at the same time, but extends more nearly in the axis of the appendage. Meanwhile the dorsal extension has grown considerably dorsad and distad, and the dorso-median evagination has extended horizontally. As a result of all these growths the parts of the ectodermic sac have come to embrace the endsac on all sides, though not completely, for it is seen in the larval stages that through a part of its extent the endsac lies against the ventral and lateral walls of the appendage.

All these growths and extensions of the ectodermic sac are evaginations, and carry with them part of the original lumen, but they are *in no respect convolutions.* The complicated lumen thus arising is suppressed, as far as actual cavities are concerned, until the latter half of embryonic life. In an embryo of 152 days (July 1st to December 1st) no actual cavity is observable, only the line marking the meeting of apposing walls, but in an embryo of 303 days (July 1st to May 1st) the lumen is an actual cavity at almost all points. In stages intermediate between these the lumen becomes more and more open as age advances. We thus see that the distention of the lumen occurs in large part prior to the junction (see p. 179) of the lumina of the endsac and ectodermic sac.

(*c.*) The endsac does not suffer much complication during its embryonic growth, but it becomes much flattened and compressed between the extensions of the ectodermic sac. The chief growth is laterad and dorsad, and gives rise to the condition found in the first larva, where the endsac lies in large part lateral to the ectodermic sac (Figure 40, Plate 5).

(*d.*) Finally the lumina of endsac and ectodermic sac become continuous (see p. 178), and the organ has then practically reached the larval condition.

C. Development in the Larvæ.

(*a.*) *In the First Larva.*

The stages at which the various phases of the development of the antennal gland in the embryo appear are not precisely fixed by time intervals because of seasonal variation in the rate of development. They may be referred to particular conditions of prominent external organs, such as the pigmentation of the eyes or the position of the tip of the telson, with much greater precision, but even this allows of no close comparisons with parallel stages in other genera or families. The stage at which the embryo hatches, marking the transition from the passive embryonic to the active larval life, is sharply defined in most free-living Crustacea, and it would seem that this is a time at which comparisons may be made most safely. Moreover, the transition to the predatory life of the larva must have a marked influence upon metabolism, and therefore upon the excretory organ and its functions. It has therefore seemed well to consider this stage in some detail.

My material was all killed within twelve hours after hatching, and hence represents the earlier part of the first larval period, the extent of which may be as much as five days (Herrick, '95, p. 172).

1. General Structure.

With the hatching of the embryo a considerable alternation occurs in the topography of the antennal gland, but this is due to mechanical causes rather than to growth. The second antenna, which has been folded back against the embryo so that its distal end is posterior to its proximal end, is released in hatching and swings — approximately in a parasagittal plane — through about 135 degrees, to a position in which the distal end is anterior to the proximal. Thus in the basal region of the appendage the dorsal face is shortened and thereby relieved of the stress which has existed at that place during embryonic life. This removal of pressure from the extensions and evaginations of the ectodermic sac brings about a change in its form, which passes from the flattened constrained shape to a more rounded one. This permits the separation of the apposing walls and the establishment of a large lumen. Likewise the endsac, which has been compressed between the dorsal and ventral portions of the ectodermic sac, is relieved from this pressure and expands as much as the larger space allows.

In Figures 32 to 38 (Plate 4) are shown the second, third, fifth, sixth, eighth, eleventh, and twelfth sections respectively from a series of thirteen sections 10 micra thick through the left antennal gland of the first larva. The sections are cut parallel to the long axis of the antenna and perpendicular to the frontal plane of the larva, and are viewed from the lateral face, Figure 32 being the most lateral one shown. The members of the series reproduced do not extend near enough to the median plane to include the opening of the duct to the exterior, but the relations of this duct to the ectodermic sac and to the external orifice may be inferred from Figure 38.

The ectodermic sac — the walls of which are represented in a lighter shade than those of the endsac — is oval in shape, flattened ventrally, and elongated in the axis of the antenna (Figures 32 to 38, *sac. ec'drm.*). The endsac (Figures 33 to 35, *sac. trm.*) lies in a depression of the ventro-lateral face of the ectodermic sac, as is readily to be understood from its position in the sections and in the series as a whole. The three evaginations of the ectodermic sac — proximal, ventral, and dorsal — are still indicated, though less prominently than in the embryo. The passage from the lumen of the endsac to that of the ectodermic sac — partly closed by the valvular flap — is shown in Figure 33.

The endsac (Figures 33, 34, *sac. trm.*) now lies closely applied to the ventral wall of the ectodermic sac, a relation which is changed in later stages (see p. 190). A ventral recess of the ectodermic sac shown in Figures 37 and 38 leads distad and mediad to the duct communicating with the external world. This is better shown in Figure 39, a section of the left gland from another series, but viewed from the *median* face. This being cut in a more favorable plane, at a slight angle with the long axis of the appendage, shows that the ventral recess continues as a duct to the external opening (*of. ex.*) at the summit of a papilla on the ventral wall of the appendage. It is clear from this figure that the duct is connected with the ventral face of the ectodermic sac. The position of the duct marks the original course of the ectodermic ingrowth in the embryo.

The conclusions reached by the examination of such parasagittal sections are supplemented by the examination of transverse sections. Figure 40 (Plate 5) is the anterior face of a transverse section through the first larva in the region of the base of the second antennæ, and shows the general position of the antennal glands, which lie almost wholly within the appendage. Figures 41 to 48 (Plate 5) exhibit the anterior faces of the third, fifth, seventh, ninth, tenth, twelfth, fourteenth, and seventeenth sections of a series through the right gland, Figure 41 being the most anterior. The sections, each 10 micra thick, are cut perpendicular to the long axis of the antenna. No section plane passes through the external orifice of the duct, but the orifice is near the plane of the section shown in Figure 46. The opening to the exterior, it will be observed, is not at the middle of the ventral face of the appendage, but more toward the median side. The communication between the lumina of the endsac and ectodermic sac does not appear, as it is small and its axis is inclined to the plane of the section (cf. Figure 33), but it lies between Figure 47 and the next following section. Its position is indicated in Figure 47 by *a*. It will be noticed that the endsac lies partly ventral and partly lateral to the ectodermic sac (Figures 44 to 48), and that its free margin extends dorsally, while the ectodermic sac extends ventrally. This is the beginning of a process of growth that is destined to reverse the relative positions of the two parts as found in the embryonic stages, where the endsac was ventral and the ectodermic sac dorsal (cf. Figs. 26, 27, 28, Plate 3).

Finally, Figure 49 (Plate 6) represents the dorsal face of a frontal section of the right gland, — the tenth, counting from the dorsal face of the gland, in a series of eighteen, each 10 micra thick, — in which is seen the lateral position of the endsac and the communication between the endsac and the ectodermic sac at *a*. The passage is situated at the lateral and proximal part of the endsac.

The evidence from sections in the three planes shows that the endsac lies ventral and lateral to the ectodermic sac; that the ectodermic sac is elongated in the axis of the antenna, and gives off the duct to the exterior from its ventral face well over on its median border; and that the gland lies almost wholly within the appendage and not in the cavity of the body proper.

The greatest diameter of the gland measured in each of the three axes gave as a result of the average[1] of several cases the following: —

Maximum	proximo-distal axis,	0.3 mm.
"	dorso-ventral axis,	0.2 "
"	latero-median axis,	0.2 "

The average length of the first larva is 7.8 mm. from tip of rostrum to tip of telson.

---

[1] The extremes of measurement vary from these mean averages 20% in some cases, which is probably due to slight differences in the age of larvæ, or to individual differences independent of age.

2. Histology.

The histological character of the endsac differs distinctly from that of the ectodermic sac, and the dividing mes-ectal line is sharply marked (Plate 6, Fig. 51, *ln. mes-ec.*). The valve-like flap (*vlv.*) in the orifice between the two sacs lies on the dorsal side, and its cells are connected directly with those of the wall of the endsac, and are of the same nature. In the region where the walls of the two sacs are adjacent, they are not applied to each other continuously, but are separated by spaces (Figure 51, *lac. sng.*) which constitute blood lacunæ. This is proved by the frequent presence in them of blood corpuscles (Figure 59), the structure of which is characteristic. These blood spaces are separated at intervals by partitions or pillars (Figures 49, 51) connecting the basement membranes of the two sacs. In structure these partitions resemble closely the tissue of the endsac. I have not traced the continuity of these blood spaces with the general circulatory system. They are not lined by an endothelial layer, as far as I am able to discover.

The cells of the endsac are all of the same general type, but show two different forms, one (Fig. 52, Plate 6) being more flattened than the other (Fig. 53, Plate 6). The more flattened cells occur in those regions of the wall which are not adjacent to the wall of the ectodermic sac (Fig. 51). All of the cells of the endsac have large nuclei, which lie close against the free wall of the cell and in most cases cause a protrusion of the cell into the lumen (Figs. 51, 53). The nuclei in the flattened cells are more elongated in a direction parallel to the surface of the wall than is the case in the more rotund cells of the other region (cf. Fig. 52 with Fig. 53). Both kinds show a chromatic network. By the methods used it was impossible to demonstrate any definite lateral cell boundaries, but the extent of the cell territories is indicated by the position of the nuclei and by the contour of the free face of the cells. The cytoplasm is finely granular, and in most cases distinctly striated, the rows of granules being perpendicular to the surfacs of the wall of the sac (Fig. 53). This granular striation would seem to indicate a secretory activity. There is, however, no bounding striate cuticula on the inner face of the cells. The wall of the sac presents a basement membrane, which is however much less marked than that of the wall of the ectodermic sac, and appears as a single line even under the amplification of a $\frac{1}{18}$ oil immersion (Zeiss) and ocular 4.

The cells of the ectodermic sac are very different in character from those of the endsac, and the transition at the mes-ectal line is, as I have said, abrupt, there being no cells of intermediate character (Fig. 51, *ln. mes-ec.*). The cells of this ectodermic part differ considerably in size and shape, although not essentially in structure. Figures 54 to 57 (Plate 6) are all drawn from the same series of sections, and with the same amplification, but from different regions in the wall of the ectodermic sac; they fairly illustrate the variation in the size and the shape of the cells. The cells from the dorso-median wall (Fig. 56) are more columnar, and the nuclei are relatively farther from the basal end of the cell than in other regions. Those from the ventral face (Fig. 55) are much smaller and show fewer striations. The cytoplasm in all these regions is granular, more densely so than in the endsac, and in all but the ventral wall (Fig. 55) the granules are arranged in rows perpendicular to the basement membrane and separated by clearer areas of periplasm. This striation is found both in the basal and free ends of the cell. In some cases the clear area between rows of granules is expanded to form large vacuoles (Fig. 56, *vac.*). The nuclei are bounded by a definite nuclear membrane and have a coarse chromatic network, which stains deeply in hæmatoxylin. Where the strands of this network cross, there are formed chromatic masses of greater density; these are usually triangular in section (Figs. 54, 57, and 58). Nucleoli are found in some cells (Fig. 55).

Mitotic phenomena, though not abundant in these cells, are now and then met with. One such cell in process of division is shown in Figure 57. The plane of division is in all cases perpendicular to the basement membrane, so that the tissue remains only one layer thick. The rarity of these indications of cell division, in spite of the considerable increase in the size of the gland in the beginning of the second larval stage, is perhaps an indication that the cell increase in the organ is more rapid in the latter part of the first larval period than in the earlier part, at which time my material was killed.

The basement membrane is seen in all cases. Under high powers it has an appreciable thickness (Fig. 58, Plate 6, *mb. ba.*). I have seen no trace of nuclei in it to indicate an endothelial nature.

All the cells of the ectodermic sac agree in having a vertically striate cuticula on the free face (Figs. 54–58, *cta.*). Under high magnification this cuticula is seen to be made up of bundles of rods or strings of granules grouped into the shape of an hour-glass, the clear spaces between these bundles having in section a lenticular shape (Fig. 58, *cta.*). This cuticula agrees in a measure with that in the walls of the labyrinth of the adult gland, but in this larval stage there are no globular prominences extending out from it into the lumen.

The histological structure of the duct is shown in Figure 60 (Plate 6), which is from a longitudinal section of the appendage. Its wall is directly continuous with the body wall. The dorsal lip of the orifice (*of. ex.*) shows no abrupt transition from the wall of the duct to that of the body. On the ventral lip the limit is somewhat more precise owing to the sharp folding, but it is difficult to say to which wall the apical cells of the ventral lip belong. The cells of the dorsal wall show differences in size and shape among themselves, and a considerable difference from the cells of the ventral wall; these being smaller and imbricated. The cells of the duct do not show the granular striation characteristic of the cells of the ectodermic sac, nor is there a striate cuticula on the face of these cells. These two characters serve to distinguish the cells of the duct from those of the ectodermic sac, and lead to the inference that the former have no secretory function. However, as one follows the wall of the ectodermic sac as it merges into the wall of the duct, these two characters gradually disappear, and it is impossible to say that there is any definite line where ectodermic sac ends and duct begins, — a condition to be expected from the fact of their having had a common origin.

The cuticular layer of the external shell bends into the duct (Fig. 60), but soon thins out and disappears. It extends for a greater distance along the dorsal than along the ventral wall.

The lumen of the ectodermic sac contains a granular coagulum, which resembles in staining properties that seen in various parts of the adult gland, but there is no trace of the globular structures there seen (p. 166). This coagulum is in all probability the secretion of the walls of the ectodermic sac, indicating that the functional activity of the gland has already begun; but that function must differ in some respects from the function in the adult, as indicated by the absence of the globules. This coagulum is not seen in the lumen of the endsac. The identity of the substance found here with that found in the adult gland can only be established by micro-chemical tests, and for that my material is not suited.

It seems probable that the function, although possibly somewhat different from that of the adult, is of essentially the same nature, i. e. excretory. This would be expected both upon *a priori* grounds and from the structure of the cells as described. At this stage metabolism, consequent upon the activity of the larva, is constant, and as all the structural conditions appear favorable, it seems as if this organ, which later is certainly the chief, if not the only, excretory organ of the body, must be functional and functional in the way of its later activities. I therefore believe that the antennal gland in the first larva is a functional excretory organ.

(*b.*) *In Older Larvæ.*

The antennal gland in the *second larva* shows no marked difference from that in the first, either in shape or in histology. There is, however, as compared with the first larva (see page 184), a difference in size, which again taking averages, is now:

Maximum	proximo-distal axis,	0.3 mm.
"	dorso-ventral axis,	0.3 "
"	latero-median axis,	0.25 "

If we assume, in view of the simplicity of the organ at these stages, that its secreting surface is about equal to the *surface* of a parallelopipedon having the dimensions of the whole organ, we find that the area of the secreting surface in the second larva is 40–50 per cent greater than in the first. The average length of the second larva (see Herrick '95, Table 34) is only about 13 per cent more than that of the first. If we compare the cubes of these dimensions we get an increase of something over 40 per cent in the bulk of the larva; consequently the increase of secreting surface in the antennal gland simply about keeps pace with the increase in bulk of the larva.

In the *third larva* we get the beginning of that process of complication by which the antennal gland of the adult animal is developed from the relatively simple organ of the time of hatching. Between the conditions in the first and second larvæ there is only the difference of size. Between the conditions of the second and third larvæ there is a difference due to increase in size, by reason of which the gland comes to lie largely in the body instead of in the appendage only, and in addition a difference resulting from the development of long slender evaginations on the dorsal and median faces of the ectodermic sac. These evaginations have only a very small lumen, but the lumen is always in connection with the main cavity of the ectodermic sac, as is shown in Figure 50 (Plate 6, *evag.*). By such evaginations the secreting surface is greatly increased without a correspondingly large demand for space in the body cavity.

In the third larva there also begin to appear at the free ends of the cells composing the wall of the ectodermic sac the peculiar globular vesicles which form so marked a feature of the adult gland. They are less well marked and less abundant here than in the older larvæ.

In this stage, the vessels and blood spaces (*lac. sng.*) which lie between the endsac and the ectodermic sac are for the first time seen to be lined with endothelial cells. This vascular tissue has arisen from the cells which are between the endsac and the ectodermic invagination, and which are seen at later embryonic stages (Plate 3, Fig. 30) as attenuated cells forming a sort of sheath around the endsac.

In the *fourth larva*, the evaginations from the ectodermic sac have further increased in number; those which occupy the positions of the ones found in the third larva have elongated, and in some cases the free end is folded back upon itself. On the dorsal face of the ectodermic sac, well forward, there is an evagination which is larger and more rounded than the others. It contains a large cavity which is connected with the main cavity of the ectodermic sac by a narrow duct. This evagination is directed backward and dorsad; *it is the first differentiation of the vesicle of the adult gland.*

The globular vesicles on the free ends of the cells in the wall of the ectodermic sac are more marked, and appear very much like the condition in the adult.

My material of the older larval stages is meagre and not in good histological condition. It is difficult, in the absence of data as to the number of moults passed, to determine to what larval stage a given specimen belongs. The sole criterion available is therefore that of length.

In *larvæ 14 millimetres long*, the dorsal rounded evagination representing the vesicle has increased much in size, extending caudad and dorsad, until its walls are in contact with those of the masticatory stomach. The narrow slender evaginations have increased in number, especially in the ventral part of the organ, and are so entangled that it is futile to attempt to follow details.

Larvæ 18 millimetres long are the oldest that I have. According to Herrick ('95, Table 34), this length indicates the seventh larval stage, and life at the bottom of the sea. In these larvæ the vesicle has enlarged still more, its walls becoming thinner, until it covers dorsally nearly all the organ. The complication of the slender evaginations is now still greater, and anastomoses between adjacent evaginations are established at many points by a breaking through of their walls. This condition is found sparingly in the fourth larva, but in this (seventh ?) stage it is quite common.

I have no material of adolescent stages in which to follow this process, but there seems every reason to believe that it is by these evaginations, with subsequent anastomoses, that the complication of tubules in the labyrinth of the adult gland is attained, and not by any system of coiling of one or a few tubules.

I have already (p. 180) called attention to the fact that in the embryo the endsac is ventral to the ectodermic sac, whereas in the adult organ the endsac is dorsal to the mass of ectodermic tubules (labyrinth) which are developed from the ectodermic sac. How is this change of position brought about? In the first larva — as is seen in Figures 33–35 (Plate 4) and Figures 40, 44–48 (Plate 5) — the endsac lies chiefly ventral to the ectodermic sac, but also extends in part dorsad up along the lateral face of the latter. Sections of later larvæ show that the chief region of growth in the endsac is in this dorso-lateral projection, while in the ectodermic sac the chief area of growth and complication by evagination (see p. 189) is in the ventral region, by means of which it extends laterad ventral to the endsac and between it and the ventral wall of the appendage. There is, then, by this differential growth a rotation of the centre of mass of each of these parts of the organ. This rotation is around the antero-posterior axis of the gland, and, if one imagine himself viewing this from an anterior point, this rotation is clockwise in the right gland, and the reverse in the left. There is no actual twisting, but only a change in position of the centre of mass of endsac and of ectodermic sac. In the larva 18 millimetres long this process has progressed so far that the plane which separates endsac from ectodermic sac is approximately parasagittal in position. Since the antero-posterior extent of the endsac is much less than that of the ectodermic sac, the former can grow dorsad and then mediad without disturbing the stalk which connects the evaginated vesicle with the ectodermic sac, because the endsac lies entirely posterior to this stalk. This process also makes it easy to understand how it comes about that the endsac in the adult gland empties into the lateral anterior lobe of the labyrinth (see p. 164), but has no direct connection with the median anterior lobe.

I have not at my command the material to enable me to follow this process of differential growth in the adolescent stages; but as far as I have been able to examine the larvæ, the conditions found agree with the process which I have mentioned, and I believe that it is in this way that the relative position of ectodermic sac and endsac as found in the embryo comes to be reversed in the adult, where the endsac is dorsal to the ectodermic sac or labyrinth.

III. Theoretical Considerations.

A. Homology of the Antennal Glands with the Nephridia of Annelids.

Leydig ('60, p. 28) was the first to suggest that the antennal glands of Crustacea and the nephridia of Annelids performed similar duties. He, however, ascribed to both a respiratory instead of an excretory function. Since that time there has been much discussion in regard to the functional likeness of these organs in the two groups of animals. Naturally, this consideration has led to the discussion of their possibly being homologous. This discussion was inaugurated by Kowalevsky ('71). Upon grounds of analogy, and from a comparison of the structure of the adult organs, it came to be pretty generally accepted that this homology was valid. Confidence in this view was, however, shaken by the publication of Reichenbach's ('77) description of the ectodermic derivation of the antennal gland in Astacus. Kowalevsky ('71) had given proof of the mesodermic origin of the nephridia in Euaxes (p. 19) and in Lumbricus (p. 25) and had formulated the germ-layer theory, holding "that the homologies of the germ layers in different types afford a scientific basis for comparative anatomy and embryology, and must be recognized as the starting point for the proper understanding of the relationships of the types" (p. 60). So great was the influence of the germ-layer theory that the results of Reichenbach in deriving the antennal gland of Astacus entirely from the ectoderm served, for the time being, completely to check its comparison with the mesodermic nephridia of Annelids.

Grobben ('79) showed, however, that the shell gland of Moina was in part mesodermic, and thus partially restored the grounds for homologizing it with the nephridia of Annelids; but Ishikawa's ('85) evidence that the antennal gland in Atyephira is derived solely from the ectoderm, and the conclusions reached soon after in Reichenbach's ('86) memoir, — in which the ectodermic origin of the antennal gland in Astacus was described and figured in detail, — not only reaffirmed the obstacles to establishing a homology between the antennal glands and the nephridia of Annelids, but also placed in different categories the shell glands of Entomostraca and the antennal glands of Malacostraca.

The contrary conclusions reached by Kingsley ('89) in his description of the development of the antennal gland in Crangon threw some doubt upon the accuracy of the observations and interpretations of

Reichenbach, and served to restore tentatively confidence in the homology of the antennal glands of Malacostraca with the nephridia of Annelids. Since that time the idea that the antennal gland is in part mesodermic has gradually gained ground, but the question is still treated in current writings as in a degree an open one, though nearly all the text-books, following Reichenbach, state that it is entirely ectodermic in origin.

No one has repeated, as far as I know, Reichenbach's work on the development of the gland in Astacus. With the exception of the work of Boutchinsky ('95),[1] — which unfortunately is little known because of its being in Russian, — no satisfactory account of the embryology of the antennal gland in any Malacostraca has appeared since Kingsley ('89) wrote. It seems probable, in view of the agreement of Kingsley, Boutchinsky, and myself, that Reichenbach's figures and descriptions are misleading, and that he entirely failed to see the endsac. Lebedinski ('92, p. 231), however, endeavors to reconcile Reichenbach's results with those of Kingsley, and with his own on the shell gland of Eriphia, by holding that the mesodermic sheath described by Reichenbach ('86, p. 98) is homologous with the mesodermic constituent forming the endsac in Crangon and in Eriphia. I do not think that Lebedinski's point is well taken, because in Crangon, Eriphia, Gebia, and Homarus the endsac appears before the ectodermic invagination, whereas in Astacus — accepting for the moment Lebedinski's interpretation — it arises much later. Further, the mesodermic sheath described by Reichenbach is, according to his own words, only an enveloping sheath of connective-tissue elements and not at all glandular. This sheath is recognizable in Homarus, where it becomes in part the investing sheath of the gland proper and of the vesicle, and in part the tissue of the blood vessels, but has no part whatever in the formation of the secreting epithelium.

We now know that the antennal gland is of double origin — mesodermal and ectodermal — in Crangon (Kingsley), Gebia (Boutchinsky), and Homarus. These, to be sure, are all in a rather limited group, the Macrura; but it is my belief that similar conditions will be found in other Malacostraca.

The ontogenetic development of the nephridia of Annelids has received attention from many investigators since the pioneer work of Kowalevsky ('71). The stimulation to these researches in the earlier part

---

[1] The preliminary paper was published a year earlier, Boutchinsky ('94).

of the period came from the problematical nature of the organ, and to this was later added the interest occasioned by the prominent place given this system of organs in the discussion of the Annelid ancestry of Vertebrates.

Since no one has held that the endoderm takes part in the formation of the nephridia in Annelids, the organ presents three possibilities as to origin: (1) that it arises entirely from the ectoderm; (2) that it is wholly mesodermic; or (3) that both ectoderm and mesoderm contribute to its formation. The first of these possibilities has not been advocated by any one, although Wilson ('89)[1] comes very near to such an interpretation. He says (p. 423) that the nephridia "arise in connection with a continuous cell-cord of ectoblastic origin. . . . Each nephric cord terminates behind in a pair of teloblasts derived from the ectoblast. The entire nephric cord is formed by the continued divisions of these 'nephroblasts,' which agree precisely with the 'neuroblasts' in structure, action, and mode of origin." The nephridium (p. 424) is later invested by a sheath of mesoblastic cells which become the peritoneal investment. Wilson believes that the funnel and the investing cells alone arise from the mesoblast, i. e. separately from the rest of the nephridium, and his conclusions are in the main in agreement with those of Whitman ('87, p. 161) in the case of Clepsine. Wilson (p. 426) admits that, in view of the observations of Vejdovský, he cannot "deny the possibility that the glandular part *may* be differentiated from the somatic mesoblast at a very early period, fusing immediately with the cells of the nephric cord, which *may* give rise only to the end vesicle." If this be admitted, his results agree in general with those of Vejdovský (see p. 194).

The other extreme, represented by the second possibility, is reached by Bergh ('88). He finds (pp. 226, 227) in Criodrilus a single funnel-cell differentiated at the point of origin of the septum, from which is proliferated a cord of cells extending posteriorly. This is the beginning of the segmental organ, which soon becomes covered with a sheath. The external terminal part (Endstück) is in no way connected with the epidermis (p. 229), the segmental organ arising entirely from the "Hautmuskelplatte." The same condition is found by Bergh ('90, p. 501) in Lumbricus, in the development of the nephridia in which "Trichter-, Schlingen- und Endabschnitte differenziren sich aus einer einheitlichen Anlage heraus, die in den inneren Muskelplatten ohne Betheiligung der Epidermis entsteht." Bergh finds support in Lehmann's ('87, p. 348)

---

[1] I refer to his later paper only, as it includes all the essentials of the earlier (Wilson, '87) one.

statement that the epidermis takes no part in the formation of the gland, but concedes ('88, p. 229) that in certain Hirudinea the Endstück arises by an invagination of the epidermis.

The middle ground between these extremes is the position taken by Vejdovský ('84 and '92). In early stages of Rhynchelmis ('84, p. 123), on the posterior face of the dissepiment there is a large cell, from which there is proliferated posteriorly a solid cord of cells. These cells later form a double row and acquire a lumen. This becomes the glandular portion of the organ, which therefore arises from the mesoblast. The nephrostome appears independently on the anterior face of the dissepiment, and later joins the glandular portion by piercing the dissepiment. The cord of cells proliferated posteriorly from the dissepiment is met, at a later stage, by an ectoblastic invagination in the form of a solid cord. From this invagination is derived the lining of the end vesicle and the efferent duct. This ectoblastic lining is, at a subsequent period of development, surrounded by mesoblastic tissue in the form of a sheath. In his later paper ('92, pp. 339–342) he reaffirms the results of his earlier publication. This general plan of development, with slight modification of details, holds, in his opinion, for the nephridia of all Oligochæta ('84, p. 123), as also for Polychæta and Hirudinea ('92, p. 357).

Vejdovský's results are in agreement with those of Kowalevsky ('71) and Boutchinsky ('81), and in part are confirmed by the work of several other writers. It will be noticed that they do not depart widely from Bergh ('88), except in the conditions at the peripheral end.

After comparing these various papers it seems to me that Vejdovský's descriptions and figures are more convincing of accuracy of observation and reliability of interpretation than are those of the writers who adopt one or the other of the extreme views; and yet it is not permissible to disregard the work of such able investigators as Bergh and Wilson. If we except the positive statements of Bergh, which lack the corroboration of later investigators, we may conclude that the evidence goes far to show that both mesoderm and ectoderm share, though unequally, in the development of the nephridium in Annelids, and therefore that, as far as origin from germ layers is concerned, there is no insurmountable obstacle to homologizing the nephridia of Chætopod Worms with the antennal glands of Macruran Crustacea.[1]

---

[1] Postscript. — Bergh ('99) has repeated Vejdovský's work on Rhynchelmis, but disagrees with him in regard to the conditions and the interpretation to be put on them: "Nach alledem meine ich meine ursprüngliche These, dass Trichter-, Schlingen- und Endabschnitt bei den Oligochäten aus einer einheitlichen Anlage hervorgehen, auch für Rhynchelmis festhalten zu müssen" (p. 446).

Granting, then, that in the antennal glands of Macrura and in the nephridia of Chætopoda both ectoderm and mesoderm are involved, can these organs be compared part for part?

The chief point is to determine in each case the boundary between the ectodermic and mesodermic constituents in the two sets of organs. Where is this in the antennal gland of Macrura? In Homarus, as I believe I have shown, it lies where the lumina of the endsac and of the ectodermal sac (labyrinth) become confluent. Kingsley's results ('89, pp. 29, 30, Figs. 61, 74) in Crangon seem to me to be capable of the same interpretation, the mes-ectal line being at the junction of endsac and ectodermal sac (canal). Boutchinsky's ('95) results on Gebia, since they do not go beyond the earlier embryological stages, are not so precise, but I find nothing in his descriptions or figures irreconcilable with my conclusion, that the epithelium lining the endsac is also of mesodermic origin, while that lining the labyrinth is derived from the ectoderm.

There is difference of opinion as to the corresponding boundary in the nephridia of Annelids. In the permanent nephridia of Rhynchelmis, as well as all other Annelids, according to Vejdovský ('84 and '92), the lining of the efferent duct and of the contractile endsac is, as has been said, ectoblastic, whereas all the glandular part and the nephrostome are mesoblastic in origin. Wilson ('89, p. 425), as we have seen, concludes that the nephrostome and the investing peritoneal sheath of the glandular portion are alone mesoblastic, whereas the epithelium lining the glandular portion, the duct, and the end vesicle are ectoblastic, arising from the "nephric cord." Finally, Bergh ('88, p. 230, '90, p. 501) concludes that in Criodrilus and Lumbricus the entire organ is mesoblastic, there being no ectoblastic constituent whatever. Thus according to Vejdovský the mes-ectal line is at the junction of the glandular region and the efferent duct; according to Wilson it is at the base of the nephrostome, and according to Bergh the gland presents no such line.

It seems impossible to draw any satisfactory conclusion from this conflicting evidence. These differences of opinion are not solely explicable upon the assumption of differences of methods in accomplishing the result in different worms, for all of these observers have worked and based their conclusions in part upon Lumbricus. The only point of complete agreement is that the nephrostome is mesoblastic.

If it is impossible to determine so fundamental a question as where mesoblast ends and ectoblast begins, it is idle to attempt more detailed comparisons. In the present unsettled state of knowledge as regards the origin of the nephridia of Annelids, the most that can be said is, that the endsac of the antennal gland in Crustacea may be homologous with the nephrostome of the nephridium in Annelids, together with perhaps a part or all of the nephridium peripheral to the base of the nephrostome.

In some points there is considerable difference between the nephrostomic end of a nephridium in an Annelid and the endsac of an antennal gland in Macrura. The lumen of the former is usually in direct continuity with the cœlom, and is ciliated; the latter is closed and non-ciliated. After the work of Grobben ('79) on the shell gland, this question occasioned considerable discussion, and it was claimed that these differences must invalidate any proposed homology between the two organs; but later investigation has shown that the blood sinuses surrounding the endsac of the antennal gland are not homologous with the nephrostomic spaces in Annelids, and therefore the premise upon which this discussion was based is destroyed.

Eisig ('87) holds that the nephridium of Annelids has two functions: (1) the elimination of solid particles from the cœlomic spaces, a duty performed by the nephrostome and in which the cilia take an active part; and (2) the excretion of soluble products from the blood and cœlomic fluid, a function exercised by the excretory cells. If this view be correct, — and there are many things which support it, — the nephrostomic function is not directly represented in the antennal gland of Crustacea, and we therefore cannot expect close morphological resemblance. Hence it seems probable that the closed endsac, in place of an open nephrostome, does not necessarily invalidate a general homology between the two sets of organs.

B. THE NUMBER OF METAMERIC ORGANS OF THIS NATURE IN CRUSTACEA.

Thus far I have considered the glands in Crustacea from one segment only, — that of the second antenna. In Annelids the nephridia are repeated through a relatively large, although varying, number of segments. Is such metameric repetition realized in Crustacea?

Boutchinsky ('95, p. 170, Tab. VI. Fig. 145, Tab. VII. Figs. 157, 162) has described in the first maxilla of Gebia the development of a mesodermic structure which takes on the form of a tubule closely resembling the antennal gland in histological detail, inclusive of staining qualities. Only the earlier stages of this organ are described, but from this evidence the author thinks the organ is probably excretory, and that it belongs to the same series as the antennal gland.

The shell gland of the second maxillary segment has long been considered as representing an Annelid nephridium, both from its resemblance in function to that organ and from the fact that it is derived from both ectoderm and mesoderm. This gland is widely distributed in Crustacea. It is known as an adult organ, the shell gland, in many Entomostraca and some Malacostraca; moreover, an organ similar in development and appearance is found during embryonic and larval life in the basal segment of the second maxilla of certain Malacostraca, although it disappears before the adult stage is reached. As a *larval* organ the shell gland has been described in the fifth segment of Palæmonetes (Allen, '93[a]) and in some Schizopods and Decapods (Claus).

Thus in many Entomostraca and Malacostraca glands closely resembling one another are developed in both the second (antennal) and fifth (second maxillary) segments; but in some cases — chiefly Entomostraca — that of the fifth segment remains as an adult organ (shell gland), while that of the second segment atrophies. On the other hand, in most of the higher Malacostraca, it is the organ of the second segment (antennal gland) which persists in the adult, while the organ of the fifth segment, if it appears at all, degenerates before adult characters are assumed.

According to the comparative anatomical work of A. Dohrn, Claus, and Grobben, the shell gland is composed of the same parts as is the antennal gland.

The development of the shell gland in the different families of Crustacea has been treated of by several authors. It appears that the gland arises from two sources; the mesodermic part forms the endsac, the ectodermic portion the "canal." Hence it agrees in the main with the development of the antennal glands. We may therefore conclude that the antennal and shell glands in Crustacea are serially homologous organs, being similar in structure and development.

Lebedinski ('89, p. 197, Tab. III. Figs. 79–81, '90, p. 184) describes in Eriphia spinofrons the development of a "Segmentalorgan" as an evagination of the somatopleure, which becomes tubular and grows forward until it ends blindly within the base of the first maxilliped. There arises concurrently an ectodermic invagination in the wall of the coxopodite of this appendage, which meets the evagination from the somatopleure, and their lumina become continuous. We have, then, in this Crustacean a gland in the *sixth* segment, which is apparently of the same series as the antennal and shell glands.

The branchial glands of Crustacea were first noted in Crayfish, Crabs, and Paguridæ by Cuénot ('87, p. xlv), but were considered as of a lymphatic nature. In his later and more complete work Cuénot ('91, pp. 76–80) describes these glands in several Decapods as found between the two branchial blood channels (Crabs and Pagurus), or as closely investing the walls of either the efferent vessels (Palæmon), or of the afferent vessels. He still ascribes to them lymphatic functions, and makes no mention of Kowalevsky's paper, which had appeared two years before.

Kowalevsky ('89) studied these organs from a physiological point of view. He found (pp. 35–42) that by *intra vitam* injection of a one per cent solution of ammonium carminate into the body spaces of Astacus, the endsac of the antennal gland soon became red. If indigo-carmine be injected, the labyrinth becomes colored blue, but the endsac remains uncolored; and if a thorough mixture of these two pigments be used, the endsac and labyrinth rigidly select the colors. Injection of tincture of litmus gave reactions showing the endsac to be acid, the labyrinth in part alkaline and in part neutral. Palæmon yielded almost identical results, as far as regards the antennal glands, but in addition there were produced by the injection of tincture of litmus two red streaks in each gill, one on each side of the shaft. There were eight double streaks on each side of the body, viz. on the five gills and the appendages of the three maxillipeds. This coloration was caused by rows of cells in which were the same color appearances as in the cells of the endsac of the antennal glands. Further, these cells acted toward the mixture of ammonium carminate and indigo-carmine precisely as did the cells of the endsac, from which it is to be inferred that there is in each gill tissue of the same function as that of the endsac. These glandular regions are the so called branchial glands.

The purely physiological work of Kowalevsky was supplemented by Allen ('92, p. 79), who describes the structures of these glands in the gills of Palæmonetes. They are spherical and composed of conical cells, the apices of which border a central area. There are two varieties of the gland cells, somewhat different in shape and in position. Allen tentatively considers these spherical branchial glands as belonging to the series of ectodermal glands. It should, however, be noticed that, according to Cuénot and Kowalevsky these glands agree in function with the mesodermic portion of the antennal glands.

The description and figures given by Allen strongly remind one of the tegumental glands described by Herrick ('95, p. 125, Plates A and 49) from the pleopods of the female Homarus, the function of which is the secretion of the glutinous material by which the eggs are fastened to the hairs on the pleopods. Glands of the same general structure are of wide distribution in the integument in Homarus and other Crustacea, as well as in the alimentary tract. Lang ('89–'94, p. 338) says that the dermal glands of Crustacea take part in excretion.

It is still questionable whether the branchial glands are modified tegumental glands, or are segmental and therefore belong to another category. The physiological evidence points strongly to their being nephridial organs, and this is strengthened by the fact that Cuénot ('94, p. 249) has found in the branchial glands chemical products closely resembling those which, according to Marchal ('92), are found in the antennal glands. In histological structure, too, they resemble closely the endsac of the antennal gland. They possess, however, no duct to the exterior, and Cuénot suggests that the products elaborated in these glands may, without chemical change, be carried by the blood to the antennal glands there to be eliminated.

Boutchinsky ('95, p. 168, Tab. VII. Figs. 163, 164) has described the development by invagination from the ectoderm of certain glands whose ducts lead to the gill chamber. These lie in the gill cavity, commonly in the dorsal wall, and he considers them as belonging in the same series as the branchial glands. But even if these are to be classed with branchial glands, they certainly are not, like the branchial glands, homologous with the endsac of the antennal glands, but rather with its labyrinth. I believe, however, that Boutchinsky has erred in classing these with the branchial glands of Cuénot, Kowalevsky, and Allen, for they seem to me to belong rather to the category of tegumental glands.

The position of the branchial glands in the axis of the gill, and in close relation to the blood vessels, as described by Cuénot and Allen, leads one to believe them to be mesodermic rather than ectodermic structures, and with this their physiological activities are in harmony. They have no duct as far as known, and there are several of them in a single gill. If in each gill they represent a single segmental organ, this organ must be in a diffuse condition.

So far as the meagre evidence goes, it shows, in my opinion, that the branchial glands belong to the same category as the antennal and shell glands, but that they represent only the mesodermic parts (endsac) of these. It must, however, be confessed that the evidence for this conclusion is not very satisfactory. A careful examination of the development of the branchial glands will go far toward establishing or invalidating this homology. I hope soon to undertake such a study.

Kingsley ('89, p. 32, foot-note) has suggested that the genital outlets represent part of a metamerically repeated series of ducts. The female and male genital openings in Decapods, for example, occupy the bases of the eleventh and thirteenth pairs of appendages respectively; their similar position is, in Kingsley's opinion, "inexplicable upon any other ground than that the oviducts and *vasa deferentia* are themselves modifications of pre-existing metameric organs, and the only organs in the Annelids which would answer the requirements of the case are the nephridia."

The first part of his proposition is strengthened by evidence given by Bateson ('94, pp. 152–155), who found that in over three per cent of the females of Astacus fluviatilis examined, there appeared supernumerary oviducal openings. These were either bilaterally symmetrical, or on one side only, and were not necessarily situated in the segment adjacent to the normal opening, but were sometimes removed to the thirteenth segment. Dissection showed that, in cases where such supernumerary openings appeared, the oviduct was branched and communicated with all the openings, which were presumably functional. Oviducal openings were found on the eleventh (normal), twelfth, and thirteenth segments, but no such repetition of genital openings was noted in males. It is probable, then, that Kingsley's proposition that the genital ducts are members of a metameric series is valid; but whether or not they are homologous with the nephridia of Annelids is quite another question. There are in Annelids other metameric organs of somewhat similar position, of which these ducts in Crustacea might be representatives, e. g. the setigerous glands or the dorsal pores. The fact that in Annelids the genital products are in many cases carried to the exterior by the nephridia, or by modified nephridial ducts, lends support to Kingsley's contention; but we cannot rely solely upon the evidence of analogy from which to draw conclusions as to homology.

The evidence on the ontogeny of the genital ducts and their openings in Crustacea is not very complete, but in the main it points to their peripheral portions at least as being ectodermic invaginations entirely distinct from the primary reproductive organs. If this be confirmed, it will add support to the view that they are homologous with the ectodermic portion of the nephridium of Annelids; but it must be remembered that the setigerous glands of Annelids also have a similar origin.

It seems possible that these ducts may hereafter be shown to represent the ectodermic part of nephridia, while the branchial glands represent the mesodermic portion, in which event the homologs of the entire nephridium would exist in the eleventh and thirteenth segments in Decapods, though the ectodermic and mesodermic portions do not come into conjunction as in Annelids; and though, further, the mesodermic constituent is separated into several masses. Such a scheme must remain purely hypothetical until the conditions can be thoroughly studied from the standpoints of both development and comparative anatomy.

To sum up the foregoing discussions, I believe that there is sufficiently good evidence that representatives of the nephridium of Annelids are found in Crustacea in the somites bearing the second antenna (antennal gland), the second maxilla (shell gland of Entomostraca and some Malacostraca), and the first maxillipeds ("Segmentalorgan" of Lebedinski); and, further, that there is partial evidence of such representatives in the somites of the first maxilla (Boutchinsky), and in the eight thoracic somites of the maxillipeds and pereiopods of Malacostraca, namely, the branchial glands which exist in all these somites, and the genital ducts which are found in part of them.

Summary.

1. The antennal gland consists of three parts: gland proper, vesicle, and duct.
2. The gland proper consists of endsac (dorsal) and labyrinth (ventral), whose lumina are connected by a *single* small orifice, which is in the lateral anterior part of the organ.
3. The lumen of the endsac is connected with the exterior only indirectly, by way of the labyrinth.
4. The labyrinth leads into the duct by a series of converging canaliculi, which open by separate pores through the dorso-median wall of the duct. These canaliculi form the "white lobe," which projects ventrad from the median anterior region of the labyrinth.
5. The duct is short and opens through a tubercle on the ventral side of the coxopodite of the second antenna. The opening is guarded by an operculum.
6. The vesicle is a dorsal diverticulum from the duct, and has no direct connection with the gland proper.

7. The blood supply of the organ is from the antennal and sternal arteries.

8. The nerve supply is from the antennal nerve.

9. The endsac encloses a single chamber with numerous radiating outpocketings; the labyrinth is a complicated mass of anastomosing tubules, which are short and of varying calibre.

10. The epithelial cells of endsac and labyrinth are of distinctly different types, and there are no cells of an intermediate nature.

11. The cells of both endsac and labyrinth take part in the secretion. This is in large measure given off in the form of globular vesicles containing an irregular granular mass or clot; these are constricted off from the free ends of the cells.

12. The wall of the vesicle is made up of a single layer of epithelium without folds, surrounded, except on the ventral side, by a muscular sheath, which is variable in thickness. It is presumably by the contraction of this sheath that the secretion is forced out of the external orifice of the duct. Between the epithelial and muscular layers there is a vascular layer.

13. The endsac arises from the mesoderm occupying the axis of the second antenna, when the embryo is 15 to 17 days old. At first there are but one or two cells differentiated.

14. By nuclear division without corresponding formation of cell walls there is formed a *solid* multinuclear body, — a syncytium.

15. Vacuoles appear in the syncytium and probably by confluence form a single large vacuole.

16. The belated cell walls form around this vacuole, so that the vacuole becomes an intercellular space, — the lumen of the endsac.

17. The ectodermic ingrowth — which in the adult becomes the labyrinth — occurs on the median ventral face of the antenna, and appears when the embryo is 28 to 30 days old.

18. This ingrowth passes, first, proximad and then around the anterior side of the endsac; by separation of its cells a lumen is formed near its deep end.

19. The separation of cells progresses rapidly toward the exterior, which is reached by the end of the sixth week. The lumen thus formed becomes the permanent duct and the lumen of the labyrinth.

20. The lumina of the endsac (mesodermic) and of the ectodermic sac (labyrinth) do not become continuous until the embryo is 273 to 303 days old.

21. The adjacent walls of the two sacs break through at a single point. There is consequently an abrupt transition — marked by the mes-ectal line — from the mesodermal to the ectodermal part of the organ, the epithelial cells of the two parts being from the beginning of different types. This boundary persists in the adult.

22. The organ probably does not secrete until after hatching.

23. At hatching the lumen of the ectodermic sac increases greatly in size.

24. In the first larva the endsac is for the most part ventral to the ectodermic sac. The duct leads from the ventral region of the ectodermic sac to the exterior.

25. At this stage the cells of both endsac and ectodermic sac (labyrinth) show evidence of secretory activity. The lumen of the ectodermic sac alone contains a granular coagulum.

26. The epithelial cells of the ectodermic sac in the first larva have a vertically striate cuticuloid layer on the free end. Such a structure is not present in any cells of the endsac.

27. At this stage the epithelium of the duct differs from that of the ectodermic sac in having neither a striated cuticuloid layer nor striated cytoplasm, but there is a gradual transition from one kind of epithelium to the other.

28. The gland of the second larva differs from that of the first chiefly in size, which increases proportionally to the increase in the size of the larva.

29. The development of evaginations from the ectodermic sac (labyrinth) begins in the third larva. In later larvæ these evaginations increase in number and size, and form anastomoses. Thus the complications of the adult labyrinth result from evagination and anastomosis, not from the coiling of a single tubule.

30. Secretion by globules (as in the adult) begins in the third larva and increases in amount in older larvæ.

31. The vesicle first appears in the third larva, as a large, open dorsal evagination from the anterior portion of the ectodermic sac. In older larvæ it increases rapidly in volume and grows caudad.

32. During larval life the chief growth of endsac and ectodermic sac are in different directions. The result is that the two parts of the gland revolve around an approximately antero-posterior axis, so that the endsac comes to lie, as in the adult, dorsal to the ectodermic sac.

33. The conflicting evidence upon the development of the nephridium in Annelids makes it impossible closely to homologize this structure and the antennal glands of Macrura. The endsac may be homologous with the nephrostome of the nephridium of Annelids together with (*a*) none, (*b*) a part, or (*c*) all of the remainder of the organ, depending upon which is the correct view in regard to the development of the nephridium in Annelids.

34. The nephridium of Annelids is *probably* represented in Crustacea in the second (antennal) segment by the antennal gland of Malacostraca; in the fifth (second maxillary) segment by the shell gland of Entomostraca and some Malacostraca; in the sixth (first maxillipedal) segment of *some* Malacostraca by the "Segmentalorgan" of Lebedinski; it is *possibly* represented in the fourth (first maxillary) segment by the excretory organ described by Boutchinsky, and in the sixth to thirteenth (maxillipedal and pereiopodal) segments in part by the branchial glands, and in part (in the eleventh and thirteenth segments) by the genital ducts.

May 1, 1898.

BIBLIOGRAPHY.

Allen, E. J.
'92. On the Minute Structure of the Gills of Palæmonetes varians. Quart. Jour. Micr. Sci., Vol. 34, pp. 75–84, Pl. 10.

Allen, E. J.
'93. Preliminary Account of the Nephridia and Body Cavity of the Larva of Palæmonetes varians. Proc. Roy. Soc., London, Vol. 52, pp. 338–342.

Allen, E. J.
'93ᵃ. Nephridia and Body-Cavity of some Decapod Crustacea. Quart. Jour. Micr. Sci., Vol. 34, pp. 403–426, Pls. 36–38.

Bateson, W.
'94. Materials for the Study of Variation. pp. xvi + 598. London.

Bergh, R. S.
'88. Zur Bildungsgeschichte der Exkretionsorgane bei Criodrilus. Arbeit. Zool.-Zoot. Inst. Würzburg, Bd. 8, pp. 223–248, Taf. 13, 14.

Bergh, R. S.
'90. Neue Beiträge zur Embryologie der Anneliden. I. Zur Entwicklung und Differenzirung des Keimstreifens von Lumbricus. Zeitschr. f. wiss. Zool., Bd. 50, pp. 469–526, Taf. 19-21.

Bergh, R. S.
'99. Nochmals über die Entwicklung der Segmentalorgane. Zeitschr. f. wiss. Zool., Bd. 66, pp. 435–449, Taf. 30.

Boutchinsky, P.
'81. Къ вопросу о развитій дождеваго червяка (Lumbricus terrestris). [On the Question of the Development of the Earthworm (Lumbricus terrestris). Записки Новоросс. Общества Естествоиспытателей. [Mem. Soc. Nat. New-Russia.] Tome 7, Pt. 2, pp. 11–71, Tab. 1–3.

Boutchinsky, P.
'94. Zur Entwicklungsgeschichte von Gebia littoralis. Zool. Anz., Jahrg. 17, pp. 253–256.

Boutchinsky, P.
'95. Наблюденія надъ эмбріональнымъ развитіемь Malacostraca. [Observations on the Embryonic Development of Malacostraca.] Записки Новоросс. Общестба Естествоиспытателей. Mem. Soc. Nat. New-Russia.] Tome 19, Pt. 2, pp. 1–216, Tab. 1–7.

Brandt, J. F., und Ratzeburg, J. T. C.
'33. Medizinische Zoologie. 2 Bde, 4to, Berlin. Der Flusskrebs. Bd. 2, pp. 58–70, Taf. 10, 11.

Bumpus, H. C.
'91. The Embryology of the American Lobster. Jour. Morph., Vol. 5, pp. 215–262, Pls. 14–19.

Butschinsky, P. See Boutchinsky, P.

Claus, C.
'63. Ueber einige Schizopoden und niedere Malacostraken Messina's. Zeitschr. f. wiss. Zool., Bd. 13, pp. 422–454, Taf. 25–29.

Cuénot, L.
'87. Études sur le sang, son rôle et sa formation dans la série animale. Partie 2, Invertébrés. Note préliminaire. Arch. de Zool. expér. et gén., sér. 2, Tome 5, Notes et Revue, pp. xliii–xlvii.

Cuénot, L.
'91. Études sur le sang et les glandes lymphatiques dans la série animale. Partie 2, Invertébrés. Arch. de Zool. expér. et gén., sér. 2, Tome 9, pp. 13–90, 365–475, 593–670, Pls. 1–4, 15–18, 23.

Cuénot, L.
'94. Études physiologiques sur les Crustacés Décapodes. Arch. de Biol., Tome 13, pp. 245-303, Pls. 11–13.

Dohrn, A.
'70. Untersuchungen über Bau und Entwicklung der Arthropoden. 6. Zur Entwicklungsgeschichte der Panzerkrebse (Decapoda Loricata). Zeitschr. f. wiss. Zool., Bd. 20, pp. 248–271, Taf. 16.

Dohrn, H.
'61. Analecta ad historiam naturalem Astaci fluviatilis. Inaug.-Dissert., 8vo, 28 pp., Berlioni.

Eisig, H.
'87. Monographie der Capitelliden des Golfes von Neapel. Fauna und Flora des Golfes von Neapel, Mem. 16, pp. xxvii + 906, Taf. 1–37. 4to, Berlin.

Gerstaecker, A.
'95. Arthropoda: Besondere Drüsen. Bronn's Klassen und Ordnungen des Thierreiches, Bd. 5, Abth. 2, Lief. 41–43, pp. 982–1010, Taf. 97, 98.

Griffiths, A. B.
'85. On the Extraction of Uric Acid Crystals from the Green Gland of Astacus fluviatilis. Proc. Roy. Soc. London, Vol. 38, pp. 187, 188.

Grobben, C.
'79. Die Entwicklungsgeschichte der Moina rectirostris. Arbeit. Zool. Inst. Wien, Bd. 2, pp. 203–268, Taf. 11–17.
Also separate. 65 pp., 7 Taf., Wien, 1879.

Grobben, C.
'80. Die Antennendrüse der Crustaceen. Arbeit. Zool. Inst. Wien, Bd. 3, pp. 93–110, Taf. 9.

Herrick, F. H.
'95. The American Lobster: A Study of its Habits and Development. Bull. U. S. Fish Comm. for 1895, pp. 1–252, Pls. A–J and 1–54.

Ishikawa, C.
'85. On the Development of a Freshwater Macrurous Crustacean, Atyephira compressa, De Haan. Quart. Jour. Micr. Sci., Vol. 25, pp. 391–428, Pls. 25–28.

Kingsley, J. S.
'89. The Development of Crangon vulgaris. Third Paper. Bull. Essex Inst., Vol. 21, pp. 1–42, Pls. 1–3.

Kirch, J. B.
'86. Das Glykogen in den Geweben des Flusskrebses. Inaug.-Dissert. 8vo, Bonn.

Kowalevski, A.
'71. Embryologische Studien an Würmern und Arthropoden. Mém. Acad. Imp. Sci. St. Pétersbourg, sér. 7, Tome 16, No. 12, 70 pp., 12 Taf.

Kowalevsky, A.
'89. Ein Beitrag zur Kenntnis der Exkretionsorgane. Biol. Centralbl., Bd. 9, pp. 33–47, 65–76, 127, 128.

Lang, A.
'89–94. Lehrbuch der vergleichenden Anatomie der wirbellosen Thiere. xvi + iv + 1197 pp., Jena, 1888–94.

Lebedinsky, J.
'89. Наблюденія надъ резвитіемъ каменнаго краба (Eryphia spinifrons). [Observations on the Development of the Crab (Eryphia spinifrons).] Записки Новоросс. Общества Естествоиспытателей. [Mem. Soc. Nat. New-Russia.] Tome 14, Pt. 2, pp. 131–200, Tab. 1–3.

Lebedinski, J.
'90. Einige Untersuchungen über die Entwicklungsgeschichte der Seekrabben. Biol. Centralbl., Bd. 10, pp. 178–185.

Lebedinsky, J.
'91. Die Entwicklung der Daphnia aus dem Sommereie. Zool. Anz., Jahrg. 14, pp. 149–152.

Lebedinski, J.
'92. Наблюденія надъ развитіемъ каменнаго краба (Сравнительная и теоретическая частъ). [Observations on the Development of the Crab (Eryphia spinifrons). Comparative and Theoretical Part.] Записки Новоросс. Общества Естествоиспытателей. [Mem. Soc. Nat. New-Russia.] Tome 17, Pt. 1, pp. 137–256.

Lehmann, O.
'87. Beiträge zur Frage von der Homologie der Segmentalorgane und Ausführgänge der Geschlectsprodukte bei den Oligochaeten. Jena. Zeitschr., Bd. 21, pp. 322–360, Taf. 20.

Lereboullet, A.
'62. Recherches d'embryologie comparée sur le développement du brochet, de la perche, et de l'écrevisse. Mém. Acad. Sci. Inst. France (Savants étrangers), Tome 17, pp. 447–802, Pls. 1–6.

Leydig, F.
'60. Naturgeschichte der Daphniden (Crustacea Cladocera). pp. iv + 252, 10 Taf., Tübingen.

Marchal, P.
'92. Recherches anatomiques et physiologiques sur l'appareil excréteur des crustacés décapodes. Arch. de Zool. expér. et gén., sér. 2, Tome 10, pp. 57–275, Pls. 1–9.

Rathke, H.
'29. Untersuchungen über die Bildung und Entwicklung des Flusskrebses. viii + 98 pp., 5 Tab., 4to, Leipzig.

Reichenbach, H.
'77. Die Embryonalanlage und erste Entwicklung des Flusskrebses. Zeitschr. f. wiss. Zool., Bd. 29, pp. 123–196, Taf. 10–12.

Reichenbach, H.
'86. Studien zur Entwicklungsgeschichte des Flusskrebses. Abhandl. Senckenberg. Naturf. Gesellschaft, Bd. 14, Heft 1, pp. 1–137, Taf. 1–14 [19 Taf.].

Rösel von Rosenhof, A. J.
1755. Der Fluskrebs hiesiges Landes, mit seinen merkwürdigen Eigenschafften. In Der monathlich-herausgegebenen Insecten-Belustigung, Theil 3, pp. 305–350, Suppl. Tab. 54–61, Nürnberg.

Semper, C.
'61. Reisebericht (Fortsetzung) [aus Manila]. Zeitschr. f. wiss. Zool., Bd. 11, pp. 100–108.

Szigethy, K.
'85. Anatomie, Histologie und Physiologie der grünen Drüse des Astacus fluviatilis. Értekezések a Természettudományi osztály köréböl [Trans. Dept. Nat. Sci.], Bd. 14, 2 Taf. 1884.

Abstract in Math. u. Naturwiss. Berichte aus Ungarn, Bd. 3, pp. 108, 109.

Vejdovský, F.
'84. System und Morphologie der Oligochaeten. 172 pp., 16 Taf., Folio, Prag.

Vejdovský, F.
'92. Entwicklungsgeschichtliche Untersuchungen. Hefte 3 u. 4, vi + 491 pp., 32 Taf., 8vo, Prag.

Waite, F. C.
'98. Structure and Development of the Antennal Glands in Homarus americanus (Abstract). Science, Vol. 8, pp. 178, 179.

Weldon, W. F. R.
'89. The Cœlom and Nephridia of Palæmon serratus. Jour. Mar. Biol. Assoc., N. S., Vol. 1, pp. 162–168, Pls. 13–15.

Weldon, W. F. R.
'91. The Renal Organs of Certain Decapod Crustacea. Quart. Jour. Micr. Sci., Vol. 32, pp. 279–291, Pls. 21, 22.

Whitman, C. O.
'87. A Contribution to the History of the Germ-Layers in Clepsine. Jour. Morph., Vol. 1, pp. 105–182, Pls. 4–6.

Will, F., und v. Gorup-Besanez, E.
'48. Guanin ein wesentlicher Bestandtheil gewissen Secrete wirbelloser Thiere. Gelehrte Anz. d. kön. bayer. Akad. Wiss., Bd. 27, No. 233, col. 825–828.

Wilson, E. B.
'87. The Germ-Bands of Lumbricus. Jour. Morph., Vol. 1, pp. 183–192, Pl. 7.

Wilson, E. B.
'89. The Embryology of the Earthworm. Jour. Morph., Vol. 3, pp. 387–462, Pls. 16–22.

EXPLANATION OF PLATES.

All figures were outlined with the camera lucida.
The orientation of figures is given for each plate separately.

ABBREVIATIONS.

art. sac.	Sacculary artery.
at. 1.	First antenna.
at. 2.	Second antenna.
cl. lby.	Cells of the labyrinth.
cl. sac. trm.	Cells of the endsac.
cœl.	Body cavity.
cry.	Crystals.
cta.	Cuticula.
drm.	Dermis.
ec'drm.	Ectoderm.
evag.	Evagination.
fas. ax.	Axillar bundle.
fos.	Depression.
glb.	Globule.
gl. e'drm.	Tegumental gland.
gn. opt.	Optic ganglion.
gn. su'œ.	Superœsophageal ganglion.
hi.	Hilum.
i'vag. ec'drm.	Ectodermic invagination.
lac. sng.	Blood lacunæ.
la. cx.	Non-pigmented calcified layer of the shell.
la. cx'.	Pigmented calcified layer of the shell.
la. e'th.	Epithelial layer.
la. mu.	Muscular layer.
lby.	Labyrinth.
lig.	Ligament.
ln. mes-ec.	Mes-ectal line.
lob. l-a.	Lateral anterior lobe.

lob. m-a.	Median anterior lobe.
lob. p.	Posterior lobe.
lu.	Lumen.
marg.	Border.
mb. ba.	Basement membrane.
md.	Mandible.
ms'drm.	Mesoderm.
mu.	Muscle.
mx. 1.	First maxilla.
oc.	Eye.
of. ex.	External orifice.
of. i.	Internal orifice.
op.	Operculum.
par. cl.	Cell wall.
par. vs.	Wall of vesicle.
sac. ec'drm.	Ectodermic sac.
sac. trm.	Endsac.
set. sns.	Sensory hairs.
tis. con't.	Connective tissue.
vac.	Vacuole.
vas. sng.	Blood vessel.
vlv.	Valve-like fold.
a.	In Fig. 2, marks junction of walls of endsac and labyrinth; in Figs. 47, 49, marks region of communication between lumina of endsac and ectodermic sac.

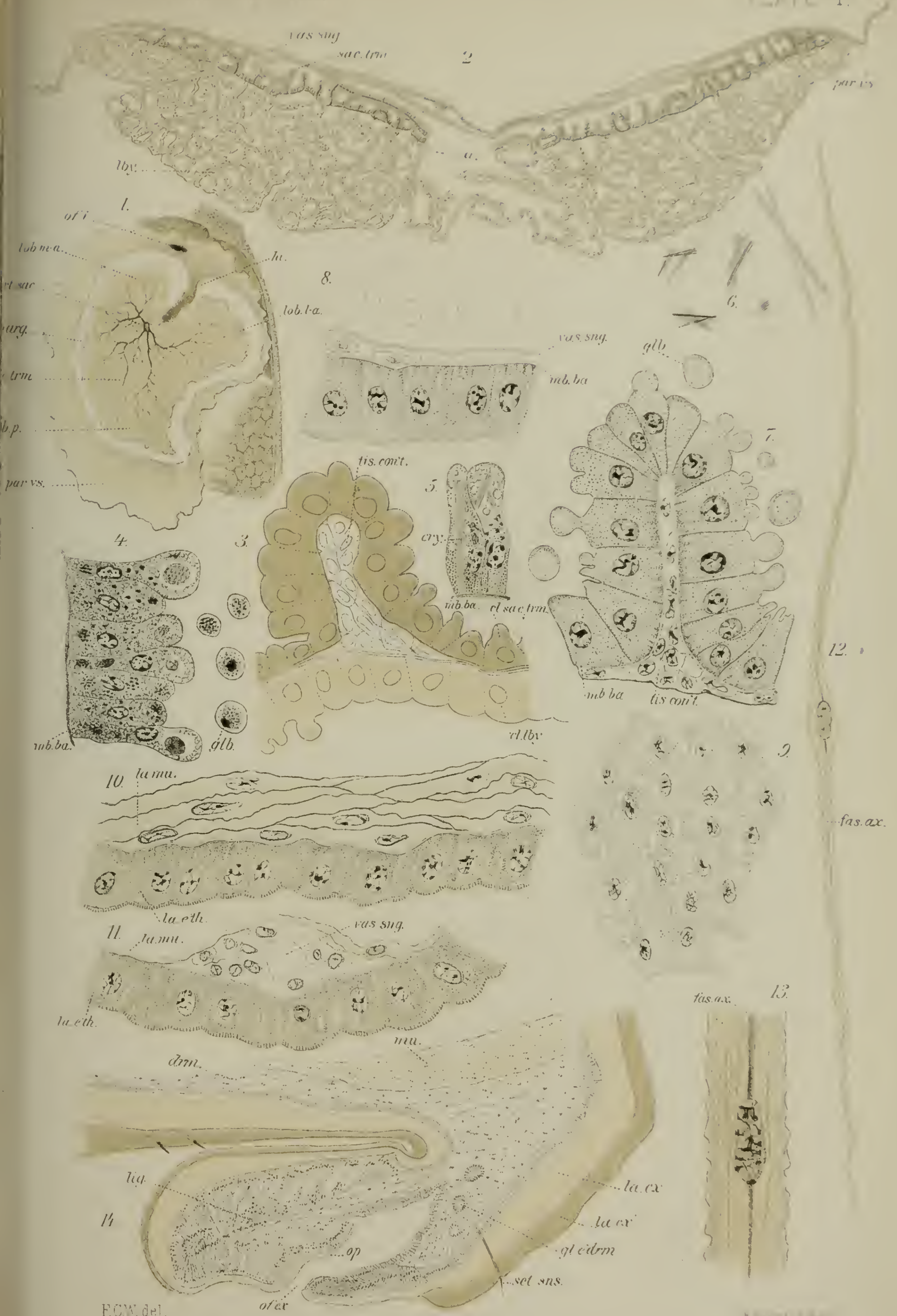
PLATE 1.

(In Fig. 1 anterior is up on the plate ; in Fig. 2 the dorsal edge of section is up ; in Fig. 14 the ventral edge of section is down, the posterior edge to the right.)

Fig. 1. Dorsal view of right gland of adult with greater part of vesicle removed. × 2. (Drawn by Mr. K. Hayashi.)
Fig. 2. Anterior face of a transverse section through left gland of adult about $\frac{1}{2}$ mm. posterior to hilus. × 14.
Fig. 3. Section of a fold in the floor of the endsac, together with adjacent walls of labyrinth tubule. × 350.
Fig. 4. Cells, showing globules, from wall of endsac. × 410.
Fig. 5. Cells, containing crystals (see Fig. 6), from wall of endsac. × 410.
Fig. 6. Crystals (probably artifacts, see p. 164 of text), from cells of endsac wall. × 410.
Fig. 7. Section of fold in wall of a labyrinth tubule showing formation of globules. × 410.
Fig. 8. Section of wall of labyrinth tubule showing striate cuticula of epithelial cells. × 410.
Fig. 9. Surface view of epithelium from posterior region of vesicle. × 410.
Fig. 10. Transverse section of wall of vesicle through a region where muscular layer is thick. The muscle cells are cut obliquely. × 410.
Fig. 11. Transverse section of wall of vesicle through a region where muscular layer is thin. × 410.
Fig. 12. A single muscle cell teased from wall of vesicle. × 410.
Fig. 13. Region of nucleus from a cell similar to that of Figure 12. × 900.
Fig. 14. Lateral face of a proximo-distal section through left second antenna in the region of the tubercle on which the duct opens. × 27.

WAITE: ANTENNAL GLANDS

PLATE 1.



F.C.W. del.

PLATE 2.

(In Figs. 15–17 anterior is up on the plate; in Figs. 18–24 (except 23) dorsal is up; in Fig. 23 lateral is up; in Figs. 18, 20, 22, 24, anterior is to the right; in Figs. 19, 21, 23, anterior is to the left; in Fig. 25 mediad is to the right. In Figs. 18–25 the mesoderm is distinguished by the darker shade.)

Fig. 15. Ventral view of an embryo 15–17 days after extrusion of egg. × 72.

Fig. 16. Similar view of an embryo 16–18 days after extrusion of egg (stage at which gland first appears). × 72.

Fig. 17. Similar view of an embryo 23–25 days after extrusion of egg. × 72.

Fig. 18. Part of parasagittal section through second antenna of embryo 15–17 days old, showing undifferentiated mesoderm in axis of antenna. × 410.

Fig. 19. Similar section of embryo 16 to 18 days old (Fig. 16), showing (in the mesoderm) first differentiation of endsac with two nuclei. × 410.

Figs. 20–22. Parasagittal sections through antenna at slightly more advanced stages. (Fig. 20 is youngest, Fig. 22 oldest.) × 410.

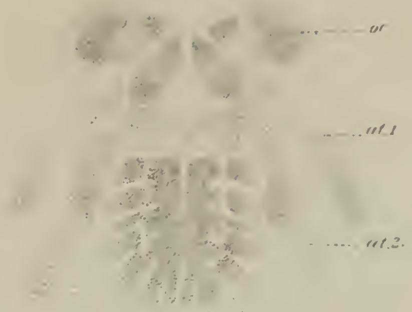
Fig. 23. Section inclined slightly to the frontal plane at a stage when the endsac is ovate in form and contains in all 12 nuclei. × 410.

Fig. 24. Parasagittal section through antenna in which a vacuole appears in the endsac. × 410.

Fig. 25. Anterior face of a transverse section through right antenna at stage when invagination of ectoderm first begins. (Embryo 28–30 days old.) × 410.

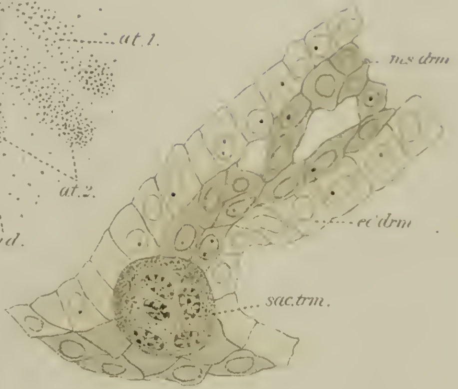
16.

17

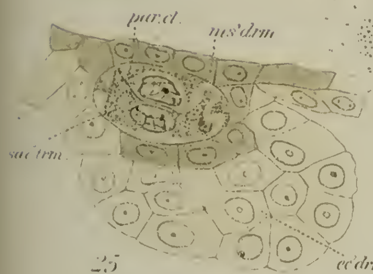


15.

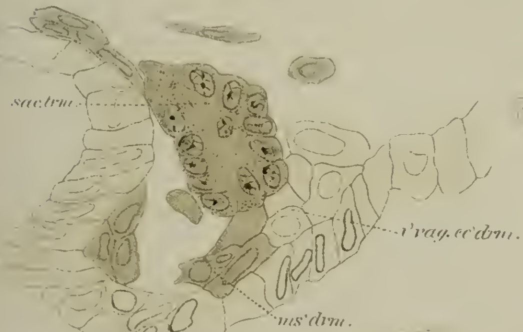
23.



19.



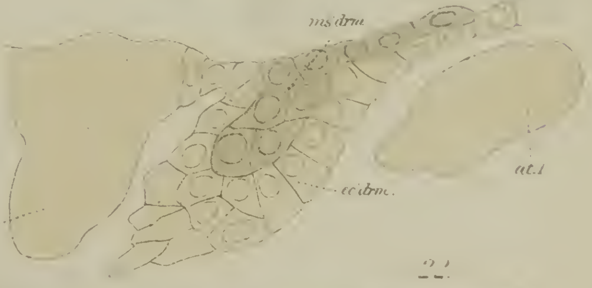
25



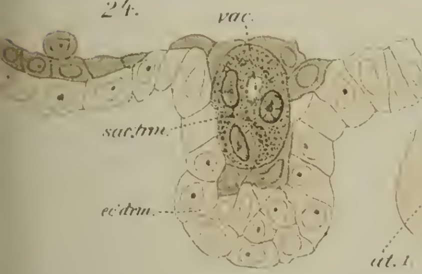
21

20.

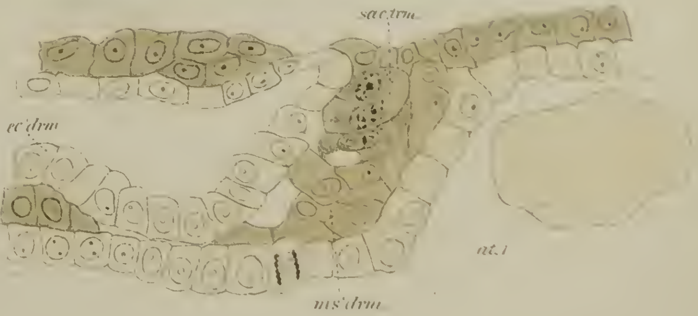
18



24.



22.



F.C.W. del.

PLATE 3.

(Dorsal is up on the plate in all figures. In Figs. 26, 27, 28, 30, anterior is to the right; in Figs. 29, 31, median is to the right. Mesoderm is distinguished by the darker shade.)

Fig. 26. Lateral face of a parasagittal section through left antenna of embryo, showing vacuolation in the endsac and the path of the ectodermic invagination. The invaginated cells in Figs. 26, 27, are more deeply shaded than the rest of the ectoderm. × 410.

Fig. 27. Similar section in slightly older embryo, showing expansion at deep end of ectodermic invagination, and a lumen formed in the endsac. × 410.

Fig. 28. Similar section in embryo about 35 days old, showing position of future lumen of ectodermic sac. × 410.

Fig. 29. Anterior face of transverse section through right antenna of an embryo about 40 days old, showing lumina of endsac and ectodermic sac and duct to exterior. × 410.

Fig. 30. Lateral face of a parasagittal section through left antenna of embryo 60–70 days old, showing growth of ectodermic invagination around the endsac. × 410.

Fig. 31. Anterior face of transverse section through right antenna of embryo 3 to 4 months old, showing extension of ectodermic invagination. × 410.


ec'drm
ms'drm.
31.
sac.trm.
gn.su'oe.
sac.ec'drm.
mu.
of.ex.
sac.trm.
27.
lu
i vag.ec'drm
26.
vac.
sac.trm.
fos.
i vag.ec'drm
i vag.ec'drm.
30.
sac.trm.
mu.
lig
mu.
lig.
i vag.ec'drm
lu
sac.trm.
sac.trm.
lu
ms'drm.
of.ex.
29.
i vag.ec'drm
ms'drm
28.

F.C.W. del.

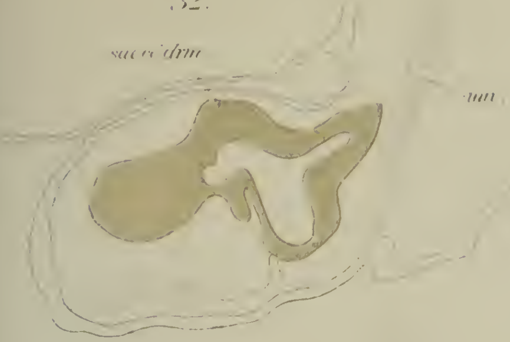
PLATE 4.

(Dorsal is up on plate in all figures. In Figs. 32–38 anterior is to the left; in Fig. 39 anterior is to the right.)

Fig. 32–38. Lateral face of the second, third, fifth, sixth, eighth, eleventh, and twelfth sections respectively from a series of thirteen parasagittal sections through the left antennal gland of the first larva. × 128.

Fig. 39. Median face of a nearly parasagittal section through the left gland and duct of the first larva. × 128.

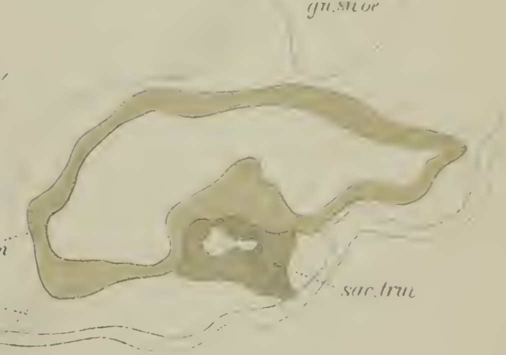
32.



33.

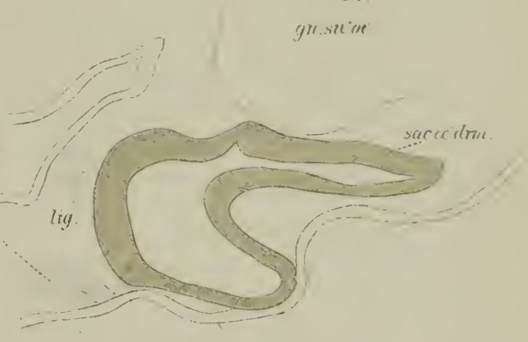
34.

35.



36.

37.



38.

39

F.C.W. del.

PLATE 5.

(Dorsal is up on all figures. Median is to the right in Figs. 41–48.)

Fig. 40. Anterior face of a transverse section through the region of the base of the second antennæ in the first larva. (The dorso-ventral axis has been slightly shortened in cutting.) × 42.

Fig. 41–48. Anterior face of the third, fifth, seventh, ninth, tenth, twelfth, fourteenth, and seventeenth sections respectively from a series through the right antennal gland of the first larva. × 128.

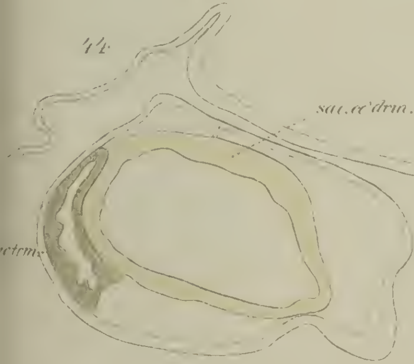
40.

41.

42

43.

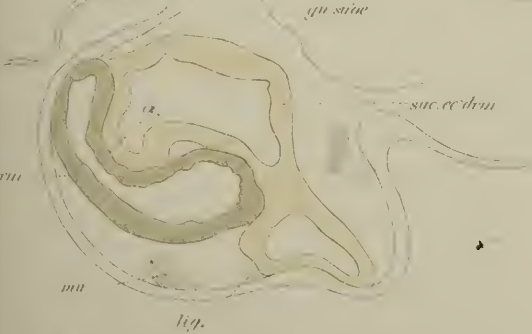
44.



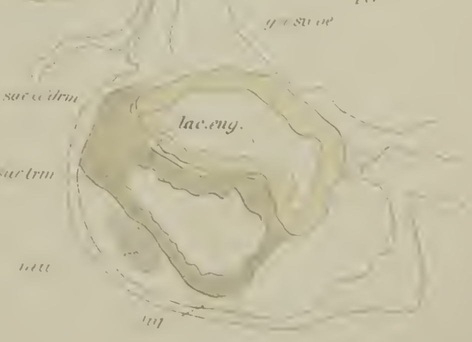
45.

46

47



48



F. W. del.

[illegible]

PLATE 6.

(In Fig. 49 anterior is up, lateral to the right; in Figs. 50, 51, 60, dorsal is up; in Figs. 50, 60, anterior is to the right; in Fig. 51 anterior is to the left.)

Fig. 49. Dorsal face of a frontal section (the tenth of a series of eighteen) through the right antennal gland. × 128.

Fig. 50. Lateral face of a parasagittal section through right gland and duct in the third larva. × 128.

Fig. 51. Parasagittal section through the orifice connecting the lumina of endsac and ectodermic sac in the first larva. × 350.

Fig. 52. Cell from section of wall of endsac of the first larva in a region not adjacent to the ectodermic sac. × 900.

Fig. 53. Cells from section of wall of endsac in the first larva in a region adjacent to the ectodermic sac. × 900.

Fig. 54. Cells from section of dorso-lateral wall of ectodermic sac in first larva. × 900.

Fig. 55. Cells from section of ventral wall of ectodermic sac in first larva. × 900.

Fig. 56. Cells from section of dorso-median wall of ectodermic sac in first larva. × 900.

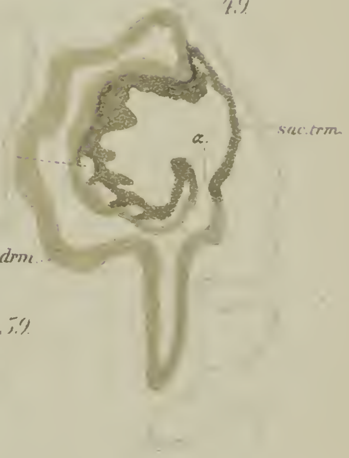
Fig. 57. Cells from section of dorsal wall of ectodermic sac in first larva, one showing mitotic figures. × 900.

Fig. 58. Cell from section of dorsal wall of ectodermic sac in first larva. × 1600.

Fig. 59. Blood corpuscle from blood lacunæ of antennal gland in first larva. × 900.

Fig. 60. Longitudinal section of duct of the antennal gland in first larva. × 350.


evag
50.
lig
lac.sng.
sac.ec'drm.
lig
sac.trm.
mu
of.ex


49.
lac.sng.
a.
sac.trm.
sac.ec'drm.

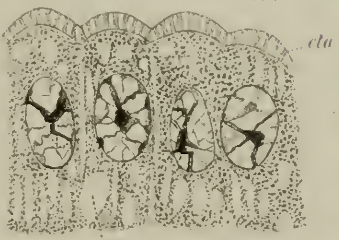

57.
cta.

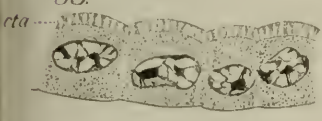

58.
cta.
mb.ba.

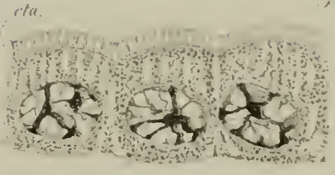

53.


52.


59.


56.
cta
vac


55.
cta


54
cta.


coel.
coel.
60.
of.ex.


lac.sng
51
ch.
lumen ce

F.C.W. del.

No. 8. — *Maturation and Fertilization in Pulmonate Gasteropods.*[1]

By Henry R. Linville.

CONTENTS.

INTRODUCTION.

In the Autumn of 1896 I undertook this investigation at the suggestion of my teacher, Professor Mark, to whom I am under many obligations for helpful suggestions and criticisms.

In the beginning my plan was to study the maturation and fertilization of Limax maximus L. and Limax agrestis Müller, but owing to ill fortune and inexperience I was unable to preserve a sufficient amount of properly prepared material of the desired stages, and consequently I have been obliged to supplement my work with the results obtained

---

[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College, under the direction of E. L. Mark, No. 109.

from a study of two species of Limnæa. The results on Limnæa to some extent repeat the most excellent work by Kostanecki und Wierzejski ('96) on Physa, a near relative of Limnæa. However, additional points of interest in regard to chemical phases in the centrosome, together with some facts concerning reduction division in the second maturation spindle, make this something more than a mere repetition of their work.

Since the publication of Professor Mark's monograph on Limax campestris, in 1881, the technique of embryology has been so much developed that a re-investigation of the maturation and fertilization of this genus of pulmonates with special attention to the history of the centrosome seemed likely to yield interesting and important results. The incompleteness of my series of stages in Limax material will, however, necessitate further work on this genus, which I hope to complete at some time in the near future.

By each addition to the already great mass of cytological literature, it becomes more apparent that if the centrosome is a permanent organ of the cell, it is an organ which goes through various and complicated phases. Certain facts impel us to believe that there is a variation in the chemical condition of the centrosome. For example, in some preparations, at a certain stage of maturation, there is no centrosome (nor centriole) to be distinguished as a deeply staining body at the poles of a perfectly formed spindle, whereas in other preparations at apparently the same stage and treated in the same manner, one may observe centrosomes which are deeply stained and of enormous size in comparison with the volume of the cell. This great variation of the centrosome is, however, not inconsistent with the idea of its permanence in the first maturation spindle, where the astral rays always indicate its presence. When, however, no astral rays are visible, the difficulties in the way of identifying the centrosome are exceedingly great, so great in fact as to render it well-nigh impossible to distinguish it from the yolk granules.

Collection of Material.

I have collected and preserved eggs of Limax agrestis, Limax maximus, and of two species of Limnæa. Limax maximus lays in the vicinity of Cambridge, Mass., during October, November, and December. Limax agrestis begins laying in early summer, and may, under especially favorable circumstances, continue to lay late into the winter. The eggs of

Limax maximus may be found in the vicinity of Cambridge in damp, protected places, under rotting wood, or under waste lumber and straw, and especially about greenhouses, where these slugs, and also Limax agrestis, are found most abundantly. The eggs of Limax maximus are not covered with earth, as are those of Limax agrestis. It is seldom that one finds the eggs of Limax agrestis lying exposed on the surface of the ground. Limax maximus in captivity apparently lays its eggs wherever it happens to be; sometimes on the bare side of the box or can in which it is confined; at other times under a piece of rotting wood or other protection. Limax agrestis, on the other hand, almost invariably bores into the loose soil in the box, sometimes nearly an inch, and lays its eggs in a single heap. Its eggs do not cohere as do those of Limax maximus.

In general, early morning is the time when eggs are laid by both species of Limax, although the laying may take place at any time of the day or night. The duration of the time of laying is not great. No continuous observations of the time consumed in laying were made, because of the desirability of getting eggs in as early stages as possible, the animal being killed as soon after the beginning of laying as possible. Considering the time required to extrude several eggs one after another, however, it does not seem likely that more than thirty minutes would be required to complete the extrusion of the largest number deposited at a single laying.

About the 15th of March, 1897, I collected a large number of Limnæa elodes Say, one of the common pond snails. Many pairs were found in the act of copulation. In the course of two days eggs were laid in the aquarium in great abundance. These snails can be stimulated to lay simply by supplying plenty of fresh water and keeping the vessels free from any decaying matter. Laying usually takes place early in the morning, but a sudden change from impure water to pure water will cause them to lay at any time of day.

Technique.

The eggs of Limax were taken either just after laying or from the sexual organs before being laid. The latter were obtained from the uterus, from the albumen gland, or from the oviduct. The eggs just deposited and those abstracted from the uterus, where they lie one after another ready to pass to the exterior, were "shelled," freed from the albumen and fixed. The albumen gland and the oviduct of individuals which had begun to lay were sectioned; eggs were found in both of these regions.

In freeing the egg cell from the shell and the albumen, I have found the best method to be the one recommended by Kofoid ('95). This consists in placing the eggs, a few at a time, in a watch glass containing normal salt solution, care being taken not to let any eggs remain in the solution longer than ten or fifteen minutes. Taking an egg carefully in a pair of fine forceps, one can either snip the membrane with a pair of sharp-pointed scissors, or, with the aid of a sharp needle, rend it by catching it between one arm of the forceps and the needle. After the egg has escaped through the opening in the egg-shell, the albumen can be washed away from it by a gentle current produced by a pipette. As soon as the eggs are free from albumen they are transferred to the fixing solution. Sometimes I have thrown the entire egg, without shelling it, into the fixing solution, and have subsequently removed the membrane and as much of the albumen as could be taken away with safety to the yolk. The egg membrane must be removed within a short time after the egg has been thrown into the fixing fluid, because otherwise it becomes too hard to be cut successfully. Eggs that have been killed (fixed) without shelling, then washed to remove the killing agent, and dehydrated in alcohol, may be returned through weaker grades of alcohol to water for the purpose of shelling and removing all but a small portion of the surrounding albumen; but far better conditions of yolk and cytoplasm were obtained by removing the albumen from the egg as soon after killing as possible, and usually the result was better still, if the egg was freed from albumen before it was killed. The latter, indeed, is the best of all methods for Limax, but in the case of the eggs of Limnæa, which are quite small, much time can be saved, and apparently quite as good results obtained, by thoroughly fixing the eggs before shelling, providing the egg-shell is removed before the albumen has had time to harden.

For killing and fixing, the following solutions were used: Saturated aqueous solution of corrosive sublimate with 3 per cent to 5 per cent acetic acid, Flemming's fluid, Perenyi's fluid, and three of the mixtures employed by Kostanecki und Siedlecki, viz. (I) a mixture consisting of saturated aqueous solution of corrosive sublimate one part, 3 per cent nitric acid one part, absolute alcohol one part; (II) a solution similar to the last in which acetic acid is substituted for the nitric acid; and (III) a simple 3 per cent solution of nitric acid. Sublimate-acetic is well known for its good preservation of cytoplasmic structures. Flemming's fluid has no advantage over other methods, and has the decided disadvantage of causing very great brittleness. Series of sections, even after being mounted and subsequent to the hardening of the balsam, frequently break into small bits under very slight pressure. Perenyi's fluid was used much more successfully. The excessive brittleness noticed in the Flemming preparations was not present in those made with this mixture; moreover, with Perenyi's fluid nuclear structures were well preserved, and when stained the elements came out clearly. Cytoplasmic structures, including the astral rays, were in most cases sharply marked. The methods proposed by Kostanecki und Siedlecki were not tried with Limax material. In the eggs of Limnæa the nuclear and the cytoplasmic structures were preserved very well by the three methods of Kostanecki und Siedlecki; of the three, the 3 per cent nitric acid solution gave the best results, the preservation by this method being exceptionally good.

Heidenhain's iron-hæmatoxylin was used exclusively in staining. Slides with sections affixed were immersed in the 2 per cent iron-alum mordant for a period varying from three to twelve hours, and after washing in a gentle current of tap water for several minutes, were placed in the ½ per cent aqueous solution of hæmatoxylin and left for periods varying from eighteen to forty-eight hours. A 2 per cent iron-alum solution was used for decolorizing, the process being carefully watched by frequent examination under a low power of the microscope. In most cases the yolk could be decolorized sufficiently to disclose the centrosomes, for example, without decolorizing the centrosomes themselves.

A. MATURATION.

I. General Account.

1. Limax Eggs in the Oviduct.

My study of the eggs of Limax as they occur in the hermaphrodite gland has been very limited. As far as the position of the nucleus in such eggs is evidence, I cannot discover that the egg has any pre-established axis, the nucleus being always central.

The earliest observed stage in the first maturation spindle was seen in eggs found in the oviduct and apparently not long freed from the hermaphrodite gland. Indeed, judging from the proximity of these eggs to the hermaphrodite gland, it seems highly probable that changes leading to the formation of the first maturation spindle begin before the egg is set free from that organ. The least developed of the eggs found in the oviduct showed the first maturation spindle already established, and nearly the whole of the germinative vesicle involved in the spindle.

2. Limax Eggs in the Albumen Gland.

I found a few eggs in the albumen gland imbedded in a small mass of albumen; there was no trace of an egg membrane. In these eggs the first maturation spindle was in every case completely formed and lying near the middle of the egg. There was no indication of the presence of a spermatozoön in the eggs found either in the oviduct or in the albumen gland.

3. Limax Eggs in the Uterus.

In the uterus of Limax agrestis I found a few eggs in which the first maturation spindle had not yet begun to move toward the periphery. The earliest stage of the eggs of Limax maximus secured was found in the uterus, no eggs of this species having been obtained either in the oviduct or in the albumen gland. In these (L. maximus) eggs the first maturation spindle was eccentric in position, the centre of one centrosphere being near the periphery of the egg. Uterine eggs were kept separate from eggs already laid, and likewise from eggs obtained from the oviduct or the albumen gland, but no note was taken of the exact location of eggs in the uterus, whether they were nearer the albumen gland or the external opening of the uterus.

The eggs of Limax maximus found in the uterus ranged from a stage in which one centrosphere of the first maturation spindle was nearly peripheral in position to a stage in which the first polar cell was completely formed. Since these eggs were found in the uterus of an animal killed while engaged in laying, one is safe in assuming that the earliest stage likely to be found in an egg of Limax maximus already laid is one in which the first polar cell has been formed. Unfortunately, not a sufficient number of eggs of Limax agrestis were preserved to furnish any definite notion of the earliest and latest stages to be found in the uterus of this species. In the few eggs from the uterus that were sectioned and examined, the first maturation spindle was nearly central.

The earliest indication of a spermatozoön within the egg was noted in uterine eggs. The fact that in some cases (L. agrestis) the head of the spermatozoön was still attached to the filament indicates that penetration had taken place only a very short time before fixation by the killing fluid. In sections of the oldest uterine eggs from Limax maximus (first polar cell completely formed) the head of the spermatozoön — still a single, oval, homogeneous, and slightly swollen body — lies near the centre of the egg, its long axis being directed more or less definitely toward the egg-aster.

4. Eggs of Limnæa.

All the material of Limnæa elodes was obtained from eggs already laid. In the earliest stages thus secured, the first maturation spindle had begun to move from the centre of the egg. In only one instance (Plate 1, Figure 2) have I seen distinct remnants of the germinative vesicle.

II. Centrosome and Centrosphere.

Recent investigation of the nature of the centrosome and the centrosphere has thrown considerable light on the variable nature of these structures. The *centrosphere* cannot at present be considered a permanent structure, but merely a temporary manifestation of an unknown force. As long as the centrosphere appeared to be the region of the beginning of the astral rays, there was good reason for assigning to it a considerable degree of importance. In the light of the recent work on Physa by Kostanecki und Wierzejski ('96), and on Ascaris by Kostanecki und Siedlecki ('96), however, the centrosphere becomes of less significance. They find that the astral rays extend into the centrosphere and even to the centrosome itself. The centrosphere, according to these authors, with whom I agree, is formed merely by a thickening of the rays. Wilson ('96, p. 234) calls attention to the concentric rings of microsomes on the astral rays in the spermatogonium of Salamandra as seen by Drüner, and says that the innermost two rings, being especially prominent, mark off a centrosphere composed of a medullary and a cortical zone. Another case in point which Wilson discusses is that of the rings of microsomes found by Heidenhain in leucocyte asters. The condition shown in leucocytes, with the astral rays beginning at the centrosome (the ultimate structure at the centre), tallies well with what Kostanecki und Wierzejski found in the egg of Physa. If the centrosphere is to be taken out of the category of the permanent organs of the cell, it nevertheless represents a condition in the chemical and physical phases of the cell which is worthy of further investigation.

In the introduction to this paper, I have referred to the variable size and condition of the *centrosome*. This is so intimately connected with the variation in the centrosphere as to render it advisable, and even necessary, to discuss the two structures together. I shall first take up the results obtained from the study of the maturation of Limax maximus, and then follow with a more complete account of the history of the centrosome and centrosphere in Limnæa elodes.

1. Limax.

(*a*) *First Maturation Spindle.*

The earliest stage of the egg of Limax maximus that I have found is one showing the first maturation spindle fully formed (not figured; compare with next older stage, Plate **3**, Figure 16). The spindle, with all the chromosomes in the telophase, has moved half the length of the egg radius toward the animal pole. At either end of the spindle is to be seen a large distinct centrosphere, composed of a central, pale, reticulated area, and a very thick wall. The wall is nearly one third as thick as the diameter of the whole sphere. Figure 16 represents a later stage, but does not differ essentially from the earlier one as far as the condition of the centrosphere is concerned. Careful examination of the centrosphere in both shows that the very fine reticulum of the clear region at the centre is, to all appearances, continuous with the more compact reticulum composing the wall. The astral rays emerge from the outer portion of this wall, but, because of the density of the substance composing the wall, it is impossible to say whether or not the central reticulum is continuous through the wall of the centrosphere with the astral fibres. The thickened wall of the centrosphere and the fine central reticulum are not occasional phenomena, but are present in every first maturation spindle in Limax maximus up to the stage represented in Plate **3**, Figure 16. *The most thorough search through specimens fixed by different methods and stained for varying lengths of time has failed to reveal any trace of a centrosome in the kind of centrosphere just described.* Between the stage represented in Plate **3**, Figure 16, and the one represented in Plate **3**, Figures 17 and 21, is a gap in the condition of the centrosome which I am not able to bridge over by intermediate stages. However, the stages are not so far apart that the changes through which the centrosphere would pass may not be fairly inferred.

Whatever the influence that causes the condition of the centrosphere, it is clear that the process is one of increase in volume of the central finely reticulated area. Figures 17 and 21 are particularly instructive in this regard. In each two centrosomes have made their appearance.

In addition to the fact that in Figure 21 the centrosomes have moved further apart than in Figure 17, the more completely fused condition of the elements composing the "Zwischenkörper" in Figure 21 gives conclusive evidence that it has progressed in development further than Figure 17. I have not been able to follow closely the fate of this central reticulated area after the stage represented in Figure 21.

It will be noticed that in Figure 17 the long diameter of the centrosphere is nearly coincident with the chief axis of the egg, and likewise with a line connecting the two minute centrosomes. In Figure 21, on the contrary, the long diameter of the centrosphere is nearly perpendicular to the chief axis of the egg, and forms a very sharp angle with the line connecting the two small centrosomes. This relation of centrosphere-axis with centrosomes suggests a causal connection, but when compared with the position of the centrosomes in Plate 3, Figure 22, it seems probable that the reason for the variation in the direction of the long axis of the centrosphere, as compared with the chief axis of the egg, in these three cases must be sought in something else than the position of the centrosomes.

Before turning to the consideration of the centrosome, it will be interesting to call attention to the astral rays of Figure 17. Here one set of the astral rays begins at the centrosphere and extends two thirds of the way to the vegetative pole, while another set is composed of very short rays scattered among the long rays. Beginning near the distal end of the long rays and continuing in the same general direction to the periphery of the egg are rather broad, indistinct band-like radiations (unfortunately not well reproduced from the drawing). On examination with a one-twelfth inch immersion lens, the bands were found to be composed of exceedingly fine granules, different from the ordinary yolk granules, and distinct also from the "microsomes" which are visible among the long astral rays. The same faint bands appeared in other eggs of the same stages as those shown in Figures 17 and 21.

There is a point concerning the astral rays in Figure 21, to which I wish to call particular attention, since it may serve to throw new light on the question of the centrosphere. Beginning at the periphery of the central finely reticulated area, the rays extend outward a short distance as a set of extremely fine fibres, then suddenly become thicker, and retain this condition to their peripheral ends. I cannot demonstrate any ring of microsomes at the region of transition from the finer to the coarser fibres, but nevertheless the zone embracing the finer rays is a distinct modification of the aster, and is of interest because of its bearing on the question of the limits of the centrosphere. Other instances of this phenomenon will be referred to further on.

It will be remembered that no centrosome, as that structure is generally understood, is to be made out in connection with the first maturation spindle of Limax maximus. After the formation of the first polar cell, however, we have (in Figures 17 and 21) within the centrosphere the centrosome already divided, presumably in preparation for the formation of the second maturation spindle. In Figure 17 the centrosomes are extremely small, and only one of them gives indication, even with the best immersion lens, of having rays in connection with it, but in Figure 21 the small dense bodies have all the characteristics of centrosomes. Although the centrosomes in Figure 21 are very minute, they may still be made out with certainty at points from which several very delicate rays diverge. These rays may have some connection with rays outside the reticulated area, but if they do, it is only a secondary connection. The rays extending from either centrosome toward the other have united into a very small but fairly distinct spindle (not well shown in the figure).

(*b*) *Second Maturation Spindle.*

My study of Limax maximus points to the conclusion that after the formation of the first polar cell, and possibly during that process, the centrosphere remaining in the egg increases in size to many times the volume it had in the first maturation spindle. Neither after the formation of the first polar cell, nor after the formation of the second, have I been able to trace *continuously* the modification of the centrosphere. In Figure 20, however, the periphery of the centrosphere is very faint; and it seems as if the whole structure were on the verge of disappearance. In a subsequent part of this paper I shall take up the discussion of the fate of the inner centrosphere and also the centrosome of the second maturation spindle.

2. Limnæa Elodes.

(*a*) *First Maturation Spindle.*

My observations on the first maturation spindle of Limnæa elodes have resulted in a number of interesting facts bearing on the relation of centrosphere to centrosome. As stated in the introduction, the centrosome sometimes appears stained faintly, sometimes very deeply. When deeply stained, it varies in size from an extremely small body to one of the size of the centrosphere itself. The existence of the latter extreme affords strong reason for believing that the entire centrosphere may become stained, for, by a proper serial arrangement of several preparations, one can see that the clear region of the centrosphere surrounding the centrosome is gradually encroached upon by the centrifugal advance of the stainable region, until the entire centrosphere is deeply and homogeneously stained. It is quite possible that the cases of faintly stained centrosomes may be due either to understanding, or, what is more probable, to protracted decolorizing.

In taking up the detailed description of the maturation spindles, I shall follow the order indicated in the discussion of the same structures in Limax maximus; that is, I shall begin with the earliest stage in the first maturation spindle. It will be remembered that in Limax maximus the earliest stage obtained was one in which the condition of the chromosomes of the first maturation spindle already indicated the telophase. That was a uterine egg.

All the eggs of Limnæa elodes were taken after being laid. The earliest stage obtained was that shown in Plate **1**, Figure 2.[1] The spindle is fully formed; it surrounds the disintegrating germinative vesicle, and already has a radial, though deep, position. At either pole of the spindle is a well-developed aster, at the centre of which appears a mass of minute granules, stained yellowish-brown. In the midst of this mass it is possible with an immersion lens to distinguish a very small and faint centrosphere, containing an extremely small centrosome (not to be seen in the drawing). The inner aster is curiously modified by the sperm aster, a phenomenon to which I shall refer later on.

A stage in the egg of Limax agrestis, similar to this, is shown in Plate **3**, Figure 14. In this case the germinative vesicle, judging from the rather uneven arrangement of the chromosomes, has just disappeared. The spindle here is central, and in this respect differs from the condition shown for Limnæa in Plate **1**, Figure 2, where one pole of the spindle is near the centre of the egg. In Figure 14 both the position of the spindle and the condition of the spermatozoön indicate a stage younger than that of Limnæa (Figure 2), but the condition of the germinative vesicles indicates that it is older than Limnæa.

In the eggs of Limnæa I have seen frequently the typical flattening of the animal pole preceding the formation of the first polar cell (Plate **1**,

---

[1] (Plate **4**, Figure 25, represents the egg of Limax agrestis before it leaves the hermaphrodite gland, and shows the condition of the germinative vesicle at this stage.)

Figure 1). The "polar depression" described by Kostanecki und Wierzejski ('96) for Physa is also not a rare phenomenon in Limnæa. Conklin ('94) suggests that the flattening of the animal pole preceding the formation of the first polar cell is caused by the contraction of the spindle fibres. Perhaps, in a similar way the "polar depression" is produced by a more active contraction of the spindle fibres which lie in the prolongation of the axis of the spindle. But even before the outer centrosphere has reached the cell membrane (Plate **1**, Figure 1), the polar depression has disappeared, and a marked flattening of the centrosphere accompanies that of the animal pole of the egg. On either side of the outer centrosphere, as seen in optical longitudinal section of the spindle (Figure 1), there is a projecting "wing" of deeply staining substance. Careful examination shows these wings to be composed of closely crowded astral rays, which have stained near their proximal ends. Since the "wings" are to be seen in all longitudinal sections of this spindle, it follows that the appearance is due to the presence of a continuous disk of staining substance.

Studying the different figures of the first maturation spindle of Limnæa with special regard to the deeply staining portion at the poles, one must, I think, conclude that both centrospheres shown in Figure 1 have taken the stain throughout their whole extent. The roughness of the outline of the stained centrospheres, as compared with those of smaller size, is due to the increasing distance between the astral rays, as one passes outward from the centre. This condition suggests the idea that even parts beyond the limit of the centrosphere may have been stained; for if only the centrosphere were stained, the outline should be more regular. Those investigators who have discovered enormous centrosomes should examine Plate **4**, Figure 23. The dense mass shown there at each pole of the spindle looks more like a precipitate lodged about a central point than like an organ of the cell. In Figure 24 the outlines of the centrospheres may be seen. The great irregularity in the form of the stained portions proves beyond question, it seems to me, that the dense masses at the poles of the spindles represented in Plate **1**, Figures 1 and 3, and in Plate **4**, Figure 23, are simply portions of the cell protoplasm which have not been decolorized.

Many investigators, notably Mark, Garnault, and Kostanecki und Wierzejski, have given in detail for pulmonates the process of the actual formation of the polar cells. It is my purpose in this division of the paper to note only the modifications of the centrosome and centrosphere. In the part devoted to the discussion of the nucleus, I shall make special mention of the differences in the character of the division of the chromosomes in the first as compared with the second maturation spindle.

Turning now to the question of the centrosome, I find that after the first polar cell has been nearly or quite formed the centrosphere belonging to it, when it can be made out at all, gives evidence of disintegration. This is shown in Plate **2**, Figure 8. Nothing which can be maintained to be a centrosome appears in the outer centrosphere of the polar cell. There is, however, in Plate **2**, Figure 12, in the only polar cell represented in that figure, a distinct centrosome, with fibres radiating to the chromosomes. The region of the supposed connection of the polar cell with the egg in this section was covered by a mass of foreign substance, so that it is not certain, though highly probable, that the polar cell was joined to the egg. The aster remaining in the egg shown in Figure 8 resembles the condition of the centrosphere shown in Figure 21. In the present case (Figure 8) the centrosphere may be said to be composed of two parts, a very small, central clear area, of spherical form, and a very much larger non-spherical enveloping structure. The two are not concentric, the inner sphere being much nearer to the peripheral flattened wall of the enveloping structure than to its deep rounded extremity. It is to be observed that in Figure 8, at the exact centre of the inner, small centrosphere, there is a minute centrosome, but with no indication of division in preparation for the next maturation spindle. The inner centrosphere, though small, is very distinct. Within this centrosphere no rays could be distinguished ; in fact, the contents, under the highest magnification, appeared to be entirely homogeneous. Rather prominent rays, few in number, can be seen passing from the periphery of the inner centrosphere out through the outer or enveloping structure. This outer structure stretches from the plane of the deep ends of the series of chromosomes belonging to the egg, toward the centre of the egg, a distance equal to nearly twice its width. The walls, beginning at the chromosomes, run for a short distance perpendicular to the plane of the chromosomes and then gradually converge and nearly come together, but the lines bounding this outer centrosphere decrease in distinctness in passing from the plane of the chromosomes. The outer structure is to be conceived of as a cylinder, truncate at the peripheral end, dome-shaped at the deep end, and containing a spherical inner centrosphere located much nearer the truncate than the opposite end.

The enlargement of the centrosphere during the completion of the polar cell and after its formation — an occurrence so striking in Limax maximus — has not yet begun in the specimen from which Figure 8 was drawn. In many other cases, however, at a slightly later stage the centrosphere shows a decided increase in size, as is seen, for example, in Plate 2, Figure 7. The peculiar arrangement of the chromosomes, the disappearing spindle fibres, and the enlarged centrosphere shown in Figure 7 represent a stage I have seen many times. In earlier stages I have never seen the centrosphere as large as it is in Figure 7. This phenomenon of an increase in the size of the centrosphere which has performed its function, was described by Miss Esther F. Byrnes for Limax agrestis in a paper read at a meeting of the American Morphological Society in December, 1896.

b. Second Maturation Spindle.

I have searched with considerable care for evidence of two centrosomes within the enlarged centrosphere of the first maturation spindle of Limnæa elodes, but I have found them in only a single case (Plate 1, Figure 4), a very early stage in the formation of the first maturation spindle. There is no evidence of a spindle forming between the centrosomes, as, indeed, nothing of the kind could be expected at so early a stage. Hence I am unable to say, as far as Limnæa is concerned, what relation the enlarging centrosphere bears to the formation of the second maturation spindle; whether the new spindle is formed *de novo* within the still persisting centrosphere, or whether the centrosphere disappears before the second maturation spindle comes into existence.

A good example of a second maturation spindle near the height of its development is shown in Plate 2, Figure 11. In this case the two astral figures are conspicuously unlike. Frequently I have found in *first* maturation spindles one centrosome differing from the other in size, and also the centrospheres differing in condition, but the variation shown in Figure 11 appears to be of quite another nature. In this case one centrosome, the peripheral one, has no centrosphere surrounding it, and the centrosphere at the deep pole of the spindle is flattened in a plane perpendicular to the axis of the spindle. I have not enough material of the proper stages to allow me to make a careful study of the second maturation spindle with reference to the centrosomes and centrospheres, and hence do not pretend to say whether Figure 11 represents a typical condition.

The phenomenon of concentric centrospheres is not confined to the first maturation spindle. The aster of the second maturation spindle shown in Plate 2, Figure 13, is not altogether like that shown in Figure

8, for Figure 13 shows that the small centrosphere is very faintly outlined and that the centrosome is very small. There can be no doubt that rays begin at the small centrosphere and continue through the outer centrosphere and beyond ; in fact the outer centrosphere is limited by a very faint outline, which does not interrupt the course of the fibres. There appear to be vacuolations within the space enclosed by the irregular outline of the outer centrosphere, a condition which is not well shown in the figure. The outline itself is not a distinct membrane, but on the contrary marks the extreme limit of what seems to be a progressive vacuolation, which advances outward in all directions except toward the animal pole. Neither in the first nor in the second polar cell of the specimen from which Figure 13 was drawn could any trace of a centrosome or centrosphere be found.

The question of the fate of the deep centrosome of the second maturation spindle involves the question of the origin of the first cleavage spindle. The principal part of the discussion of the latter question I shall leave for another division of this paper. There are, however, certain points which may be considered here.

Unlike the egg-nucleus in sea-urchins and tunicates,[1] the egg-nucleus in gasteropods moves but slightly from the region where the polar cells are formed. Hill ('95) has shown for Sphærechinus that while the egg-nucleus is in the resting stage at the centre of the egg, it has no rays indicating the presence of a centrosome. The sperm-nucleus, with its centrosome, may be seen at this time a sufficient distance away from the egg-nucleus to enable one to determine readily the relationship of the single aster present in the egg. The case with gasteropods is quite different. Not only is the egg-nucleus eccentric in position, but the astral rays belonging to it persist till a very late stage in the development of the two nuclei. Kostanecki und Wierzejski find for Physa that as the sperm-nucleus, with the aster in advance, moves toward the egg-nucleus, the astral rays of the egg-nucleus begin to disappear, as if they were being assimilated by the sperm-aster, while the two are still a considerable distance apart. In both Limax and Limnæa I have seen quite the opposite conditions and have never seen the phenomena these authors describe. Instead of a diminution of the area affected by the deep aster of the second maturation spindle, I find that, as the egg-nucleus develops, the centrosphere enlarges and the extent of the rays

---

[1] The statement with regard to the movement of the egg-nucleus in tunicates is based on unpublished evidence, which Dr. H. E. Crampton of Columbia University has kindly permitted me to refer to.

becomes greater (Plate 3, Figure 20). I have never seen for Limnæa the stage shown for Limax in Figure 20. Although every indication of an egg-aster finally disappears, the time of its disappearance is very much delayed as compared with many other animals.

There are many interesting questions which arise in connection with the disappearance of the egg-centrosome. There are difficulties in proving either that the disappearance is permanent or that it is only temporary. If one maintains that the centrosome after the formation of the second polar cell simply goes into a resting stage, and thus becomes invisible, but finally reappears, the only answer that can be made is, that such a statement is an assumption that can neither be proved not disproved. It is an easy matter to find small dense bodies in the region of the egg-nucleus, and even bodies surrounded by radiations. Often many of these small dense bodies may be found in such positions with reference to the two nuclei in the egg as to seem to be significant, but the difficulty comes in deciding which, if any, of these many centrosome-like structures are really centrosomes. For, not only may these structures be found in close relation to the nuclei, but similar appearances are frequent throughout the egg. With such difficulties as these to contend against, it is of the greatest importance that the phases in the regressive metamorphosis of the egg-centrosome be followed with the closest scrutiny.

III. The Nucleus.

In my original plan of work I was little concerned with the nucleus, but as the investigation progressed two problems of great interest and importance claimed my attention. These are: first, the relation of the nucleoli or karyosomes to the chromatin in the resting nuclei, and, secondly, the question of the reduction division in the Roux-Weismann sense; that is to say, a reduction of qualities by a transverse division of the single chromosomes in the second maturation spindle. I shall take up the second of these questions first, because it comes first in the stages of development which I have studied.

1. Division of Chromosomes.

The apparent variation in the number, size, and form of the chromosomes in the maturation spindles of Limax maximus made the study of these elements a particularly difficult and perplexing one. As long as I worked exclusively with this material, the possibility of ever being able to find evidence concerning a reduction division in the second maturation spindle seemed to me very remote. The number of chromosomes in the first maturation spindle of Limax maximus varies from sixteen to twenty, and sometimes twenty-one or twenty-two of them may be seen. Platner ('86) and Garnault ('88) found for Arion sixteen to twenty chromosomes; but it is quite possible, as Boveri ('90) suggests, that the normal number is really sixteen, — a number which seems to be typical for gasteropods. The fact that in Limax maximus the chromosomes exhibit such variation in size and form, leads me to believe that in the telophase of the first maturation spindle of this species, and possibly of Arion also, not all the bodies seen are simple chromosomes, but rather that some of them are the result of an appreciable separation of the elements composing the "dyads," so that, while some of the supposed chromosomes are unseparated dyads, others are simply one of the components of a dyad. I believe the tetrad formation of the chromosomes to be characteristic of the prophase of the first maturation spindle. When the elements of the dyads are very close together, the resulting appearance is that of a very large chromosome, much larger than the smaller ones. The smaller chromosomes occur most frequently near together, either in pairs or suggesting a paired arrangement. That they are actually joined together, I could not demonstrate satisfactorily. There are cases, however, in which it is a matter of considerable doubt whether a mass of chromatin is a single body with a constriction at the middle, dumb-bell fashion, or whether there are really two chromosomes very near together. In one case I was able to make out the sixteen dyads very distinctly in the polar cell (Plate 3, Figure 17), but the chromosomes remaining in the egg were so closely massed that it was impossible to count them. A curious condition is to be noticed in Figure 21. The number of dyads in the polar cell is fourteen, and the number of chromosomes remaining in the egg is also fourteen. This is quite an unusual variation, and it is probable that two chromosomes at either end of the spindle were obscured in some way. The evidence afforded by a single instance, even though as satisfactory as that shown in Figure 17, is alone not sufficient to carry conviction, but taken with the results I have obtained from my study of Limnæa, affords reasonable ground for believing that the explanation which I have offered of the appearance of chromosomes in excess of the number sixteen is the correct one.

The eggs of Limnæa are more favorable for following the phases of the maturation divisions. Material fixed in 3 per cent nitric acid showed better preservation than that fixed by any other method. The earliest stage of the chromosomes derived from the germinative vesicle that has come under my observation is shown in Plate **1**, Figure 2. The outline of the germinative vesicle has only partially disappeared, and the chromosomes are still indefinite in number and unlike in form. Their arrangement on the spindle can hardly be said to have more than begun. I have no stages between this condition and that represented by Figure 4, but I have in other specimens abundant corroboration of the appearance which Figure 4 shows in regard to the method of separation of the chromosomes in the first maturation division (compare Figure 1). In the first maturation spindle I have always found sixteen chromosomes, some of them more or less completely divided, others not only divided but separated a short distance. Examination of Figure 4 will show that some chromosomes are considerably longer than others. The shorter ones lie end to end on the same spindle fibre. These I take to be chromosomes which have completed their separation, and have now begun to move toward their respective poles. At the middle point of the longer chromosomes, which corresponds with the equator of the spindle, there is an "elbow." Chromosomes in which this elbow is less prominent, are longer than those in which it is large. The meaning is quite clear. The appearances seen in the chromosomes of the first maturation division of Limnæa are due to the more or less complete *splitting* and separation of elongated chromosomes.

Leaving now for a time the discussion of the phases immediately following metakinesis in the first maturation spindle, I shall take up the consideration of the chromosomes in the prophase of the second maturation division. Figure 11 (Plate **2**) illustrates a condition which represents partly the prophase and partly the metaphase of division : that is to say, some of the chromosomes are undivided and some have just divided. The chromosomes of this spindle are distinctly dumb-bell shaped, and lie with their long axes parallel with the axis of the spindle. Here, as in the first maturation spindle, I find sixteen chromosomes, all of which are arranged on the outer, thicker fibres of the spindle, never, as is usual in Limax, through the axis of the spindle. Careful examination of the successive sections from which Figure 11 was constructed showed that some of the dumb-bell shaped chromosomes were completely divided across the "handle," and that migration from the equator had barely begun. Not only is the form of the chromosomes in the prophase of the second maturation division that of a dumb-bell, but even as early as the telophase of the first maturation division all the chromosomes, both those in the group that is to go into the first polar cell and those that are to remain in the egg, have this dumb-bell shape. Even in the metakinesis of the first maturation division I have occasionally seen evidence of a transverse constriction of the chromatin rods. Thus we seem to have in Limnæa a partially concealed "tetrad formation." The presence of the transverse constriction so soon after the longitudinal splitting leaves little doubt that the division as it finally takes place in the second maturation spindle agrees in position with the early constriction.

This observation does not accord with the results Boveri ('90) obtained for Carinaria, one of the heteropods. He found the chromosomes of the first maturation spindle to be quadruple. This quadruple group splits longitudinally in the first maturation division, and then, after the rearrangement of the chromosomes on the second maturation spindle, the division takes place by a longitudinal splitting, exactly as in the first maturation spindle. Naturally one is disposed to ask, What, then, is the meaning of the quadruple groups?

The thing of importance now to be decided for Limnæa is the manner of formation of these "Vierergruppen" or tetrads. To make sure of an exact answer to that question a study of the processes going on in the rearrangement of the chromatin in the germinative vesicle in preparation for the maturation divisions would be necessary. If the tetrads are formed by two longitudinal splittings of segments of the original spireme thread, as in Ascaris (Boveri, '87), and if the two pairs of elements composing the tetrad are elongated and pressed closely together, as at least they seem to have been in the case of Carinaria, then the two maturation divisions would be "equation divisions," and not reducing, except in the sense of a quantitive reduction. If, on the other hand, the length of the masked tetrads represents the length of the original spireme which, in breaking up, first divides longitudinally and next transversely, then the second maturation division is a reduction division in the Roux-Weismann sense. Apart from the evidence which a study of the early stages in the formation and fission of the spireme thread would give, I have little hesitation in holding that we have in Limnæa a reduction division of the Roux-Weismann type, because soon after the evident longitudinal splitting of the chromosomes there occurs a transverse constriction in each of the resulting halves, which continues until there is complete separation of each half into two parts, which then move toward their respective poles.

2. Nucleoli, or Karyosomes.

After the formation of the second polar cell the egg-nucleus becomes vacuolated, and in most of the cases that I have observed the sperm-nucleus also becomes vacuolated at the same time. Both contain many nucleoli or karyosomes varying in size and situated either at the crossing of linin fibres or arranged along such fibres in bead-like fashion. The nucleoli frequently stain with varying intensity in the same nucleus, but generally the staining of all nucleoli is very faint. The larger ones appear to be vacuolated. I have no doubt of the integrity of these karyosomes as distinct elements. Platner (**'86**) believed them to be distinct elements; but the opposite view was maintained by Boveri (**'90**, p. 357), who is inclined to think that Platner's "Karyosomen" are artefacts produced by a crowding together of net-knots and numerous large achromatic nucleoli by an unfavorable method of preservation, and that the mistaken interpretation is in part due to the appearance given in very thin cross-sections. I believe, however, that the structures in question can be shown to actually exist as distinct normal bodies, not artefacts. Moreover, I can bring observations to support Platner's claim that the chromosomes which are taking shape for the first cleavage spindle are to be seen surrounding karyosomes as rings. Platner (**'86**, p. 53) says, "Die Karyosomen nur erscheinen auf den ersten Blick *völlig* farblos, eine aufmerksame Beobachtung lehrt aber dass die Chromatinsubstanz welche anfangs diffus in ihnen vertheilt war, sich in der Form kleiner Körnchen an der Peripherie concentrirt hat."

"Diese Chromatinelemente sind anfangs noch sehr klein und in grösserer Anzahl vorhanden und entziehen sich dann leicht der Beobachtung. Später sammeln sie sich aber zu einigen wenigen grössern Körpern an und treten dann deutlich hervor. Von diesen Chromatinkörnern enthält die Mehrzahl der Karyosomen zwei Stück, welche meist an zwei diametral gegenüberliegenden Punkten der Peripherie gelegen sind. In den kleinern erkennt man zuweilen nur ein solches Element."

I have not studied the karyosomes sufficiently either to confirm or deny Platner's quoted statement, that the chromatin is diffused through the karyosomes preceding the time of its accumulation into a ring on the periphery. I should say, however, that the fact that the karyosomes show staining reaction before the chromatin is collected on the periphery, and that afterwards they do not (a statement which I have not quoted), is not absolute proof that the chromatin is contained in the substance of the karyosomes. The variations in the stainability of these bodies may, it seems to me, be due to causes which have nothing to do with the movement of the chromatin. It is a well known fact that the centrosome goes through certain chemical phases, in which it does not stain at all by a method which at other times stains it deeply. It seems quite possible that the karyosomes may also have chemical phases independent of any physical accumulation of chromatin.

Whether the chromatin in the resting stage of the nucleus is distributed through the substance of the karyosomes, or whether instead it is distributed through the nuclear sap, as Klinckowström ('97) thinks is the case with Prostheceræus, I believe Platner is right in saying that chromatic substance is to be found at one period in the resting stage of the nucleus collected in rings about the karyosomes. I have frequently noticed densely staining rings, irregular in outline, surrounding faintly stained karyosomes. My best evidence concerning the points in question is shown in Plate 1, Figure 6. This figure represents the formation of the first cleavage spindle, and, quite exceptionally, the two so-called pro-nuclei have fused. Rays from each aster have extended into the substance of the fused nuclei, one bundle of rays running nearly through the nuclei. Scattered along this bundle of fibres are numerous deeply stained, bent rods. Similar rods may be seen here and there in the nucleus, apparently unattached. Still others are found lying very close to the faintly stained karyosomes and in more or less intimate contact with them. The chromatin particles surrounding the karyosomes, those lying loose in the nuclear sap, and those being drawn along the penetrating astral rays, are so evidently of the same origin that investigation of the history of the chromatin within the resting nucleus would involve an examination of the changes in the so-called nucleoli or karyosomes.

B. FERTILIZATION.

I. The Early History of the Spermatozoön in the Egg.

1. General Description.

As I stated at the beginning of this paper, the first evidence of the presence of the spermatozoön in the egg of Limax that I have seen, was in specimens taken from the uterus. Not only was the first evidence of penetration of the spermatozoön seen in uterine eggs, but in *all* uterine eggs that I have examined penetration had taken place. Whenever I have found eggs in the oviduct (L. agrestis), great numbers of spermatozoa have always been present surrounding the egg and completely filling the oviduct. This condition suggests simultaneous movement of the eggs and spermatozoa from the hermaphrodite gland. I have never found either eggs or spermatozoa alone in the oviduct.

Under these conditions one might expect self-fertilization, and I have looked carefully for evidence of it. That self-fertilization has not taken place, at least in the oviducal eggs that I have examined, may be explained by what seems to be a fact, viz. that the spermatozoa occupying the oviduct are in an immature condition. In the developing sperm element, as the head of the spermatid begins to take on the form characteristic of the mature condition, the tail is continually growing in length. The end of the tail of the spermatid exhibits a large knob. In the fully developed free spermatozoön there is no indication of this knob. Now, in the oviducal spermatozoön of Limax agrestis I have seen this knob-like structure and I am inclined to think all the spermatozoa in the oviduct are in this immature condition.

So far as I know, the spermatozoön has never been observed in the act of penetrating the egg in gasteropods. It is not very important, however, in gasteropods that this phenomenon should be observed, since the tail in following the head into the egg affords the observer the means of determining the topographical relations necessary for noting certain preliminary processes of fertilization.[1]

In the case of Limax maximus I have found, in one instance, a spermatozoön very near the periphery of the egg, which it apparently had but recently penetrated, while the first maturation spindle was migrating to the periphery to form the first polar cell (Plate **3**, Figure 16). When, in other instances, the spermatozoön was in practically the same stage as represented in the figure just mentioned, I have found the first polar cell completely formed (Plate **3**, Figure 21). In one instance (L. agrestis, Plate **3**, Figure 14) I found the spermatozoön with head and tail still connected, and the germinative vesicle of the egg just disappearing. Kostanecki und Wierzejski ('96) found in Physa that a spermatozoön may penetrate the egg and a large sperm-aster may be developed by the time the first maturation spindle is formed. On the other hand, they found that, in the same species, the spermatozoön may not penetrate the egg until both polar cells have been formed.

---

[1] I may anticipate criticism of this statement by calling attention to what is probably a fact, that the viscidity of the egg-cytoplasm prevents *great* whiplash movements of the spermatozoön; it is not likely therefore that the tail is "fixed" in a position far from the path along which the spermatozoön has progressed.

A very suggestive phenomenon in the early history of the spermatozoön in the egg is shown in Plate **3**, Figure 15. It seems as if the attraction which caused the spermatozoön to penetrate the egg were only a general attraction, and not located in a definite region of the egg; for after penetration the head made almost a complete circle before it came within the more definite influence of the egg-centrosome, or before the egg-centrosome and the sperm-centrosome had entered upon the proper phases for attracting each other. At other times, as in Figure 14, the spermatozoön on entering moved straight ahead, not stopping until it had come in contact with the membrane on the other side of the egg. Here it would have remained until the head and tail had separated.

In a preceding paragraph I have referred to the preliminary processes through which a spermatozoön in the egg may be said to go. These processes are: first, the change in form of the sperm-head; and, secondly, the separation of the head from the tail. I shall describe these processes in turn.

2. Changes in the Sperm-Head.

The sperm-head in its fully developed condition, and before it has entered the egg, has the form of a skewer with one, more or less complete, spiral turn. The sperm-head in Figure 15, although broken away from the tail, still retains the general form it had before it entered the egg. As a rule, however, immediately after penetration it undergoes a modification in form. The nature of this modification is well shown in Figure 14. The fact that the head is still attached to the tail, enables one to see that, in this case at least, the long axis of the head is now at right angles to its original long axis. Kostanecki und Wierzejski ('**96**, Figure 1) show the same condition for Physa. Apparently the change begins very soon after the spermatozoön enters the egg, for in only two instances (one of them shown in Figure 15) have I seen the normal form preserved. It also seems probable that the sperm-head, after becoming elliptical, does not increase in size for a considerable time, for many sperm-heads are found having the same elliptical form, and apparently the same size, both when they are at the periphery of the egg (Plate **1**, Figure 1, Plate **2**, Figure 8, and Plate **3**, Figure 17) and when advanced in their course toward the egg-aster (Plate **3**, Figure 21). This fact is brought out better by the figures of Kostanecki und Wierzejski than by mine. I do not believe any especial significance can be attached to this change in the form of the sperm-head. At first thought, the comparison of the sperm-heads in Figures 14 and 21 would seem to lead to the conclusion that the centrosome in the egg represented in Figure 21 had moved from the side to the end of the head (if the change in form shown in Figure 14 is typical); but such a change in position it seems to me would be meaningless. The difference between the two may be explained by the fact that the sperm-head would naturally present the smallest surface while being drawn through the yolk granules and the protoplasm.

Besides the modification of the sperm-head, there is another phenomenon which, like the one just described, is incidental rather than essential. I refer to the early appearance of a clear area about the sperm-head. The conditions are represented in Figures 14, 15, 21, etc. The outer limit of this area is usually marked by a fine sharp line, so that the whole has the appearance of a clearly defined vacuole, with the sperm-head at the centre. One can make out fine threads radiating from the sperm-head to the margin of the vacuole. In the eggs that I have examined there is no visible modification of the form of the sperm-head by these radiating threads in the vacuole, except in two cases. One of these is represented in Figure 15, where I find that the radiating threads have caused a modification of the outline of the sperm-head. Wherever a thread comes in contact with the sperm-head, a projection, apparently from the head, is formed. The origin and meaning of these radiating threads seem to me of considerable interest in connection with the subsequent changes in the sperm-nucleus, and hence I shall discuss that subject in the next division of this paper.

3. The Sperm-Head and the Beginning of the Sperm-Centrosome.

The change of most importance in the early history of the spermatozoön in the egg is the breaking away of the sperm-head from the tail. The interval of time between the penetration of the sperm-head and its separation from the tail may be short or long according as we interpret the conditions shown in the figures I have made. In some cases it appears probable that the spermatozoön has travelled over a considerable part of the substance of the egg before the head is separated; in others (Figures 1, 7, 8, 11, 16, 17, etc.) either the sperm-head on entering has left the tail outside, or the tail, though entering, has been resorbed. However, the *time* of separation of the head from the tail is not so important as the *manner* of separation. It is to the manner, and still more to the *cause*, that I desire now to direct attention.

Kostanecki und Wierzejski in their Figure 1 give a stage of an egg of Physa which is slightly more advanced than my Figure 14. The head in their figure, as in mine, is represented as being still attached to the tail. Between the head and the stainable tail there is the so-called middle piece, containing the densely stained body supposed to be the centrosome. I have tried to demonstrate the existence of a middle piece and a centrosome in the specimen from which my figure was drawn. Although the sperm-head and a portion of the tail lie in a single section, I am unable to make out any differentiation in the tail near the point of union with the head, the only modification of the tail at that point being a slight swelling. Unfortunately I have but this single specimen showing the head still connected with the tail.

In the work of Wilson and others on the changes of the spermatozoön in the egg, it has been established that the centrosome, in many animals at least, lies in the middle piece of the spermatozoön, and the discovery of any granule within the middle piece has come to be considered as the discovery of a centrosome. Waiving the question of the existence of a differentiated middle piece in the spermatozoön of gasteropods, there are proofs, beside those brought forward by Kostanecki und Wierzejski, that a centrosome exists near the base of the sperm-head. Wilson and Mathews ('95) among others have shown that the sperm-head soon after penetration turns so that its basal end is nearest the egg-aster. At the time of turning a small aster is visible at the base of the sperm-head. An important point in the turning of the head is, that the centrosome is located at the base of the sperm-head. Now, if the tail is present in the egg, it serves as a landmark to show when the turning of the sperm-head takes place and how great is the angle through which the axis of the sperm-head passes. In sea-urchins the tail does not enter the egg with the sperm-head and centrosome; hence the degree of turning cannot be noted as accurately as is possible in the eggs of gasteropods. The difficulty with gasteropod spermatozoa, however, is that because of the early change in the form of the sperm-head and its separation from the tail, the observer is unable to distinguish apex from base. Fortunately this difficulty does not exist in two of the series of preparations that I have. Figure 14 illustrates one of them. In this case the head and tail are still attached. In the other case (Figure 15) the form of the detached sperm-head is very nearly the same as that of a mature sperm-head before penetration. Whatever movements the tail may have gone through while still attached to the head, it is fair to assume that the position of the tail shown in the drawing (Figure 15) is the position it had when the sperm-head separated from it. In this series of sections, and in another of mine similar to it, the base of the sperm-head is turned toward the egg-nucleus; in the section represented in the drawing (Figure 15) the turning has been through an arc of 90 degrees. The fact that in both series the base is turned toward the egg-aster shows that the force which caused the turning must have acted at the base. The difficulty comes now in finding the structure in which that force resides. I have said that I have been unable to find a centrosome in the series represented in Figure 14, and I am not certain of having seen it even in the preparation from which Figure 15 was drawn. However, from what we know of the turning of the sperm-head in other forms, we can assume that the centrosome exists in this case, even if it is not visible. I have shown in the figure two structures which *may* be centrosomes. Extending from the base of the sperm-head in advance and to the left of it I have shown two fibres, thicker than the others that surround the sperm-head, each containing at its middle point a minute granule. On examination of the specimen with a $\frac{1}{18}$ inch homogeneous Zeiss lens these two fibres are seen to be composed of numerous very fine fibrils. This recalls the condition that Kostanecki ('96, Figure 1) shows for the free sperm-head of the sea-urchin. In the sea-urchin, however, there is only one bundle of rays, and that extends from the base directly toward the centre of the sperm-aster. In the other series (not figured) of the same stage as the one represented in Figure 15, there is evidence of a granule in a bundle of fine fibres which extends from the base of the sperm-head. Fibres can also be seen radiating from this granule into the surrounding vacuole, but these radiations have no connection, as far as I can determine, with the more prominent threads extending from the sperm-head through the vacuole. Since in Figure 15 — a stage in which the centrosome is known to be active — there is no evidence of connection between a centrosome and the fibres radiating from the sperm-head, the radiating threads about the sperm-head shown in Figure 14 can hardly be said to be due to the influence of a centrosome.

The evidence I have of the existence in the egg of a structure which I can say positively is a sperm-centrosome in its earliest stages is very meagre. I have seen in the egg many appearances in close proximity to the free sperm-head which suggested an aster, but examination in other parts of the cell afforded many examples of similar ill-defined aster-like structures. In Figure 21 I have drawn a structure that may be the sperm-aster in an early condition; it lies within the vacuole of the sperm-head at the end nearest the egg-aster. The fact that it lies on the side of the sperm-head which is directed toward the egg-aster is, I believe, a strong argument that this particular structure is the spermaster. The discussion of examples of undoubted sperm-asters I shall leave for the next sub-division of this paper.

II. The Sperm-Centrosome.

Kostanecki und Wierzejski ('96) have shown that after the spermatozoön has entered the egg and the sperm-head has taken on a spherical form, the centre of activity is within the sperm-aster. These authors have also shown that at the earliest appearance of the sperm-aster in the egg it is very small and near the sperm-head. As the aster increases in size, it is found sometimes at a considerable distance from the sperm-head. Later in the progress of development the sperm-aster and sperm-head (the latter now considerably vacuolated) are found near together moving toward the egg-aster, the sperm-aster leading the way. Frequently, even at a very early stage, the sperm-centrosome divides into two parts, and a gradually developing spindle forms between them.

It has been supposed generally that the sperm-aster in its course toward the egg-aster takes a position somewhere between the egg-aster and the sperm-head. Some of the figures by Kostanecki und Wierzejski show exceptions to this. For example, in their Figure 3, showing the first maturation spindle at the top of the figure, the sperm-head lies to the left near the periphery of the egg, but the sperm-aster is below the centre. Likewise in their Figure 14, the sperm-aster, instead of lying between the sperm-nucleus and the deep end of the second maturation spindle, is situated so that the line joining it to the sperm-nucleus makes a right angle with the line uniting sperm-nucleus and the inner end of the second maturation spindle. At first I was inclined to think that a second sperm-head in the egg had escaped their observation; but since that time I have found that in my own material it is far easier to make out sperm-nuclei than sperm-asters. Furthermore, I am able to corroborate for Limnæa (Figure 7) some of the conditions which they have shown for Physa. I have no important additions to make to the accounts of these authors on the early changes of the sperm-centrosome in the egg. The facts I have collected are all corroborative of the results obtained by Kostanecki und Wierzejski. I shall therefore describe my observations only briefly.

The sperm-nuclei shown in Figures 5 and 7 are pointed on the side nearest the sperm-aster. This condition was first noticed by Mark for Limax campestris in 1881. In Figures 13, 20, 29, of Kostanecki und Wierzejski are shown striking modifications in the form of the egg-aster and sperm-aster. Apparently each aster is repelled or possibly, as Kostanecki und Wierzejski suggest, is being assimilated by the other. The interesting facts shown in these figures and in my own Figures 2 and 7 are: first, in each of the five cases the process of maturation is not completed, and, secondly, there *has been* an attraction existing, else the sperm-aster and the egg-aster never would have come as near together as they have. The fact that the functions of the egg-aster are not yet completed, may be sufficient to account for the temporary repulsion.

Considerable attention was given in Part A of this paper to the variable form of the centrosome. In the study of the egg-centrosome, the centrosphere afforded a sort of standard for comparison — a very unsatisfactory one, however. The sperm-centrosome has no centrosphere. The condition of the sperm-centrosome in the specimens I have observed which is most nearly typical of the conditions of centrosome structures in general is that shown in Figure 5. The centrosome in that figure is a small dense granule, which is at the point of origin of the astral rays.

The sperm-centrosome shown in Plate **2**, Figure 10 is the largest I have seen. In fact, I imagined when I first saw it that it was a sperm-head with possibly a centrosome beneath it, but I now believe that the dark body seen in close proximity to the radiations from the large centrosome is the sperm-nucleus belonging to it. Another sperm-head is visible in the egg, but it is near the periphery and is still homogeneous, whereas the more central sperm-head gives evidence of being vacuolated (a condition not shown in the figure).

Another condition of the sperm-aster is shown in Figure 2. I have not been able to make out anything in the central region of the aster that has the appearance of a centrosome, there being instead a large, faintly stained, thickly reticulated area, from which astral rays extend. This central region is very much flattened, apparently owing to a repulsion between this aster and the deep aster of the maturation spindle. The repulsion apparent in the astral rays of both these asters is manifest also in the flattened condition of their central reticulated areas. The peculiar distortion and partial displacement of the reticulated area of the deep maturation spindle affords perhaps the strongest evidence I have presented of a repulsion of one aster by another. The centrosomes could be found only in the peripheral aster of the maturation spindle.

III. The Origin of the First Cleavage Spindle.

The fact that a fully formed sperm-spindle exists in the egg while the processes of maturation are going on, does not of itself prove that the sperm-spindle will become the first cleavage spindle; but nevertheless a strong presumption is created that such is the case. If a spindle arising from the division of the egg-centrosome should also be found after the formation of the second polar cell, the reason for the existence of a sperm-spindle could not be easily explained. As far as I know, however, the egg-centrosome has never been found to divide and produce a spindle after the formation of the second polar cell; but that does not end the matter. In the first place, it is impossible to know whether every sperm-centrosome divides to form a spindle; and in the second place, the sperm-spindle, whether formed, or only potentially existing in the sperm-centrosome, nearly disappears from view during the resting stage of the germ-nuclei.

Kostanecki und Wierzejski maintain that they have followed the history of the sperm-centrosome through even this almost quiescent stage to the actual formation of a cleavage spindle. Their Figure 33a represents the centrosome as having nearly disappeared. Even on this evidence, how is one to prove that the egg-centrosome has totally disappeared "because of inability to carry on the division of the cell," while the sperm-centrosome, a new organ, becomes predominant and develops into the first cleavage spindle? If at any time a link is missing in the chain of the history of the sperm-spindle, it seems to me we cannot exclude the possibility that the egg-centrosome may come again to view, and actually take part in forming at least a part of the first cleavage spindle.

In my discussion of the changes of the egg-centrosome, I have said that, although the disappearance of the egg-centrosome and the astral rays is long delayed, they nevertheless come to a condition in which it is impossible to distinguish them from the yolk granules and the protoplasm. I have also said that I have not seen a stage such as Kostanecki und Wierzejski represent in their figures, where the rays of the egg-aster are apparently being assimilated by the rays of the sperm-aster; but I have not seen exactly the conditions of germ-nuclei which these authors find at the time assimilation is going on. However, their figures as a whole do not bear out the "assimilation" theory completely, as, for example, in Figure 27, where the egg-aster (even though the germ-nuclei are nearer together than in Figure 25 or 28) is still apparently active. When we come to the stage represented in their Figure 33a, and still further to conditions such as I have found where no aster can be detected in connection with either egg-nucleus or sperm-nucleus, then we may well question the value of the "assimilation" theory.

I have referred in an earlier part of this paper to the clear evidence brought forward by Hill ('**95**) to show that in the egg of Sphærechinus the egg-aster completely disappears. The sperm-aster, from the time it appears at the base of the sperm-head till the first cleavage spindle is formed, is clearly visible; and the sperm-centrosome and its product, the sperm-spindle, are accompanied by the only astral structures that are visible. Fick ('**93**) finds the first cleavage spindle to be of spermatic origin, but the proof to be found in the existence of an "archoplasmic" mass is not so satisfactory as the evidence produced by Hill.

Some of the most recent work on the history of the centrosomes in the egg tends to re-open the question of the origin of the first cleavage spindle. Foot ('**97**) maintains for Allolobophora that whatever the evidence of an aster about the spermatozoön in the egg, the cleavage aster comes from the egg itself. According to this investigator, the spermatozoön gives to the developing embryo only the sperm-head. The first cleavage spindle comes from the egg-aster, although that structure is invisible during the resting stage of the egg-nucleus. Klinckowström ('**97**) finds in a planarian that both egg-aster and sperm-aster disappear during the resting stage of the germ-nuclei. When two asters make their appearance to form the first cleavage spindle, they are at a considerable distance from each other and in such relation to the two germ-nuclei that it is impossible to decide their origin.

The conditions encountered by Klinckowström are apparently the same as those represented in my Figures 12, 18, and 19, referred to above; and since he, as I, could not follow the changes in the centrosome continuously, we can not say, as others have said of centrosomes in practically the same relation to nuclei, that both are of spermatic origin. Hence, if anything leading toward conclusive proof is to be known, it must be learned from facts striking enough to counterbalance the weakness incident to a break in the series of phases through which the centrosomes are seen to pass. I believe I have in Plate **4**, Figures 26, 27, and 28, evidence which proves, just at the stage of development when evidence is most conclusive, that *the first cleavage spindle is wholly of spermatic origin.*

The relation of egg-nucleus and sperm-nucleus in the egg of Limnæa is so constant that the sperm-nucleus is never found between the polar cells and the egg-nucleus. Frequent observation of the stages in the development of the sperm-nucleus enables one to know, even by a hasty examination of the series of sections, which nucleus is the sperm-nucleus. When, therefore, we find, as in Figure 27, that the sperm-nucleus, although partly overlying the egg-nucleus, is nearer to the two centrosomes, and indeed, between the egg-nucleus and the centrosomes, we know that both centrosomes more definitely belong to the sperm-nucleus than to the egg-nucleus. More important than the position of the centrosomes with reference to the sperm-nucleus, and still dependent on that position, is the fact that the astral rays from either centrosome have extended toward the sperm-nucleus; and, having touched the nuclear membrane, have caused indentations in it, and have even penetrated the nucleus itself and united to form a spindle there. The most careful scrutiny of the sections through the egg-nucleus fails to reveal the slightest trace of its being affected yet by the presence of the asters.

Although many changes take place in the nucleus between the stages represented in Figures 27 and 26, the formation of the cleavage spindle has proceeded just far enough to show that the process of first involving the sperm-nucleus in the spindle continues without interruption until that nucleus is wholly within the spindle, while the egg-nucleus is still outside of it. The series of changes leading up to the formation of a perfect first cleavage spindle with the chromosomes in their prophase position is nearly completed in the stage represented in Figure 28.

In conclusion I desire to answer an objection that may possibly be raised and then to call attention to an important additional fact. It may be urged that at least one of the centrosomes represented in each of the Figures 12, 18, and 19 may still be the egg-centrosome, since it is as near to the egg-nucleus as it is to the sperm-nucleus. In reply to this possible contention, I should say, that, while the various positions which the two nuclei *may* occupy with reference to each other, would easily bring one centrosome into a situation where it would be as near to the egg-nucleus as to the sperm-nucleus, nevertheless such a position in the light of the subsequent history of the centrosome can be shown to be *temporary* and *incidental.* It must be remembered also that the sperm-centrosome, sometimes single and sometimes divided, precedes the sperm-nucleus as the two move toward the egg-nucleus in the early stages of fertilization. The fact that one and sometimes both centrosomes later migrate from a point between the two nuclei and away from the egg-nucleus toward the sperm-nucleus tends to emphasize the interpretation I have given: — that the centrosomes of the first cleavage spindle are related to the sperm-nucleus alone. Although one centrosome is often found very near the egg-nucleus, and even extends astral rays toward it, I have *never found both centrosomes coöperating to involve the egg-nucleus in a spindle before the sperm-nucleus was involved.* This seems to me a point of vital importance, precluding, as it does, the possibility of even one centrosome, being of other than spermatic origin; for if in Limnæa elodes one of the centrosomes comes from the egg, then the incipient first cleavage spindles would be as likely to involve the egg-nucleus as the sperm-nucleus first.

SUMMARY.

The centrosome and the centrosphere are extremely variable structures, both in size and in their reaction to stains.

In the processes leading to the formation of the first polar cell in Limax maximus, no centrosome is visible. The astral rays apparently begin in the thickened wall of a pale centrosphere.

After the formation of the first polar cell, and also after the formation of the second polar cell, the centrosphere is found to be greatly enlarged. This condition is characteristic of both Limax maximus and Limnæa elodes.

In the egg cell of Limnæa elodes great variation in the condition of the centrosome and the centrosphere is observed. Two facts tend to show that the *centrosphere* is not a permanent organ of the cell: First, the centrosphere is sometimes invisible on account of the increased area at the centre of the aster which reacts to the stain, and, secondly, astral rays beginning in the centrosome continue *through* the centrosphere. The centrosphere then appears to be no more than a region of thickenings in the astral fibres.

The *centrosome* in the first maturation spindle of Limnæa, when it is visible, varies from a very minute granule to a condition in which its diameter is as great as the transverse dimension of the spindle itself, or even greater. In the first maturation spindle of Limnæa the centrosome was invisible in only a few cases, the astral rays usually giving evidence of its existence. The centrosome of the second maturation spindle of Limnæa never appeared as a large structure; the number of preparations, however, was limited.

In both Limax and Limnæa after the formation of the second polar cell, the disappearance of the egg-centrosome and the egg-aster, though long delayed, is complete.

A reduction division of the chromosomes in the Roux-Weismann sense was observed in the second maturation division of the egg of Limnæa elodes. The process consisted of a *transverse* division of the dyads resulting from the longitudinal splitting of the masked tetrads of the first maturation division.

In fertilization the tail follows the sperm-head into the egg, but later is resorbed by the egg cytoplasm. The sperm-head, after breaking away from the tail begins, under the influence of the sperm-centrosome, to move, with its base in advance, toward the egg-aster. At the beginning of this movement the sperm-centrosome is not visible; later it becomes distinctly visible, and often very large, giving evidence of variations comparable in a measure to the variation in the egg-centrosome of the first maturation spindle of Limnæa.

Occasionally the sperm-centrosome of Limnæa divides into two while on its way toward the egg-nucleus, a process prophetic of the existence of these centrosomes at either pole of the first cleavage spindle.

On account of the fact that in Limnæa both egg-centrosome and sperm-centrosome at certain stages disappear for a time, it is impossible to ascertain the source of the first cleavage spindle by following the history of the centrosomes. However, reasonably satisfactory proof that the first cleavage spindle is wholly of spermatic origin is found in the facts that the incipient cleavage spindle involves the sperm-nucleus first, and that the egg-nucleus, so far as my observations have extended, is never involved in the spindle before the sperm-nucleus is entirely drawn upon it.

BIBLIOGRAPHY.

Boveri, T.
'87. Zellen-Studien. Heft 1. Die Bildung der Richtungskörper bei Ascaris megalocephala und Ascaris lumbricoides. Jena. Zeit. Bd. 21, pp. 423–515. Taf. 25–28. Also separate. 93 pp., 4 Taf. Jena, 1887.

Boveri, T.
'90. Zellen-Studien. Heft 3. Ueber das Verhalten der chromatischen Kernsubstanz bei der Bildung der Richtungskörper und bei der Befruchtung. Jena. Zeit. Bd. 24, pp. 314–401. Taf. 11–13. Also separate. 88 pp., 3 Taf. Jena, 1890.

Conklin, E. G.
'94. The Fertilization of the Ovum. Biol. Lectures, Mar. Biol. Lab. Wood's Holl. Vol. 2, pp. 15–35. 10 Figs. in text.

Fick, R.
'93. Ueber die Reifung und Befruchtung des Axolotleies. Zeit. f. wiss. Zool. Bd. 56, pp. 529–614. Taf. 27–30.

Foot, K.
'97. The Origin of the Cleavage Centrosomes. Jour. Morph. Vol. 12, pp. 809–814. Pl. 39.

Garnault, P.
'88. Sur les phénomènes de la fécondation chez l'Hélix aspersa et l'Arion empiricorum. 1. Zool. Anz. Jahrg. 11, pp. 731–736. 2. Zool. Anz. Jahrg. 12, pp. 10–15. 3. Zool. Anz. Jahrg. 12, pp. 33–38.

Hill, M. D.
'95. Notes on the Fecundation of the Egg of Sphærechinus granularis, and on the Maturation and Fertilisation of the Egg of Phallusia mammillata. Quart. Jour. Micr. Sci. Vol. 38, pp. 315–330. Pl. 17.

Klinckowström, A. von.
'97. Beiträge zur Kenntniss der Eireifung und Befruchtung bei Prostheceraeus vittatus. Arch. f. mikr. Anat. Bd. 48, Heft 4, pp. 587–605. Taf. 28–29, 3 Textfiguren.

Kofoid, C. A.
'95. On the Early Development of Limax. Bull. Mus. Comp. Zoöl. Harvard Coll. Vol. 27, No. 2, pp. 35–118. Pl. 1–8.

Kostanecki, K.

'96. Ueber die Gestalt der Centrosomen im befruchteten Seeigelei. Anat. Hefte, Abth. 1, Heft 22 (Bd. 7, Heft 2), pp. 217–237. Taf. 13–14.

Kostanecki, K., und Siedlecki, M.

'96. Ueber das Verhältniss der Centrosomen zum Protoplasma. Arch. f. mikr. Anat. Bd. 48, pp. 181–273. Taf. 10–11.

Kostanecki, K. von, und Wierzejski, A.

'96. Ueber das Verhalten der sogen. achromatischen Substanzen im befruchteten Ei. Nach Beobachtungen an Physa fontinalis. Arch. f. mikr. Anat. Bd. 47, pp. 309–386. Taf. 18–20.

Mark, E. L.

'81. Maturation, Fecundation, and Segmentation of Limax campestris, Binney. Bull. Mus. Comp. Zoöl. Harvard Coll. Vol. 6, No. 12, pp. 173–625. Pls. 1–5.

Platner, G.

'86. Ueber die Befruchtung bei Arion empiricorum. Arch. f. mikr. Anat. Bd. 27, pp. 32–72. Taf. 5–6.

Sobotta, J.

'95. Die Befruchtung und Furchung des Eies der Maus. Arch. f. mikr. Anat. Bd. 45, pp. 15–93. Taf. 2–6.

Wheeler, W. M.

'95. The Behavior of the Centrosomes in the Fertilized Egg of Myzostoma glabrum, Leuckart. Jour. Morph. Vol. 10, No. 1, pp. 305–311. 10 Figs. in text.

Wilson, E. B., and Mathews, A. P.

'95. Maturation, Fertilization, and Polarity in the Echinoderm Egg. Jour. Morph. Vol. 10, No. 1, pp. 319–342. 8 Figs. in text.

EXPLANATION OF PLATES.

The drawings on Plates 1, 2, and 4 represent a magnification of 575 diameters; those on Plate 3 about 400 diameters. Projection of the image was made by an Abbé camera lucida. All figures except 3, 5, and 9 are composites of structures extending through several, in some cases nine, sections.

PLATE 1.

All Figures are of eggs of *Limnœa elodes.*

Fig. 1. First maturation spindle, telophase. Centrosomes of large size. Sperm-head near vegetative pole. Breaking of membrane at animal pole accidental; the flattening of the egg normal.

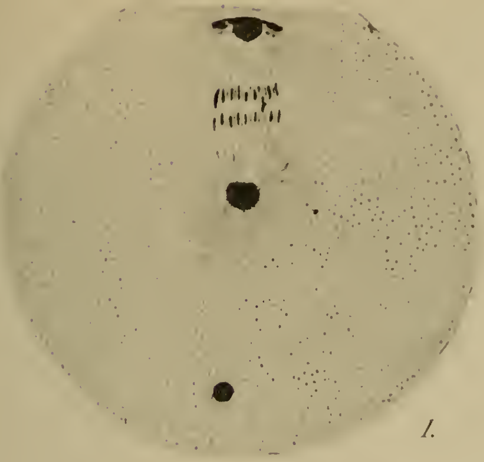
Fig. 2. First maturation spindle. Portions of the membrane of germinative vesicle still visible. Form of deep aster of spindle modified by sperm-aster.

Fig. 3. Deep centrosome and aster, to show the rays beginning at centrosome and extending through and beyond the centrosphere.

Fig. 4. First maturation spindle. The sixteen chromosomes (concealed tetrads) splitting longitudinally. Deep and peripheral centrosomes unlike.

Fig. 5. Sperm-aster and sperm-nucleus. Nucleus elongated in the direction of its aster, and pointed. Position of egg-aster indicated by dotted outline.

Fig. 6. Germ-nuclei fused into a single (?) cleavage nucleus. First cleavage spindle forming. Chromosomes being drawn to the spindle by the rays which penetrate the interior of the fused germ-nuclei. Occasional nucleoli show chromosomes attached to them.



1.

2.

3.

4.

5.

6.

H.R.L. del.

Heliotype Co. Boston.

PLATE 2.

All Figures are of eggs of *Limnœa elodes.*

Fig. 7. First polar cell destroyed. Its position indicated by dotted outline. Enlarging of centrosphere begun. Centrosome of sperm-aster divided into two, but surrounded by a single system of astral rays. Sperm-head pointed on side toward the distant sperm-aster.

Fig. 8. First polar cell; the peripheral centrosphere disintegrating. Deep centrosome surrounded by a small spherical centrosphere; this surrounded, in turn, by an eccentric larger centrosphere.

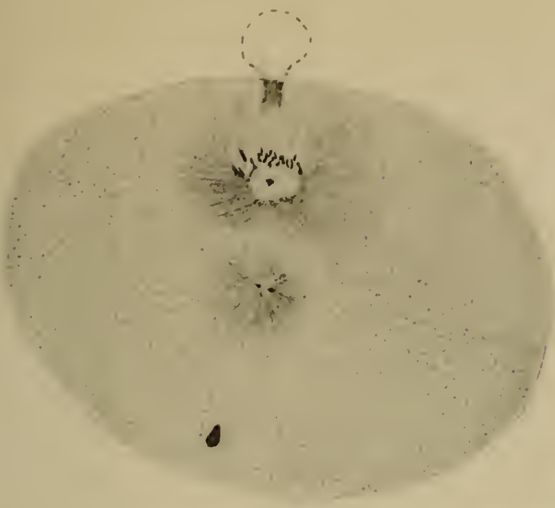
Fig. 9. Transverse section through the peripheral chromosomes of the first maturation spindle. Sixteen chromosomes present.

Fig. 10. To show large sperm-centrosome and, near by, the slightly vacuolated sperm-head. Another sperm-head at periphery of egg. The polar cell in outline projected on the plane of this section. The egg-nucleus is not shown, as it lies in another section.

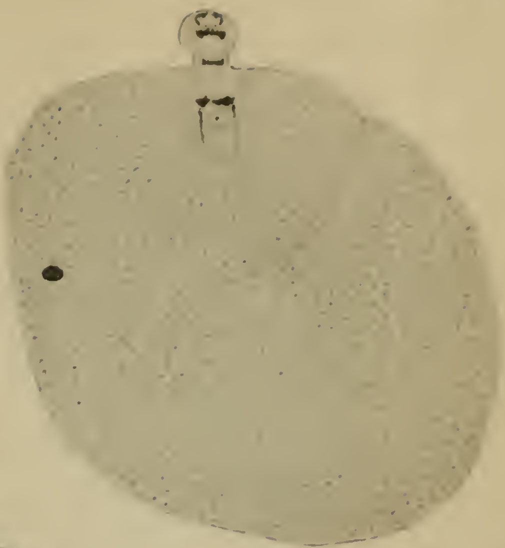
Fig. 11. Second maturation spindle. Sixteen dumb-bell shaped chromosomes (dyads) about to divide by transverse division. Constructed from successive sections.

Fig. 12. Only one polar cell (second) recognized. Its relation to egg obscured by accidental presence of a foreign body. Formation of first cleavage spindle.

Fig. 13. Telophase of second maturation spindle. Deep centrosphere surrounded by an eccentric outer centrosphere. Sperm-nucleus without sperm-aster.

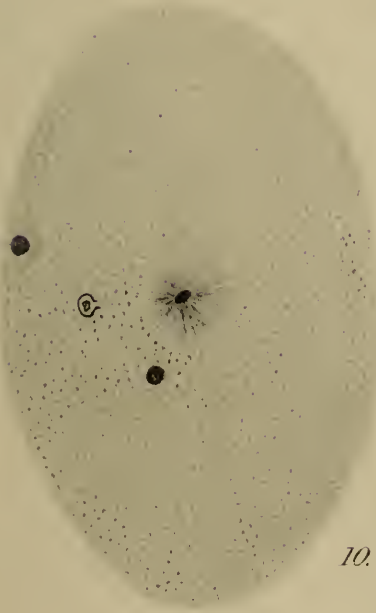


7.



8.

9.



10.

11.

12.

13.

H.R.L del.

Heliotype Co. Boston.

PLATE 3.

Fig. 14. *Limax agrestis.* First maturation spindle, germinative vesicle having just disappeared. Head and tail of spermatozoön still connected.

Fig. 15. *Limnæa sp.?* First polar cell remains. Second polar cell formed, but broken away from the egg; its "Zwischenkörper" remains near that of the first polar cell. Sperm-head just broken off from the tail, and with base turned toward the egg-nucleus. The sperm-head lies in a vacuole. Two centrosomes (?) may be seen each in a bundle of rays in the vacuole on the side away from the proximal end of the tail.

Fig. 16. *Limax maximus.* Formation of the first polar cell. Centrosphere with thick reticulated wall; no centrosome is visible. Clear area of centrosphere finely reticulated. Sperm-head in lower part of figure.

Fig. 17. *Limax maximus.* First polar cell just formed. Vacuolation or enlarging of centrosphere begun. Two centrosomes (?) in the centrosphere. Sperm-head in usual vacuole. Sixteen dyads in first polar cell.

Fig. 18. *Limax maximus.* Centrosomes about to form the first cleavage spindle.

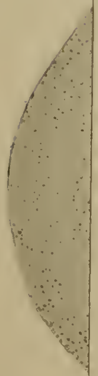
Fig. 19. *Limax agrestis.* Polar cells lost. First cleavage spindle forming.

Fig. 20. *Limax maximus.* First polar cell lost; second polar cell still united to the egg. The germ-nuclei are nearly surrounded by numerous small bodies resembling centrospheres.

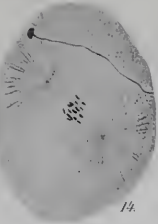
Fig. 21. *Limax maximus.* First polar cell just formed. Enlargement of centrosphere further advanced than in Figure 17. Two minute centrosomes with radiations within the centrosphere. Sperm-head with problematic centrosome within the sperm vacuole Blunt end of tail is the one to which the sperm-head was attached.

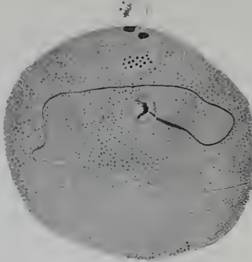
Fig. 22. *Limax maximus.* Telophase of first cleavage spindle. Nuclear membrane already formed about the chromosomes. Centrosomes divided in anticipation of the next cleavage.

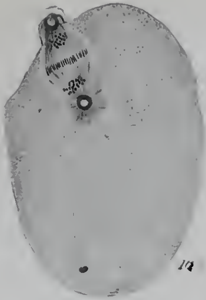
LINVILL

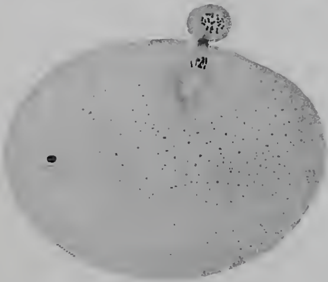


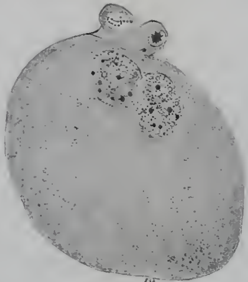
H.R.L.


14.

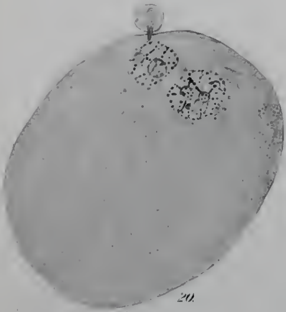

15.

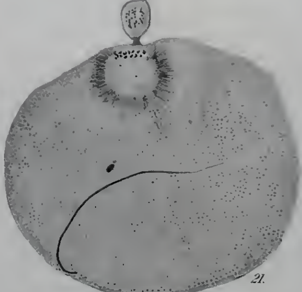

16.

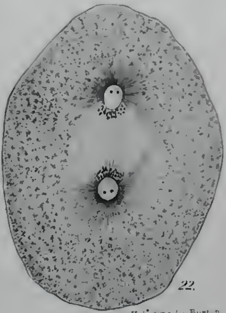

17.


18.


19.


20.


21.


22.

H.R.L. del.

Heliotype Co. Boston

PLATE 4.

All Figures, except Figure 25, are of eggs of *Limnœa elodes*.

Fig. 23. First maturation spindle. At either pole of the spindle is collected a mass of precipitate, the whole resembling a so-called centrosphere.

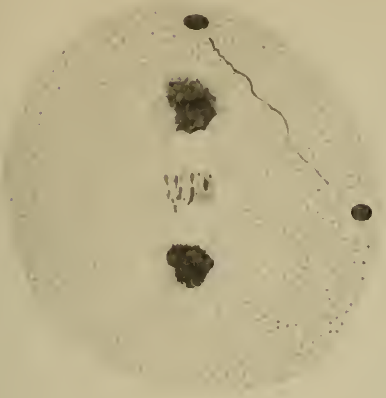
Fig. 24. First maturation spindle. Apparently the centrospheres were in the process of being decolorized when the process of decolorizing was checked.

Fig. 25. *Limax agrestis.* The germinative vesicle contains two nucleoli and "Linin" fibres with elements of future chromosomes arranged in "skein" stage.

Fig. 26. First cleavage spindle. Structures that seem to be the sperm-chromosomes now occupy the middle of the spindle, and the egg-chromosomes are about to be drawn into it.

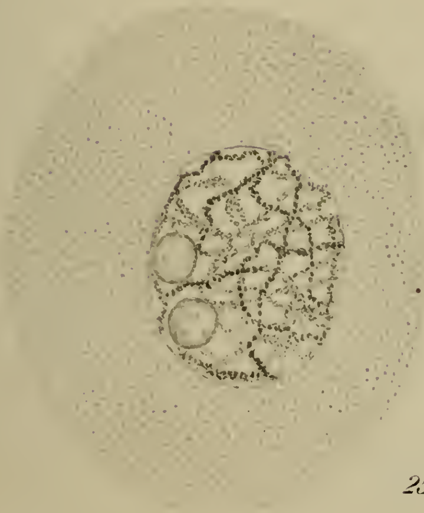
Fig. 27. First cleavage spindle. Rays near the incipient spindle are beginning to penetrate the sperm nucleus, while the egg-nucleus is still unaffected. The chromosomes are not yet formed.

Fig. 28. First cleavage spindle. The sperm-chromosomes occupy the whole breadth of the spindle, while the egg-chromosomes are at one side of the spindle. The granular funnel beneath the polar cells probably represents the path through which the egg-chromosomes were drawn to the spindle.

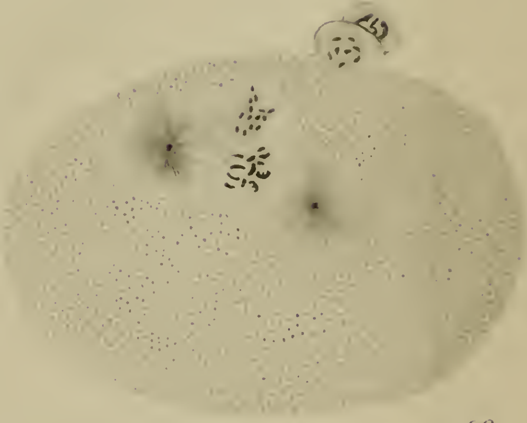


23.

24.

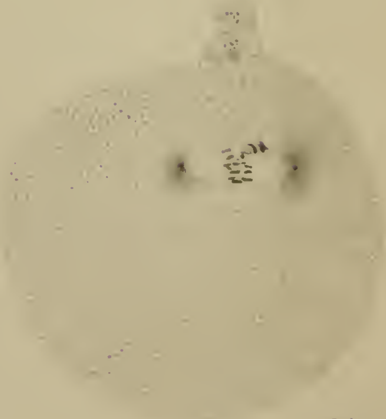


25.



26.

27.



28.

H.R.L. del.

Heliotype Co., Boston.

Harvard University. Museum
of Comparative Zoology
Bulletin