III. "On the Variable Stars of the δ Cephei Class." By J. NORMAN LOCKYER, C.B., F.R.S. Received November 9, 1895.

[Publication deferred.]

IV. "Microscopic and Systematic Study of Madreporarian Types of Corals." By MARIA M. OGILVIE, D.Sc. Communicated by Sir ARCHIBALD GEIKIE, F.R.S. Received July 24, 1895.

(Abstract.)

In the first part of this paper the author gives the results of her microscopic investigations on the structure of the skeleton in a number of typical Madreporaria.

Detailed microscopic study of the surface of the septum showed small scales lying above and against one another somewhat like the slates of a roof, and consisting solely of fine, parallel-placed, or diverging, aragonite fibres. Besides these calcareous scales, ectodermal cells (calicoblasts) could still be observed in several cases, attached to the surfaces of septa in fresh specimens. Heider and one or two other authors have already mentioned the frequent occurrence of organic polypal remnants on skeletal surfaces.

The scales observed by the author were found to agree precisely in shape and size with the calicoblasts, and to show various transitional stages from the organic cell to the calcified. It follows from this that the skeleton of Madreporaria takes its origin from an actual calcification of the calicoblasts, and not, as Koch thought, by a secretion laid down outside the cells. The author found further that the calcareous scales were arranged in extremely thin lamellæ, and that the fibro-crystalline deposit was similarly oriented in successive lamellæ.

The stages in the process of skeleton building may be thus generally stated:—

(1) Calcareous deposit is laid down within individual calicoblasts of the ectoderm. At the same time new ectodermal cells are formed next the mesoglœa, and these which are undergoing calcification become loose external layers of partly calcareous, partly organic tissue.

(2) Fibro-crystalline groups of aragonite are built up in the individual cells, and the cell-walls shrivel. Thus a connected calcareous lamella is formed, which is ultimately incorporated with the skeleton.

(3) Changes of disintegration and crystallisation still continue after the cell lamella has severed living contact with the polyp. The disintegration of organic cell-remnants produces various flecks and bands, usually carbonaceous, in the midst of the crystalline deposit. These afford the explanation of the so-called "dark streaks" and other appearances in the skeleton.

The finer structure of the septa will be readily understood when it is remembered that the septa are formed within radial invaginations of the aboral body-wall of the polyp. The septal surfaces are practically casts of the two flaps of a septal invagination. When the flaps are smooth, the calcareous lamellæ are also smooth. But, according to the author's observations, that is seldom the case in recent Madreporaria. Usually the septal flaps are pitted and goffered, resembling the pleated muscular flaps of the mesenteries, and the septal surfaces are correspondingly granulated and fluted. The author has found that in all cases the calcified calicoblasts of successive lamellæ are grouped around definite *centres of deposit* situated in the median plane—corresponding to the growing edge—of the septum. Subsequently the individual groups of calicoblasts assume the form of radiating bunches of fibro-crystalline aragonite, passing outwards from the original centre of deposit in the median plane to the surface of the septum. The author has given the name of "fascicles" to these fibro-crystalline "bunches," and has demonstrated the relation which they bear to the external sculpturing observed on lateral septal surfaces. *The emergence of a fascicle at the surface gives rise to a granulation.* The fascicles are, however, of varied size; if large, one fascicle usually corresponds to one granulation; if small, a number of fascicles may in the course of septal thickening coalesce to form a broad nodular granulation. The size of individual fascicles depends on the original closeness of the "centres of calcification" at the septal edges.

The trabecula (= "poutrelle" Edw. and H.) of a "perforate" septum is composed of *symmetrical groups of fascicles* placed in vertical series. The author has further found that those septa described by Edwards and Haime as "imperforate and leaf-like" are also composed of trabeculæ. But the individual parts of these trabeculæ have an opposite *pair of fascicles* instead of an indefinite number. The majority of Astræid genera have septa in which both kinds of trabeculæ occur. The author applies the term "simple trabecula" to a trabecula made up of successive *pairs* of fascicles, as the axis of deposit is in part or wholly common to the opposite fascicles; and the term "compound trabecula" to one made up of successive *groups* of fascicles. In the former case the fibro-crystalline deposit may be said to be bilaterally symmetrical in the opposite halves of a septum; in the latter the fibro-crystalline deposit is radially symme-

trical around ideal trabecular axes in the median septal plane. Each member of a successive series of fascicle "pairs" or "groups" in a trabecula is called by the author a *trabecular part* (*Trabekelglied*). *The "fascicle" may be regarded as the structural unit of the coral skeleton. Two or more fascicles combine to build up a "trabecular part." And the differences in the relative arrangement of trabecular parts determine the endless varieties of skeletal form within the Madreporaria.*

The author has subjected the following typical genera to a detailed microscopic investigation :—Galaxea, Mussa, Heliastræa, Goniastræa, Montlivaltia, Thecosmilia; then Fungia, Siderastræa, Lophoseris; further, Eupsammia, Haplaræa; and, lastly, Turbinaria, Actinacis, Madrepora, and Porites. This research enables the author to state that different types of septal structure are characteristic of different groups of Madreporaria. The differences relate to the microscopic structure of the trabeculæ and to the arrangement of trabeculæ in the plane of a septum. It is impossible here to do more than indicate the line of research. *Turbinaria* is an example of an extremely simple structural type. The component trabeculæ are small, uniform in size, and directed all in the same way, obliquely or almost horizontally inwards from the periphery of the septum to the inner edge. The fascicles are paired, and their axes never bend out of the median septal plane. *Galaxea* has a septum whose trabeculæ bend right and left from a definite area of divergence in the septal plane. The individual trabeculæ are large, vary in size, and the axes of the paired fascicles bend out of the median plane towards the opposite surfaces of a septum. The septum of *Mussa* is composed of a number of broad ridges, elliptical in section, and ending at the upper edge of the septum in broad "spiniform teeth." The author shows that each "spiniform tooth" is itself finely serrated, and that the serræ represent apices of trabeculæ. In short, *a single broad ridge of the Mussa septum is the precise homologue of the complete Galaxea septum*, being built up of fan-shaped groups of trabeculæ diverging right and left from the middle area of a ridge. Again, *Fungia* has, like Mussa, a septum composed of a number of ridges, but the trabeculæ in each ridge have a course almost parallel with one another. The emergent fascicles are thus so close that coalescence inevitably takes place; the soft parts of the polyp clothing the ridge are pushed outwards at the prominent middle part of the ridge, and readily give rise to synapticular union between septa. Further reference to this part of the work must be omitted here.

The author observed in sections of recent types that a larger amount of organic cell-material was usually present near the median plane of the septum than towards the lateral surfaces. This she believes may be attributed to the greater rapidity of the calca-

reous secretion and the less complete calcification of the calicoblasts present at the doubled upper edges of septal invaginations. In fossil material, secondary changes render this central part of the septum more or less conspicuous on account of the breaking down of organic products, or sometimes the complete replacement by infiltrated salts. The author strongly contends that there is no basis for the assumption of a "*primary septum*" in the middle plane of a septum in the sense at present accepted by most palæontologists. On the contrary, the author's sections show that the *fibro-crystalline structure of the septum is the same throughout its whole thickness, essentially that of a double system of thin calcareous lamellæ*, either smooth or fluted, and corresponding to a deposit from opposite flaps of an invagination.

The author's investigations afford many new microscopic facts of structure testifying that the growth in height of the polyp is accomplished at certain growth-periods, between which pauses ensue. During each growth-period a varying number of the calcareous lamellæ, "growth lamellæ," are laid down, and these always appear in intimate union with one another. Again, regular curves or lines of growth are evident on the septal surfaces, marking the intervals between successive growth-periods. The space between two growth-curves or lines on the septal surface represents the part of the septum built up in one growth-period, and it has been called by the author a septal *growth-segment.* An important observation is that the extra length added to a single trabecula in one growth-period is *invariably one trabecular part;* this length varies in the trabeculæ of one and the same septum, being greatest at the exsert portions near the wall.

Granulations mark the surfaces of trabecular parts. Edwards and Haime applied the term "synapticula" to the interseptal bars in Fungia and its allies, and described the synapticula as formed by coalescence of granulations from opposite surfaces of neighbouring septa. The author demonstrates that in Fungia the granulations *seldom* meet across interseptal loculi. But a continuous calcareous deposit is formed in a special invagination of the interseptal parts of the aboral body-wall. Together with a number of observations on other synapticulate types, this has led the author to accept a distinction made by Pratz, and hitherto discredited in the literature. Pratz proved that the fossil Fungid subfamily of Thamnastræinæ had synapticulæ formed by coalescence of granulations, and these he called "*pseudo*synapticulæ." The name of "*true* synapticulæ" he limited to such as were formed around new centres of deposit out of the septal plane; these he found in Siderastræa, but did not farther examine typical genera belonging to the families Funginæ and Lophoserinæ. The author's results are that *pseudosynapticulæ* occur not only in Thamnastræinæ, but also in the Funginæ, Lophoserinæ, and occasionally in Astræidæ and Eupsammidæ. While *true synapticulæ*

occur chiefly in Funginæ and Eupsammidæ, rarely in Lophoserinæ, and never in Astræidæ. The author regards true synapticulæ as *basal* structures representing modified dissepiments. The advantage of synapticulæ to the polyp is that they afford a basal support over which the fleshy parts and mesenterial loculi may bend and be continued to some depth. The author, in pointing this out, refers to the analogy of the internal canaliculate visceral system thus produced with the external canaliculate system attained by a porous cœnenchyme in "Perforate" colonies. At the same time she thoroughly disagrees with the prevailing opinion that the synapticulate types have any nearer relationship with Madrepora, Porites, &c., since the skeletal parts show many important differences of structure; neither is the "porous cœnenchyme" in any way homologous with the synapticulate calyx.

No essential difference is presented between septa, costæ, and wall in respect of their microscopic structure, and the author found it also for other reasons practical to distinguish in her work the septa and costæ under the inclusive name of *radial* structures, the wall, on the other hand, as a *tangential* structure. Dissepiments, tabulæ, true synapticulæ, and certain kinds of columella are regarded as *basal* structures.

The microscopic structure of dissepiments and tabulæ is demonstrated by the author to be the same. Both are composed of a series of calcareous growth-lamellæ laid down from one surface only of the aboral body-wall of the polyp. The fibro-crystalline deposit is therefore perpendicular to the plane of contact between polyp and skeleton. The distance from one platform of dissepiments to the next above coïncides in all typical Astræids with the interval between two growth-lines on the septal surface. It may be deduced from this that the polyp lays down a new basal support for itself at the close of each growth-period. The solid calcareous deposit (usually called "stereoplasm" or "endotheca") at the base of the short, simple calyces of most Turbinolids, has the same microscopic structure as tabulæ or dissepiments, differing from them only in the fact that the new groups of growth-lamellæ are always closely opposed to the foregoing.

The "columellar" or "pseudocollumellar" area of recent Madreporaria is explained by the author as the morphological equivalent of the "tabulate" area in most Palæozoic Madreporaria. The styliform or fasciculate "true" columella of Turbinolia and its allies proves itself to be, structurally considered, a basal deposit, and is merely an upwardly arched or entwined modification of the tabulæ. The "pseudocolumella" is, as already known, a mixed structure in which septal teeth or outgrowths unite with irregularly distributed basal deposit. It finds its antetype readily in the occasional warping

of the septal spines or inner ends *within* the tabulate area of certain Palæozoic genera. The "lamellar" columella is of especial interest; the author looks upon it as the remnant of a retrograde "*main septum*," affording therefore an important phylogenetic link between so-called "tetrameral" and "radial" symmetry of the septa wherever it occurs.

Considerable differences are at present found in Madreporarian literature in the use of the terms "theca" and "epitheca." The author accepts Heider and Ortmann's terms "*pseudotheca*" for a wall formed by lateral thickening of the septa, and "*eutheca*," or simply *theca*, for a wall in which independent centres of deposit are developed. Ortmann's suborders of Madreporaria, Euthecalia, Pseudothecalia, Athecalia are, however, believed by the author to be based on an erroneous principle, since all types with a porous wall are placed among Athecalia. Porosity is looked upon by the author as a secondary feature, the porous wall can be demonstrated to be the morphological equivalent either of pseudotheca or of eutheca. A still more serious objection to these suborders is the fact that not all Turbinolids possess an eutheca; neither do all Astræids possess a pseudotheca as Ortmann means, but cases occur in both those families where the only peripheral support is afforded by the epitheca. The author is inclined to think this was the primitive form of the Madreporarian calyx, and to look upon both theca and pseudotheca as later modifications associated with retrogression of the epitheca, greater prominence and rapid growth of the septa, and very often with the processes of vegetative budding.

Certain cœnenchymatous colonies, Madrepora, Turbinaria, &c., have been shown by the author to have thecal and septal structure like the Turbinolids; further absence of basal structures in the calyx other than columella. This throws a new light on the relationship of these types and brings them along with the Oculinidæ and Pocilloporidæ into a very natural affinity with the Turbinolidæ. The cœnenchyme of these colonies is treated by the author as an elaboration of a primitive *extracalycinal* deposit around individual polyps. Bourne in one of his papers suggests the possibility of cœnenchyme being epithecate in certain of these types.

In order to elucidate the "costate" portions of Astræid and Fungid colonies, the author demonstrates the exact homology of skeletal parts in the calyces of ancient Cyathophyllids and of recent Astræids and Fungids. The pseudotheca which appeared in Acervularia and other Cyathophyllid types marked out an inner from an outer area of the calyx and septa. The exact counterpart of this is found in the type-genus of the Astræidæ, Heliastræa. In it, however, only the inner part is called *calyx*, while the outer area is spoken of as a "costate"—*extracalicinal*—area. It is on this outer area

that the so-called "Randplatte" (which the author translates as "edge-zone") is supported in the living polyp, and the author takes it that the typical edge-zone has mesenteries and mesenterial loculi simply because it was originally an inherent part of the polyp. It is clear that such costate parts in Astræid colonies have an entirely different evolutionary history from the cœnenchyme in the Pocilloporidæ, &c., where no edge-zone surrounds the polyp. The author traces back this difference in recent colonial types to a difference already well-marked in Silurian Madreporaria—viz., the difference between the calyces of a typical Cyathophyllid and a typical Zaphrentid respectively. In the former a broad calycinal outer zone with dissepimental base surrounds an inner tabulate area; in the latter there is no such outer zone or the very slightest indication of it.

The author found that the families of Edward and Haime's classification must undergo considerable changes; she limits herself here to one or two of the most important changes suggested by her on the basis of microscopic septal structure and generally of the morphology of the skeleton. The family of Astræidæ E. H. hitherto included two main subfamilies, the Astræinæ and Eusmilinæ. The former is made by the author the sole representative of Astræidæ, while the latter is entirely broken up. The genera Trochosmilia, Placosmilia, and their allies are referred to the family of Turbinolidæ; the genera Rhipidogyra, Pectinia, Dendrogyra, Euphyllia, and a large number of fossil genera are placed in a new family Amphiastræidæ erected by the author. The Mesozoic representatives of this new family are proved to be direct colony-building descendants of Palæozoic Zaphrentids, while the Turbinolidæ are looked upon as simple corals descended from the same Palæozoic family. The Stylina group of Eusmilinæ E. H. are placed in the neighbourhood of the Astræidæ and Amphiastræidæ as an intermediate family Stylinidæ. Galaxea is regarded as a near ally of the Stylinidæ; in spite of its somewhat aberrant features the author ranks it provisionally within this family.

Edwards and Haime's group of Madreporaria Perforata is also broken up by the author. The Eupsammidæ show undoubted affinity with the Fungidæ, and both these families, together with the Astræidæ and Stylinidæ, are shown to have derived their structural features from leading Palæozoic types belonging to the family of Cyathophyllidæ. In all of them the septum reaches a high degree of differentiation in its trabecular structure, on lines already introduced in various of the more advanced Palæozoic types. The Madreporidæ (Turbinarinæ E. H. and Madreporinæ E. H.) are placed in the neighbourhood of Pocilloporidæ and Oculinidæ; their simple septal structure agrees with the primitive types of septum presented by Palæozoic Zaphrentids and their allies. The Poritidæ, although

having certain features in common with the Madreporidæ, differ essentially in septal structure, and are regarded as a group of Madreporaria which branched off at a very early age from the main ancestral stem of Zaphrentidæ, and followed an independent line of development.

The author's results bear inevitably to the conclusion that the suborder Madreporaria Rugosa erected by Edwards and Haime draws an entirely artificial barrier between Palæozoic Madreporaria and the younger suborders M. Aporosa and Perforata Ed. and H. In the second part of the present paper the author annuls all three suborders and follows out the evolution of Madreporaria in the light of the general morphological results arrived at in the first part of the paper. Haeckel's terms of "Tetracoralla" for the M. Rugosa and Hexacoralla for the M. Aporosa and Perforata only gave a stronger expression to Edwards and Haime's convention of tetrameral and hexameral symmetry of the septa. And although several authors have from time to time pointed out the inappropriateness of erecting subdivisions on the feature of septal symmetry, nothing farther has been done. Even now, in current literature, one may find the term *Rugosa* = Tetracoralla set in contradistinction to *Madreporaria* = Hexacoralla!

From the standpoint attained by her own investigations, the author then traces the series of changes which appeared within the group of Madreporaria during the course of the geologic ages. Some of the more important and general of these evolutionary changes may be shortly enumerated:—

(1) *Tabulæ became modified centrally* as columella and pseudocolumella, more seldom became vesicular.

(2) Instead of one to four basal pits (fossulæ) for the reception of specialised reproductive mesenterial filaments, *the whole base of the calyx became deepened*, usually around the axial columella or pseudocolumella.

(3) Septa became more prominent and exsert in growth; their structure became more elaborate, their surfaces fluted and richly granulated, their edges knobbed, toothed, serrated, spined.

(4) The "rugose epitheca" became tardy in growth, and was replaced functionally by a theca or pseudotheca.

(5) Vegetative increase was facilitated by the specialization of an "edge-zone" around the polyp (represented by the "costate" portion of a calyx, or its ancient homologue, the peripheral "dissepimental zone" of Cyathophyllids).

(6) The "*pinnate insertion*" of septa demonstrated by Kunth in primitive corals became gradually a feature of embryonic calyces, and then vanished. But the embryonic mesenteries appear in recent types in the same "tetrameral" order as the septa did in the mature

calyces of primitive types. The disappearance of "pinnate insertion" as a generic feature did not necessarily entail the abandonment of a tetrameral, more properly said, bilateral, arrangement of the septa. It induced mainly the *hastening of septal insertion, the relative position being often retained, even in adult forms.** Again, many recent types said to have radial symmetry of septa in adult calyces have well-marked bilateral symmetry in the young individual.

All the above changes indicate, in the author's opinion, merely various lines of adaptivity, correlative with one great, leading change in the living polyp:—*an increase in the number of gonad-bearing mesenteries and in the musculature of the mesenteries, resulting in improved powers of self-preservation and of reproduction.*

The evolution of recent Madreporarian families from primitive types hinges round the gradual incoming of that main change. The general law of the hastening of the developmental stages in the individual worked with this change, and the pinnate insertion of septal pairs became more and more modified to a cyclical system of insertion. The author points out in favour of this view how the untoward circumstances for coral existence which prevailed in Europe during the Upper Carboniferous, Permian, Triassic, and Liassic ages, may have given a widespread impulse towards the carrying out and confirmation of the main evolutionary change as above stated. The change, however, has been ever since in progress. The author traces its constant working within the family of Astræidæ, its influence on Eupsammidæ and Oculinidæ, and so on.

There is therefore, in the author's opinion, no greater fallacy than the idea that some universal change took place amongst Madreporaria at the end of Palæozoic time and before the Mid-Triassic era. One and the same line of evolution may be detected making its way in the group of Madreporaria. Precocity in advance was shown by the Palæozoic Cyathophyllids, hence the high differentiation of Astræids, Eupsammids, and Fungids as early as Mesozoic ages. On the other hand, the Palæozoic Zaphrentids and their descendants in Mesozoic times were remarkably backward in advance, and it is among their recent representatives that primitive structures and forms are chiefly upheld. Naturally retrogression and atavism is shown in various degree in all families, in none more so than in the Turbinolids, the family most closely allied with the ancient Zaphrentids.

The author draws up a new classificatory system of Madreporaria

* Various observations bearing out this statement have been made by the author on Mesozoic corals. These are fully described in the author's "Monograph of the Upper Jurassic Stramberg Corals," at present being published in the 'Paläontologische Mittheilungen' (Koch, Stuttgart).

into a number of independent families of equal rank. These are based on the study of skeletal structures, known facts of anatomy, and phylogenetic relationships. She arranges the families, according to the lines of descent demonstrated in the present paper, as follows:—

Zaphrentoidean Families: Zaphrentidæ, Amphiastræidæ, Turbinolidæ, Stylinidæ, Oculinidæ, Pocilloporidæ, Madreporidæ, Poritidæ.

Cyathophylloidean Families: Cyathophyllidæ, Astræidæ, Fungidæ, Eupsammidæ.

V. "On the Calibration of the Capillary Electrometer." By GEORGE J. BURCH, M.A. Communicated by Professor B. PRICE, F.R.S. Received June 24, 1895.

In my papers* "On a Method of Determining the value of Rapid Variations of a Difference of Potential," and "On the Time-Relations of the Capillary Electrometer," I showed that the photographic record of an excursion of the capillary electrometer indicates electromotive changes not only qualitatively but quantitatively, even when they last too short a time for the movements of the meniscus to be completed.

The movement of the mercury commences simultaneously with the communication to it of the E.M.F., and ceases the instant it is withdrawn, the velocity of the meniscus at any instant being proportional to the difference between the P.D. of the source and the P.D. of the charge in the electrometer. For the sake of brevity, this difference will be referred to as the Acting P.D.

I showed that if an excursion is recorded in the form of a curve, of which the abscissæ are proportional to the times and the ordinates to the acting P.D.'s, the acting P.D. at any instant is given immediately by the tangent to the curve at that point; and the method of analysis set forth in my papers was based on the determination of the tangent or its equivalent.

Since then the process has been applied to several hundred photographs, most of which were taken during the research on the electrical phenomena of muscle and nerve in which I have assisted Professor J. Burdon Sanderson.†

In the apparatus finally adopted the sensitive plate is fixed to one end of a balanced pendulum by which it is carried with uniform velocity past a vertical slit. The image of the capillary is thrown

* 'Roy. Soc. Proc.,' vol. 48, p. 89; and 'Phil. Trans.,' vol. 183, A, pp. 81—105.

† 'Physiol. Soc. Proc.,' June 24, 1893, in 'Journ. of Physiol.,' vol. 16, p. 319, and vol. 18, p. 171.